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CONTENTS

Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE FOR 1983

CalCOFI continued to evolve to new levels during the last year. The CalCOFI Committee, during a two-day retreat to define its goals, agreed that the mission of CalCOFI was to "develop a knowledge of the living marine resources and their environment in the waters off the Californias, i.e., to understand the physical and chemical ocean environment and how it changes with time; to determine productivity of the ecosystem; to make information on the biological and physical features of California waters readily available in timely fashion (e.g., publications, conferences, data bases). The ultimate goal is to understand and predict the fluctuations in marine populations and to provide the basis for wise use of resources."

Toward the above goals, several opportunities were investigated. The Committee began to consider accepting other academic or scientific institutions into CalCOFI. The Committee also received suggestions for a "CalCOFI-type" investigation of the nearshore areas in an attempt to solve some of the problems related to inshore resources. Also, a new five-year interagency CalCOFI agreement was drafted to replace the current one, which will expire in 1984. The Committee traveled to Mexico City in February to meet with representatives of Instituto Nacional de Pesca to discuss mutual needs and develop a cooperative agreement. We are optimistic that CalCOFI's scope will continue to expand in the coming months.

The 1983 CalCOFI Conference was held in October at ISOMATA in Idyllwild, California, and was attended by 137 scientists from four countries, representing twenty research institutions and two industries. A symposium entitled "Mesoscale Patterns and Processes" was convened by John McGowan. Fifty research papers and ten posters were presented. A minisymposium of papers relating to El Niño was chaired by George Hemingway.

The El Niño noted in last year's report has been watched and studied carefully in the waters off California. By October 1982, anomalously high coastal sea levels, high sea-surface temperatures, and enhanced inshore poleward flow of the California Countercurrent were being reported from Baja California to British Columbia. By December 1982 even the Gulf of Alaska was being affected. It was clear that a major El Niño event, at least as strong as that of 1957-58, was in progress in the California Current. The work of scientists aboard R/V *Townsend Cromwell* in February 1983 revealed extreme El Niño conditions off southern California. Nine transects off southern California were carried out during the remainder of the year by Scripps's Marine Life Research Group aboard R/V *Ellen B. Scripps* and R/V *New Horizon*, with additional support from the Office of Naval Research and the California Sea Grant College Program. Five other cruises off California were conducted by the Southwest Fisheries Center, La Jolla. Physical, chemical, and biological sampling was done on all these cruises. All the data, when compared with the appropriate long-term monthly CalCOFI mean, confirmed that the 1982-83 event surpassed the previous record holder, the 1957-58 event, in terms of its effects on the California Current. These effects are still seen in data taken during the 1984 CalCOFI work at sea.

Once again Julie Olfe was managing editor for *CalCOFI Reports*. The Committee would like to thank her for her continuing excellent work.

The CalCOFI Committee:
Izadore Barrett
Herbert Frey
Joseph Reid

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1983

Total California landings of fishes, crustaceans, and mollusks during 1983 have been estimated by the California Department of Fish and Game to have dropped 25% from the 1982 level and 32% from the average of the past six years. Landings of pelagic wet fishes during 1983 were almost half that of the previous year (Table 1).

The commercial sector seemed to take the brunt of changing oceanographic conditions during 1983, most notably in poundage: anchovy dropped 90%, squid 89%, salmon 86%, ocean shrimp 74%, Dungeness crab 70%, rockfish 35%, and jack mackerel 30%. The only significant increases in landings were for albacore, yellowfin tuna, and skipjack.

Meanwhile, California's sportfishing industry seemed to benefit during 1983 because of the migration of more southerly "big game" species into local waters. However, the northern and central California ports that depend primarily on salmon and rockfish had a poor year.

PACIFIC SARDINE

The moratorium on commercial fishing of Pacific sardines, *Sardinops sagax caeruleus*, remained in effect during 1983 because the spawning biomass was assessed as remaining well below the 20,000 tons necessary to initiate a directed fishery. However, good signs of a possible recovery of the sardine resource were evident. Sardines were observed and caught

more frequently during 1983 than any other time since the moratorium was enacted ten years ago.

During 1983 an estimated 388 tons of sardines were landed with mackerel. This represents a three-fold increase over the incidental catch of sardines in 1982 and a twelve-fold increase over 1981. In dockside interviews, fishermen described increasing occurrences of sardines mixed with mackerel; several instances of dumping pure schools of sardines have been reported, but are unverified. Sardines were observed by port samplers in mackerel landings during all months of the year, and landings of 10 tons or more occurred in all but three months of the year. In the eight years prior to 1982, monthly landings of 10 tons or more of sardines occurred only five times. The frequency of occurrence of sardines in observed mackerel landings climbed to 30% in 1983, almost double that of the previous year. Length frequencies of sardines showed a bimodal distribution, with the 1983 year class represented by the smaller mode (115–145 mm SL), and the 1982 year class and older fish represented by the larger mode (160–250 mm SL).

The 1983 fall midwater trawl survey captured 1,600 sardines in 37 of 133 trawls (28%). This represents a substantial increase over previous years in both number of fish and percent occurrence. Young-of-the-year fish occurred in 25 of 133 of the trawls (19%) and constituted the majority of the catch by number. In an additional trawl survey in November, 230 sardines

TABLE 1
Landings of Pelagic Wet Fishes in California in Short Tons from 1964-83

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1964	6,569	2,488	13,414	44,846	175	8,217	75,709
1965	962	2,866	3,525	33,333	258	9,310	50,254
1966	439	31,140	2,315	20,431	121	9,512	63,958
1967	74	34,805	583	19,090	136	9,801	64,489
1968	62	15,538	1,567	27,834	179	12,466	57,646
1969	53	67,639	1,179	26,961	85	10,390	105,307
1970	221	96,243	311	23,873	158	12,295	133,101
1971	149	44,853	78	29,941	120	15,756	90,947
1972	186	69,101	54	25,559	63	10,303	104,993
1973	76	132,636	28	10,308	1,410	6,031	150,489
1974	7	82,691	67	12,729	2,630	14,452	112,576
1975	3	158,510	144	18,390	1,217	11,811	190,075
1976	27	124,919	328	22,274	2,410	10,153	160,115
1977	6	111,477	5,975	50,163	5,827	14,122	187,570
1978	5	12,607	12,540	34,456	4,930	19,899	84,437
1979	18	53,874	30,471	18,300	4,681	22,025	129,369
1980*	38	47,339	32,645	22,428	8,886	16,957	128,293
1981	31	57,593	42,913	15,673	6,558	25,715	148,483
1982	145	46,364	31,275	29,110	11,322	17,951	136,167
1983*	388	4,740	35,882	20,272	8,829	2,001	72,112

*Preliminary

(40–233 mm SL) were captured in 9 of 99 trawls (9%). One catch of small sardines (40–70 mm SL) at Santa Catalina Island indicated a possible fall spawning, which may have been produced by a southern subpopulation of sardines that had moved north.

Pacific sardines continued to appear in the incidental catches of live-bait fishermen. The percent occurrence by day of sardines from voluntary bait logs remained about the same in 1983 (27%), compared to 23% in 1982. Reports of small sardines (1983 year class) in live-bait catches were frequent.

As a result of concern about the increased availability and incidental take of sardines, two pieces of legislation were enacted in 1983. Assembly Bill 394, passed in April and enacted as urgency legislation, requires the California Department of Fish and Game to monitor the incidental catch of sardines and allows the percentage of sardines that may be taken incidentally to be increased or decreased in accordance with a specified formula. This is an attempt to lessen the impact of an impending recovery of the sardine population on other fisheries, primarily mackerel.

The second bill, AB 457, takes effect in January 1984. It allows the first 250 tons per year of incidentally landed sardines to be used for any purpose, not just canning and reduction as required by previous regulations. After the first 250 tons are landed, the allowable uses of incidentally caught sardines are restricted to canning, reduction, and live bait for the remainder of the calendar year. This bill allows fresh fish dealers without cannery or reduction facilities to utilize incidental catches of sardines during a portion of the year. It also eliminates the need for market fishermen to "dump" loads containing sardines for a portion of the year, and legalizes the use of incidentally taken sardines as live bait.

Most sources of information about the relative abundance of Pacific sardines continue to indicate a moderate increase in the biomass off California.

NORTHERN ANCHOVY

By January 1983, in the southern permit area, only 1,958 tons had been landed since the 1982-83 anchovy season opened the previous September. Bad weather, low availability of commercial-sized schools, poor market conditions, and good mackerel fishing resulted in no landings for January. Similarly, in the northern permit area, conditions for fishing were poor, and only 381 tons were landed between the season's opening the previous August and the interseason closure (February-March).

In the northern area, after the closure, an estimated 191 tons were landed during April at a price of $44.75

per ton. In the southern area, no landings occurred in April, and May landings were only 250 tons, all at Port Hueneme. Fishing continued sporadically in June, with 2,484 tons landed, mostly at Port Hueneme, where the price fell from $46.00 to $44.00 per ton by the end of the season (June 30). At Terminal Island, only two landings were reported during the spring. San Pedro fishermen complained of small, unfishable schools in the area. At the end of the 1982-83 anchovy fishing season (June 30) an estimated 4,925 tons were landed in the south (Table 2), far short of the southern area quota of 140,000 tons. In the northern area, 1,270 tons were landed for the 1982-83 season (quota: 10,000 tons).

For the 1983-84 fishing season, a preliminary biomass estimate of 1,549,000 tons (1,405,000 MT) of northern anchovy was made by the National Marine Fisheries Service using a "larval census equivalent" based on an egg production estimate of 652,000 MT. The optimum yield was established at 128,100 tons. The total U.S. reduction fishery harvest limit was set at 115,500 tons, reserving 12,600 tons for nonreduction fisheries. An initial allocation for reduction was set at 56,800 tons. Allocation of the rest would be considered when 25% of the total quota (28,875 tons) had been landed. Initial allocations of 5,800 and 52,000 tons were set for the area north and south of Point Buchon, respectively.

The Pacific Fishery Management Council (PFMC) met in San Diego on September 28–29, 1983, and recommended options for several amendments to the Anchovy Management Plan. Major options included (1) 70% (U.S.)–30% (Mexico) OY allocation; (2) a

TABLE 2
Anchovy Landings for Reduction Seasons in the Southern and Northern Areas from 1966-83, in Short Tons

Season	Southern Area	Northern Area	Total
1966-67	29,589	8,021	37,610
1967-68	852	5,651	6,503
1968-69	25,314	2,736	28,050
1969-70	81,453	2,020	83,473
1970-71	80,095	657	80,752
1971-72	52,052	1,314	53,426
1972-73	73,167	2,352	75,519
1973-74	109,207	11,380	120,587
1974-75	109,918	6,669	116,587
1975-76	135,619	5,291	140,910
1976-77	101,434	5,007	106,441
1977-78	68,476	7,212	75,688
1978-79	52,696	1,174	53,870
1979-80	33,383	2,365	35,748
1980-81	62,161	4,736	66,897
1981-82	45,149	4,953	50,102
1982-83*	4,925	1,270	6,195

*Preliminary

reduction quota (OY) formula of 100% of the excess spawning biomass over 300,000 MT, with a limit of 200,000 MT; (3) a season of August 1–June 30 (north) and September 15–June 30 (south) with *no closure* for February-March; and (4) no size limit, but a 10/16-in.-mesh size restriction. The recommended options were forwarded to the Department of Commerce. Washington, D.C., with implementation expected in time for the opening of the 1984-85 season.

No reduction landings were reported through the end of the year in the northern permit area, and only 17 tons were landed in the southern permit area. Boats in the northern area fished for mackerel and did not find fishable concentrations of anchovies. Many of these fishermen did well fishing for salmon in Alaska and were not willing to spend a large amount of effort on anchovies, in spite of a disastrous year for squid and the reduction facility's apparent willingness to take anchovies. A similar situation occurred in the southern area, where good mackerel fishing occurred through mid-October, but market conditions remained poor for anchovy. While fishing for mackerel, fishermen reported no significant concentrations of anchovies. During October, the Oxnard reduction facility did place orders for anchovies, but aerial spotters were unable to locate fishable concentrations. The major facility for reduction in southern California at Terminal Island has shown little, if any, interest in taking anchovies since the spring of 1982.

The total reduction landings for 1983 statewide were 3,124 tons. Additionally, 6,409 tons were estimated to have been used for live bait and 1,616 tons for other nonreduction purposes. During 1983 the price of anchovies for reduction ranged from $39.00 to $49.00 per ton.

JACK MACKEREL

For the fifth consecutive year, jack mackerel (*Trachurus symmetricus*) contributed less than Pacific mackerel (*Scomber japonicus*) to California's mackerel fishery. Jack mackerel had been the dominant species landed in all but seven years since the 1947 inception of the jack mackerel fishery. The estimated 1983 landings of 20,272 tons accounted for 36% of all mackerel landings.

Jack mackerel were dominant in landings during only three months of the year: April, May, and June. No restrictions on Pacific mackerel were in effect during this time. However, jack mackerel became largely unavailable during August and remained so for the rest of the year. Landings declined dramatically, and most catches of this species for the remainder of the year took place around Monterey Bay. During August, September, and October, jack mackerel landings

accounted for only 10% of all mackerel landings. From September through December over 83% of jack mackerel landings occurred off Monterey.

Jack mackerel have traditionally been considered an underutilized species. It is doubtful that the unprecedented low availability of this species during late 1983 was associated with drastically reduced biomass levels. It seems more likely that behavioral responses to warm water, which reduced their availability to purse seines, had a larger effect.

PACIFIC MACKEREL

The year began with approximately 10,000 tons remaining on the 1982-83 season (July 1–June 30) quota of 29,000 tons. For the first time in several years, the season quota was not increased prior to the February 1 deadline for quota adjustments, partly as a result of information suggesting weak recruitment of Pacific mackerel (*Scomber japonicus*) in recent years. Landings during the first three months of the year were extremely poor, partly because of a prolonged period of inclement weather during February and March. However, these landings were also indicative of a fishery dominated by older year classes, and continued a pattern begun the previous year. From July 1982 through March 1983, the 1978 and older year classes accounted for an estimated 65% of the tonnage landed.

Landings increased dramatically during April and May as weather improved. In addition, age composition of Pacific mackerel samples showed a reversal in the trend of a fishery dominated by older fish: 1980 and 1981 year classes constituted 47% of the tonnage landed during the spring. Cannery interest in mackerel improved following the meager landings of the first part of the year, and resulted in an April price jump from $174 to $200 per ton at Terminal Island. However, negotiations for a new price formula in May returned the ex-vessel price per ton to $174, where it remained for the rest of the calendar year. The season was closed on June 23, when it was determined that the 29,000-ton quota had been reached.

The 1983-84 season opened on July 1 with a quota of 22,000 tons based on a total biomass assessment of 130,000 tons. This was lower than assessments of the previous two years, and resulted from lower estimated levels of recruitment. Fishing was good during the summer off both southern and central California.

Although it is difficult to assess any impacts attributable to El Niño, several circumstances developed over the summer and early fall that may have been related. First, the trend of increasing recruitment of the 1981 year class that occurred during the spring and early summer was steadily reversed into the fall.

9

These two-year-old fish contributed 44% of the tonnage landed in July, but only 11% in October. Second, Pacific mackerel began to dominate mackerel landings in July. Beginning in August and continuing into December, Pacific mackerel made up virtually 100% of all mackerel landings. This is unprecedented in the history of this dual-species fishery. Also, by late October, Pacific mackerel became largely unavailable south of Monterey, with only scattered and intermittent landings from the Southern California Bight. In November and December, Monterey landings accounted for 23% and 62% of all landings of Pacific mackerel, respectively. This represented a steady decline, beginning in July, in the percentage of landings occurring in southern California. During the first six months of 1983 nearly 100% of Pacific mackerel landings were at San Pedro or Terminal Island.

It is becoming more and more apparent that the Pacific mackerel population is in need of another strong year class. The appearance of 1983 year-class fish (125–150 mm FL) in late June was the earliest in a year that 0-age-class fish have been sampled. Evidence of spawning from late February (indicated by these early young-of-the-year fish) through at least June raised hopes for a strong 1983 year class. However, trawl survey results in the fall did not reinforce this hope. Meanwhile, the 1982 year class has contributed only trace amounts to landings as one-year-olds; the trend shown by the 1981 year class is not encouraging. The fishery may thus be faced with dealing with two or three consecutive years of poor recruitment.

By the end of December, the seasonal catch of Pacific mackerel was just short of the 22,000-ton quota, with six months still remaining in the 1983-84 season, and with poor prospects for good availability of jack mackerel during the interseason.

Annual landings of Pacific mackerel for 1983 are estimated at 35,882 tons, a slight increase over the previous year (Table 1). This brings the average landings over the last five years to 34,000 tons, with a low of 29,000 tons (1979) and a high of 42,000 tons (1981). The last time a five-year average surpassed this was the 1940-44 average of 41,000 tons, with a low of 26,000 tons (1942) and a high of 60,000 tons (1940).

Monterey landings for the year exceeded 3,000 tons and contributed approximately 10% of the total landings. This was the largest annual take for Monterey since the beginning of California's Pacific mackerel fishery, more than five decades ago, and partially reflects increased effort expended by the displaced southern California fleet. Several San Pedro boats actually made trips as far north as Santa Cruz after early October, and delivered their catches all the way

back to Los Angeles Harbor. Therefore, catches in the Monterey Bay area were substantially higher than landing data suggests.

MARKET SQUID

Both of California's market squid, *Loligo opalescens*, fisheries failed during 1983. Fishermen and biologists alike blamed El Niño.

The northern California squid fishery experienced the second poorest season on record. Landings of only 1,052 tons were recorded, and about half were caught near Half Moon Bay, resulting in an even lower catch figure for traditional fishing grounds near Monterey. The disastrous season came at a time when demand for squid was increasing, as well as the price, which was raised to $400 per ton. Local demand for squid was met with imports and Atlantic Coast species for the first time.

The poor season was not entirely unexpected. California Department of Fish and Game biologists predicted that the El Niño phenomenon that began in 1982 and caused the ocean temperature off central California to rise as much as 5°F above normal would have a serious effect on the availability of market squid to Monterey fishermen. In 1961 and 1973 less intense warm-water episodes occurred, but they also coincided with poor squid catches. However, biologists did not expect 1983 catches to be as poor as they were.

As for the 1984 season, the ocean temperature off central California has declined, and if squid respond favorably to the more normal conditions, the fishery can be expected to improve during the coming year.

The southern California fishery suffered through its worst year since it first became viable during the early 1960s. Landings for the year were just less than 1,000 tons. Ninety-nine percent of landings were made during January and February, capping off a 1982-83 winter season that fishermen described as dismal. The worst was yet to come. During November, the usual beginning of southern California's season, squid failed to show on the traditional fishing grounds off the south side of Santa Catalina Island. Only one ton was landed during the last three months of the year.

Because of poor catches and continued high demand, fishermen received record prices for landings made. During recent seasons ex-vessel prices fluctuated between $140–$160 per ton. During early 1983, fishermen received an average price of $345 per ton at San Pedro fresh fish markets.

The failure of the 1982-83 and 1983-84 southern California winter squid fishery was less predictable than the failure in Monterey Bay. Although moderate warm-water events have occurred since the early

1960s, fluctuations in landings seem to have been more closely tied to market demand. Since the fishery did not exist during a more comparable event, the 1957-59 El Niño, comparisons could not be made.

PACIFIC HERRING

The 1983 herring catch was 8,829 tons (Table 1). This represents a decline of over 2,000 tons from the 1982 catch and is primarily due to the poor herring catch at the start of the 1983-84 season. The major component of the catch comes from the seasonal herring roe fisheries in Tomales and San Francisco bays. Small fresh fish and bait fisheries also exist. The roe fishery begins in December and usually ends in February or when the quotas are taken.

Regulation changes for the 1982-83 season included elimination of the platoon system in Tomales Bay, which was possible after 16 permittees were allowed to transfer to San Francisco Bay. Quotas, adjusted because of the transfer of permittees, were set at 1,000 tons and 10,400 tons, respectively, for Tomales and San Francisco bays.

The 1982-83 seasonal catch was 10,551 tons, down slightly from the 1981-82 catch of 11,321 tons. The season was a success even though the overall quota of 11,400 tons was not taken. Weekend closures in San Francisco Bay contributed to lower catches. In Tomales Bay the largest spawning run of the season occurred in an area that was inaccessible to the fleet and was the major reason for the quota shortfall in this area.

The 1983 Tomales Bay herring spawning biomass was estimated to be 11,000 tons, one of the highest estimates recorded. The 1983 San Francisco Bay herring spawning biomass was estimated to be 59,200 tons, a 40% decline from the previous year. Recruitment of the 1981 year class was poor and contributed to the lower estimates. However, deep-water spawning was reported by fishermen in San Francisco Bay, and because the magnitude could not be determined with present sampling techniques, the biomass estimate may be artificially low.

In 1983 acoustic techniques were experimentally used for the first time to estimate the spawning biomass of herring in San Francisco Bay. Although this method needs refinement, the 1983 acoustic estimate of 77,000 tons was higher than that obtained by sampling herring spawns in shallow-water areas.

The 1983-84 herring season began slowly with poor December catches. While it is felt that El Niño has had a negative impact on herring abundance, it remains to be seen how the 1984 fishery will be affected by changes in recruitment, mortality, or distribution of adults.

GROUNDFISH

California's 1983 commercial groundfish industry experienced a difficult year. The commercial groundfish harvest declined 24% to 43,446 tons from the 1982 harvest level (Table 3). The California El Niño seemed to have a widespread and negative impact on most groundfish fisheries. Restrictive species quotas, lower levels of fishing effort, and reduced market demand contributed to decreased commercial harvests of several key species. However, the recreational groundfish harvest remained essentially unchanged, with an estimated catch of 3,500 tons, primarily rockfish, *Sebastes* spp.

Commercial rockfish landings—principally widow (*S. entomelas*), bocaccio (*S. paucispinis*), and chilipepper (*S. goodei*)—were 19,510 tons. The widow rockfish catch declined from 11,297 tons in 1982 to 3,800 tons in 1983 because of decreased abundance and more restrictive management measures. The Pacific Fishery Management Council established a coastwide optimum yield (OY) for 1983 of 11,550 tons for widow rockfish. A 75,000-pound trip limit was imposed in March to distribute widow rockfish landings over a longer fishing season; but by September, because of greater-than-projected coastwide widow rockfish landings, a 1,000-pound trip limit was imposed for the remainder of the year. As widow rockfish declined in availability, so did the capture efficiency of midwater trawls for this species. During the fall the fishery became economically nonviable for numerous midwater trawl vessels, which then switched to multispecies bottom trawling or quit California's groundfish industry for the season. Contrary to the trend for other gear types, gill net-captured rockfish increased from 1,699 tons in 1982 to 1,846 tons in 1983 because of more intensive gill net activity off San Francisco, Monterey Bay, and southern California.

TABLE 3
California Groundfish Landings (Short Tons)

Species	1982	1983*	Percent Change
Dover sole	10,967	9,242	−16%
English sole	1,586	1,278	−20%
Petrale sole	859	619	−18%
Rex sole	728	689	−5%
Thornyheads	—	1,842	—
Widow rockfish	11,297	3,800	−66%
Other rockfish	17,483	15,709	—
Lingcod	1,498	973	−35%
Sablefish	10,446	7,160	−31%
Pacific whiting	1,123	1,078	−4%
Other groundfish	1,466	1,056	−28%
TOTALS	57,454	43,446	−24%

*Preliminary

Landings of the major flatfish species decreased moderately for the year. Anomalous oceanographic conditions and decreased fishing effort seemed to contribute to these declines.

Sablefish, *Anoplopoma fimbria*, landings in 1983 were particularly sensitive to market fluctuations. In recent years, increased demand for trawl-caught small sablefish, to be marketed in fillet form and in the round, drove commercial landings to record levels. Depressed foreign and domestic markets contributed substantially to the 31% decline in 1983 landings.

Despite the lower supply of groundfish, the price structure for most groundfish species remained relatively stable. The notable exceptions were rockfish prices, which were impacted because of imports of inexpensive rockfish from other northeastern Pacific fisheries.

DUNGENESS CRAB

California Dungeness crab, *Cancer magister*, landings were only 5.3 million pounds for the 1982-83 season compared to 10.5 million pounds landed during the previous season. The statewide total was dominated by the landings of northern California. Actually the San Francisco area (central California) showed an opposite trend: landings for 1982-83 were more than double those of the previous season.

In Crescent City, Trinidad, Eureka, and Fort Bragg, 3.43, 0.36, 0.91, and 0.06 million pounds, respectively, came across the docks. Bodega Bay, San Francisco, and Half Moon Bay landings were 0.29, 0.13, and 0.15 million pounds, respectively.

The 1982-83 season opened November 9 in central California, with an opening price of $1.35 per pound to the fishermen. Favorable weather contributed to fishing success. Northern California crabbers faced exceptionally hazardous sea conditions when their season opened December 1, but were motivated by a record opening price of $0.90 per pound. In response to the northern California opening, the San Francisco crab price dropped to $1.00, but recovered to $1.30 by midmonth.

Responding to poor catches in deeper water and improving weather in late December, many northern California crab fishermen moved their gear to well inside the 10-fathom isobath. By mid-January, 90% of the season's production was met, and the price had risen to $1.53 per pound. During this time, however, the weather had worsened, and vast quantities of crab gear had been lost.

In central California, 76% of the San Francisco area landings were reported by the end of December. By season's end, the price paid to San Francisco fishermen had reached $2.00 per pound. During the season,

432 vessels had engaged in the fishery in the area from Crescent City to Fort Bragg. Approximately 125 boats participated in the San Francisco area fishery, which includes the landing sites from Bodega Bay to Half Moon Bay.

PACIFIC OCEAN SHRIMP

Historically, California's fishery for ocean shrimp, also known as pink shrimp (*Pandalus jordani*), has occurred almost exclusively off northern California in waters designated as "Area A" by state regulations. In more recent years, a fishery off Morro Bay-Avila has grown in significance.

The 1983 Area A shrimp season was an unmitigated failure: only 833 pounds were landed. An additional 221,219 pounds were caught by California shrimpers off Oregon (PMFC areas 86 and 88) and landed in Crescent City. The ex-vessel price was $0.62-$0.64 per pound at the beginning of the season and gradually increased to $0.77-$0.80 per pound in July depending upon the dealer.

To give perspective to this catastrophe, since 1958 the lowest poundage landed was 0.98 million pounds (1973), and the highest was 13 million pounds (1977). Although the cause of the failure is not known for certain, an El Niño effect cannot be ignored. The fishery to the south, however, fared much better.

Landings of 944,695 pounds of ocean shrimp were recorded in the ports of Morro Bay and Avila (PFMC area 98) during the 1983 season. This was nearly double the poundage landed in 1982, the poorest season since 1979 when the Morro Bay fishery began in earnest. Sixteen trawlers (5 single-rig and 11 double-rig) participated in the 1983 fishery, making a total of 187 trips. The season ended somewhat prematurely in September when concentrations of pelagic red crabs (*Pleuroncodes planipes*) became so dense that trawlers could not reach the shrimp before jamming their nets with crabs. Single hauls in excess of 20,000 pounds of crabs were reported. Unfortunately, there is no market for these pelagic red crabs.

The ex-vessel price for shrimp delivered to Morro Bay reached a record high of $0.80 per pound early in the season. It remained stable until season's end, probably because of the scarcity of shrimp from northern California.

From data extracted from fishermen's log books, catch per unit of effort (CPUE) remained fairly strong through August. Generally, both single- and double-rig vessels had CPUE in excess of 200 pounds per hour trawled. For the season, single-rig boats averaged 197 pounds per hour, whereas double-rig vessels averaged 231 pounds per hour. Combined CPUE averaged 221 pounds per hour for the season.

The monthly count of shrimp per pound averaged 79.3, from 211 samples taken during the course of the season. This compares to previous season averages below 65 per pound, indicating that 1983 yielded a much smaller average grade of shrimp. Monthly sex composition was also different in 1983 compared to previous seasons. In general, male composition was comparable to past seasons, but transitionals were appreciably higher and females correspondingly lower. This may indicate a slower rate of transition to female in 1983, which may also explain the higher average count-per-pound values. The overall smaller size of shrimp may reflect slower growth.

The forecast for the 1984 shrimp fishery appears bleak at this time owing to poor market conditions. Because of new foreign competition from Norway and Chile, the 1984 ex-vessel price for pink shrimp is projected to begin at around $0.40 per pound. At this price, California trawlers may not be able to fish at all, especially if shrimp availability remains low.

PELAGIC SHARK AND SWORDFISH

During 1983, 249 permits were issued to harpoon fishermen to take swordfish; 228 drift gill net permits were issued for taking pelagic sharks and swordfish. The season for harpoon fishermen is year-round; the season for drift gill netters extends from May 1 to January 31.

Harpoon fishermen suffered through their worst season since 1950, reporting, on logbooks, landings of only 422 fish. In 1950 the reported catch was less than 400. While some might be tempted to blame the recent failures in the harpoon fishery on the growing success enjoyed by the drift gill net fleet, it should be noted that the harpoon fishery has historically been subject to extreme fluctuations, and that the failure of the 1983 harpoon fishery occurred despite the creation of harpoon-only areas off southern California.

Drift gill net permittees ended 1983 with a record season for swordfish, with landings exceeding 2.6 million pounds. The previous high was in 1978, when landings were just under 2.6 million pounds, but that catch was entirely by harpoon. In numbers, drift gill netters reported 1983 landings of close to 21,000 swordfish. The season finished on a strong note, with 4,500 fish reported taken in January. The previous reported high for a January was only 400 fish.

Common thresher shark (Alopias vulpinus) landings were down in 1983 from the two previous seasons, amounting to just over 1.6 million pounds. Catches for 1981 and 1982 were 2.0 and 2.3 million pounds, respectively. During 1983, however, there were indications of an emigration of fish to the north of traditional fishing grounds, possibly in response to the 1982-83 warm-water episode.

The gill net fishery detected other biological events possibly related to this warm-water episode. Of particular interest was the first recorded occurrence in California waters of the pelagic thresher shark (Alopias pelagicus). Its distribution has been previously described as occurring entirely within subtropical and tropical waters; it is commonly taken on hook and line during the winter sport fishery off lower Baja California. It appears from catch records that during the summer of 1983 the pelagic thresher may have largely displaced the common thresher in waters off southern California.

In addition, during the past several years the log books kept by nearshore set-gill net fishermen have indicated frequent catches of young-of-the-year common threshers in their summer landings along the Los Angeles, Ventura, and Santa Barbara county coastlines. This has not been the case in 1983. Instead, these fish are being captured by gill nets in nearshore waters as far north as Point Reyes.

Further expansion of the California drift gill net fishery into northern waters was witnessed again this year. As many as 20 vessels from southern California ports spent most of the summer operating out of ports as far north as San Francisco, with most effort in the area off Monterey Bay. During the late summer, when weather conditions allowed, these vessels made substantial swordfish landings.

An official of the Washington State Department of Fisheries reported that one drift gill net vessel operating in water 80-90 miles outside Puget Sound had a very successful season targeting on the common thresher shark.

RECREATIONAL FISHERY

During 1983, southern California anglers experienced one of their most extraordinary years. The El Niño condition evident in the eastern Pacific was responsible. Biological evidence of the phenomenon was observed off southern California as early as September 1982, and physical evidence (increased sea-surface temperature) was available by November. Since changes in fish distributions were noted prior to 1983, a review of the fall 1982 sportfishery is included here.

Beginning in September 1982, sportfishermen in southern California noted a change in the availability of large (5–8-pound) Pacific bonito, Sarda chiliensis. The fish were first taken off San Diego, and catches progressed north as the month passed. Remarkable catches persisted through early December, at which

13

time a series of storms curtailed the fishery. During mid-September, an unprecedented late run of albacore (*Thunnus alalunga*) developed close to San Diego. The fish were large: many weighed 50 to 60 pounds, and some occasionally exceeded 70 pounds. The run lasted for 10 days, stopped, but resumed in November farther offshore. November's run produced good catches with many albacore in the 60–70-pound class. In addition, striped marlin (*Tetrapturus audax*) fishing in November was the best on record, with over 190 fish reported at local sportfishing clubs.

January 1983 was characterized by good weather during the first half of the month, which allowed anglers to catch many large bonito. Poor weather during the next 2½ months precluded most sportfishing activity off California. During this period, isolated commercial landings of bluefin tuna (*Thunnus thynnus*) off southern California, combined with bonito and California barracuda (*Sphyraena argentea*) off central California evidenced unusual northerly shifts in the availability of these fishes.

It wasn't until May that sport-fish catches again began to reflect the occurrence of a warm-water event. Fishermen in southern California were then greeted by remarkably good fishing for yellowtail (*Seriola lalandei*) and barracuda in Santa Monica Bay, as well as yellowtail off the Coronado islands. Additionally, long-range boats caught large (50–100 pound) bigeye tuna (*Thunnus obesus*) off Cedros Island, Baja California. During June, excellent albacore fishing occurred in an area 50 miles north of Guadalupe Island: catches of 100–200 fish per day, with the albacore averaging 22 pounds, were reported.

July marked the beginning of the summer season and continuing good yellowtail fishing at the Coronado islands. The first striped marlin of the year was taken on July 10, and by month's end over 100 had been landed. Marlin catches centered around Santa Catalina and Santa Barbara islands, an early indication of how far north the fish would go. By mid-July good fishing for bigeye tuna was occurring off San Diego, and at month's end the sportfishing fleet began catching yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Euthynnus pelamis*).

August ushered in a period that has been called the "100 golden days" in southern California sportfishing. Fishing for yellowfin tuna and skipjack tuna was phenomenal, with anglers averaging 2.5 and 1.6 fish per day, respectively, for trips on commercial passenger-carrying fishing vessels (CPFVs) operating from San Diego. Boats as far north as Ventura enjoyed similar success, although their season was much shorter. Half-day CPFVs operating nearshore from Dana Point to San Diego experienced unprecedented periods of excellent yellowfin and skipjack tuna fishing. Bigeye tuna were also available during this period, and over 1,700 were reported landed by CPFVs. Yellowtail fishing continued to improve, especially at the offshore islands and under drifting kelp. Dolphinfish (*Coryphaena hippurus*) appeared by mid-August, and sporadic catches occurred through September.

During September, the best marlin fishing ever recorded off southern California occurred in the vicinity of Santa Rosa Island. Catches of 10 fish per day per boat were common, while one angler tagged and released 16 marlin in a three-day period. Yellowfin tuna fishing was also exceptional in the same area, with several fish over 150 pounds landed. In October a bluefin tuna weighing 364 pounds was taken by hook and line; it was the largest tuna ever taken by an angler off California.

During the fall of 1983, northern and central California anglers also experienced unusual sportfishing success on more "southern" species. Albacore were taken in Monterey Bay during September, and bonito were commonly taken into November. Large bonito (> 10 pounds) were taken by shore fishermen off Crescent City, and large schools of bonito were reported off Fort Bragg. One striped marlin was landed in Monterey during September, and others were reported hooked as far north as San Francisco. Boats (CPFVs) operating from Avila and Morro Bay were catching marlin on fall albacore trips. Apparently, the most available concentration of marlin was north of Point Conception during the fall—out of range of southern California anglers. This precluded a predicted exceptional marlin season off southern California. The fish seemed to bypass southern California and remain off the northern part of the state for most of the fall.

During mid-November a series of Arctic-spawned storms ended the exceptional sportfishing season off southern California. Surface water temperatures decreased to within 3°-4°F of normal, causing most anglers to give up as success rates declined. However, 29 striped marlin were landed in November, and 7 were taken in December, a month in which they had never previously been reported caught. Fishing for large bonito did improve somewhat during late November and December, with fish in the 10–12-pound range providing notable action.

The 1983 sportfishing season off southern California easily qualifies as a success when historical CPFV landings are compared. Catches of selected species on these vessels reflect some of the exceptional biological consequences of El Niño off California. Over 99,000 yellowfin tuna and 92,500 skipjack tuna were reported landed. The previous state record for yellowfin tuna

was 10,801 (1967), and the skipjack tuna record stood at 21,423 (1977). Bigeye tuna landings increased dramatically, with 1,773 reported; the previous record was 288 (1981). Dolphinfish landings represented an all-time high, with over 997 fish reported taken in southern California waters. One truly remarkable thing about these records is that they were all set concurrently in a relatively short (100-day) period. This El Niño apparently allowed large quantities of several highly esteemed sportfish species to move much farther north than normal, thus becoming available to southern and northern California anglers.

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Allen Grover, northern anchovy
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Compiled by Richard Klingbeil

THE 1983 SPAWNING BIOMASS OF THE NORTHERN ANCHOVY

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ABSTRACT

The 1983 equivalent larval census estimate of the spawning biomass of the northern anchovy (*Engraulis mordax*) central subpopulation is 1,405,000 MT. This estimate is based on data gathered by an egg production survey conducted from February 4 to April 1, 1983. The abundance of larvae is projected from the daily production of eggs and the subsequent mortality of eggs and larvae. This equivalent larval census estimate is the basis of the anchovy fishery optimum yield for 1983-84.

The egg production method estimate of anchovy spawning biomass is 652,000 MT. This is based on the summation of three regional estimates of daily egg production and population fecundity. The standard error of the total estimate is 137,000 MT, for a coefficient of variation of 21%.

In 1983 the central subpopulation of northern anchovy was geographically distributed more offshore and poleward than in recent years. Spawning was extensive throughout the Southern California Bight (with the exception of the Santa Barbara Channel); spawning was evident along a narrower coastal band adjacent to the northern Baja California coast inside of Guadalupe Island; a small amount of spawning was detected adjacent to the coast north of Point Conception.

RESUMEN

La estimación, por medio del censo larval correspondiente, de la biomasa de reproductores en la subpoblación de la anchoveta del norte, *Engraulis mordax*, que habita las aguas de la California Central es de 1.405,000 Tm para 1983. Esta estimación se basa en los datos sobre producción de huevos obtenidos durante exploraciones realizadas desde el 4 de Febrero al 1° de Abril de 1983. La abundancia de larvas es derivada de la producción diaria de huevos y la mortalidad consiguiente de huevos y larvas. Esta estimación equivalente del censo larval sirve de base para obtener la producción óptima de anchovetas para 1983-84.

Por el método basado en la producción de huevos se estima que la biomasa de la población reproductora es de 652,000 Tm, para lo cual se considera la suma de tres estimaciones regionales de producción diaria de huevos y fecundidad de la población. El error estándar para la estimación total es de 137,000 Tm, para un coeficiente de variación del 21%.

La distribución de la población central de *E. mordax* aparecía en 1983 más alejada de las aguas costeras y se extendía más al norte que en años anteriores. La puesta se extendía por todo la Bahía del Sur de California (excepto en el Canal de Santa Bárbara); además, se observó en una franja costera a lo largo de la zona norte de Baja California, mar adentro de la Isla Guadalupe, y algo de puesta aparecía en la zona costera al norte de Punta Concepción.

INTRODUCTION

This report documents the 1983 spawning biomass estimate of the central subpopulation of northern anchovy (*Engraulis mordax*), as required by the Anchovy Management Plan, adopted by the Pacific Fishery Management Council (PFMC 1978). In recent years, anchovy biomass has been assessed using two ichthyoplankton-based methods: larval census (Smith 1972; Stauffer and Parker 1980; Stauffer 1980; Stauffer and Picquelle 1981); and egg production (Parker 1980; Stauffer and Picquelle 1980; Picquelle and Hewitt 1983). The larval census method assumes a constant of proportionality between larval abundance and spawning biomass, whereas the egg production method measures and incorporates variability in this proportionality parameter; these two methods produce estimates that consistently differ in magnitude.

This year, as well as last year, we estimated anchovy biomass using the egg production method because it is a more accurate and efficient estimator than the larval census method. However, the management plan's harvest quota is determined by an optimum yield formula based on larval census biomass estimates. The PFMC has interpreted the optimum yield formula to require a "larval census equivalent" spawning biomass estimate (Picquelle and Hewitt 1983).

This report describes the survey results, the egg production biomass estimate, and the equivalent larval census estimate of biomass. The egg production method defines the spawning biomass as the quotient of the daily production of eggs in the sea and the daily

fecundity (per ton of spawners) of the population (Parker 1980). The larval census method defines the spawning biomass as proportional to the quarterly average standing stock of larvae summed over four quarters of the year, and assumes constant quarterly reproductive output (per ton of spawners) and constant survival of the young (Smith 1972). An equivalent larval census can be estimated by measuring larval mortality and projecting the number of larvae resulting from the measured egg production (Stauffer 1983; Picquelle and Hewitt 1983).

DESCRIPTION OF SURVEY

The 1983 survey of the central subpopulation of the northern anchovy was conducted aboard the NOAA R/V *Townsend Cromwell* from February 4 through April 1, 1983. The survey ran from north to south, starting at San Simeon, California, (CalCOFI line 73.3) and ending at Bahia del Rosario, Baja California (CalCOFI line 110.0). The southern end of the survey was truncated because of the expiration of the Mexican sampling permit. Plankton samples were taken at 850 stations using a 25-cm diameter net of 150-micron mesh, retrieved vertically from a depth of 70 m; of these plankton samples, 482 contained anchovy eggs (Figure 1). Midwater trawl samples were taken at 62 stations using a 15-m² trawl with a 2-mm mesh liner;

51 trawls caught anchovies (Figure 2). For a detailed description of field operations see Cruise Report 8304-TC, dated May 18, 1983, William Flerx, Southwest Fisheries Center, La Jolla, California.)

The distribution of anchovy eggs differed greatly from recent years: the range extended much farther offshore, and a smaller proportion of eggs was taken in Mexican waters. Also unlike previous years, there was a lack of correlation between the geographic pattern of eggs and the pattern of surface temperature isotherms (Figure 1) (Lasker et al. 1981; Picquelle and Hewitt 1983). One possible explanation is the occurrence of unusually warm water over the entire range of the survey.

The occurrence of positive trawls agreed well with the distribution of eggs (Figure 2). Unfortunately, there was a lack of trawl stations in the San Pedro Channel region, even though there was a high density of eggs in this area. Another shortcoming of the survey was the decision to sample only to CalCOFI line 110, the assumed southern extent of the central subpopulation. The two largest samples of eggs were taken from the southernmost line of the survey (Figure 1), suggesting that a local high density of anchovies occurred there and presumably extended farther south. It is impossible to estimate the amount of biomass residing south of the survey, or whether these fish
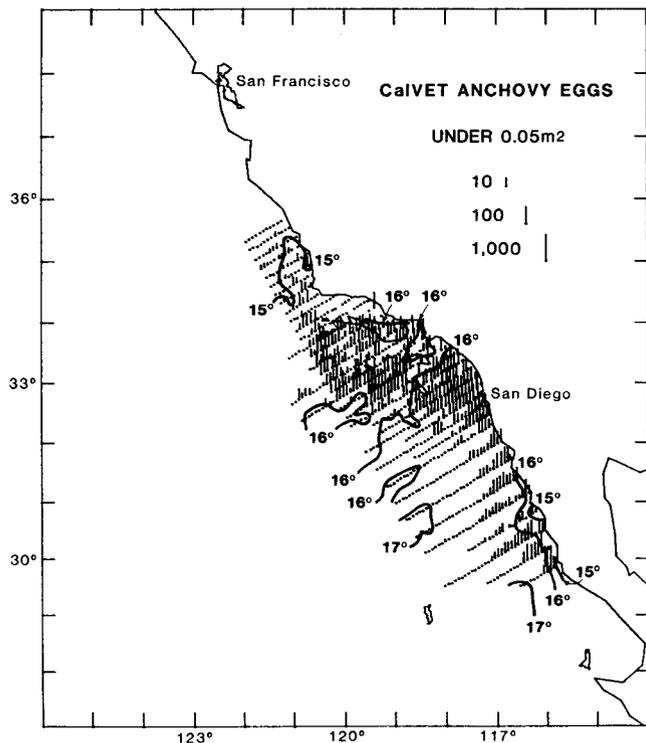
Figure 1. Geographic distribution of anchovy eggs from CalVET samples and surface isotherms.
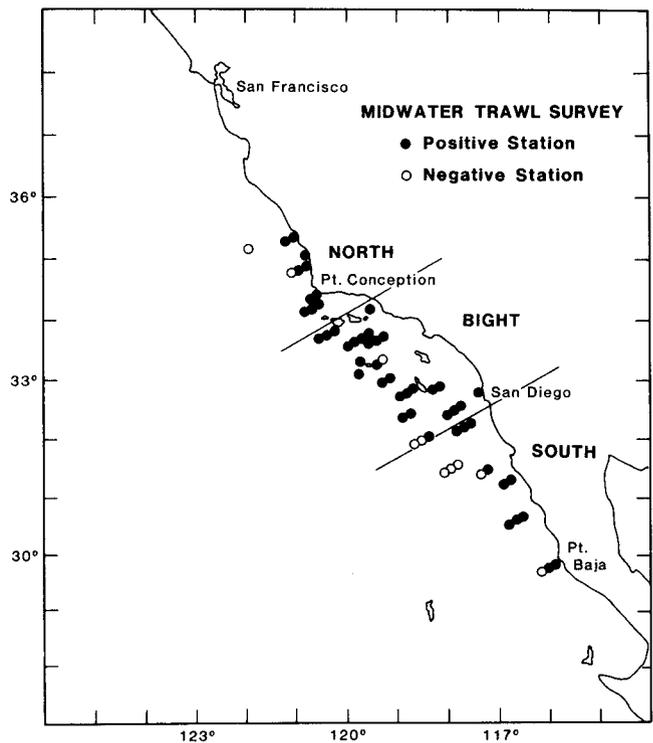
Figure 2. Geographic distribution of trawl stations and positive trawls within each region.

would be from the central subpopulation. With these two possible exceptions, the egg and trawl surveys appear to have provided good sample coverage of the central subpopulation of northern anchovy in 1983.

EGG PRODUCTION BIOMASS ESTIMATE

Biomass Model

The egg production estimate of anchovy spawning biomass, derived by Parker (1980) and modified by Stauffer and Picquelle (1980), is

$$B = P_o A \frac{k\,W}{R\,F\,S} \tag{1}$$

where B = spawning biomass (MT),

P_o = daily egg production, number of eggs produced per 0.05 meter^2,

W = average weight of mature females (grams),

R = sex ratio, fraction of population that is female, by weight (grams),

F = batch fecundity, number of eggs spawned per mature female per batch,

S = fraction of mature females spawning per day,

A = total area of survey (0.05 meter^2),

k = conversion factor for grams to metric tons.

An approximate sample variance for the egg production spawning biomass estimator, derived from the delta method (Seber 1973), is a function of the sample variances and covariances of the parameters

$$\text{Var }(B) \cong B^2 \times$$

$$\left\{ \frac{\text{Var }(P_o)}{P_o^2} + \frac{\text{Var }(W)}{W^2} + \frac{\text{Var }(R)}{R^2} + \frac{\text{Var }(F)}{F^2} + \frac{\text{Var }(S)}{S^2} + \right.$$

$$2\left[\frac{\text{Cov }(P_o W)}{P_o W} - \frac{\text{Cov }(P_o R)}{P_o R} - \frac{\text{Cov }(P_o F)}{P_o F} - \frac{\text{Cov }(P_o S)}{P_o S} - \frac{\text{Cov }(WR)}{WR} - \right.$$

$$\left.\left. \frac{\text{Cov }(WF)}{WF} - \frac{\text{Cov }(WS)}{WS} + \frac{\text{Cov }(RF)}{RF} + \frac{\text{Cov }(RS)}{RS} + \frac{\text{Cov }(FS)}{FS} \right]\right\} \tag{2}$$

The quantity $P_o A$ is the daily production of eggs in the sea. Estimating this parameter requires the assumption that the rate of instantaneous egg mortality is constant over the range and duration of the survey; mortality was not measured with sufficient precision to test this hypothesis. The quantity $RFS/(kW)$ is the daily fecundity (per ton of spawners) of the population; the model assumes that this parameter is also constant over the range and duration of the survey. It was possible to test this hypothesis, and for this survey it was rejected. The value of average female weight
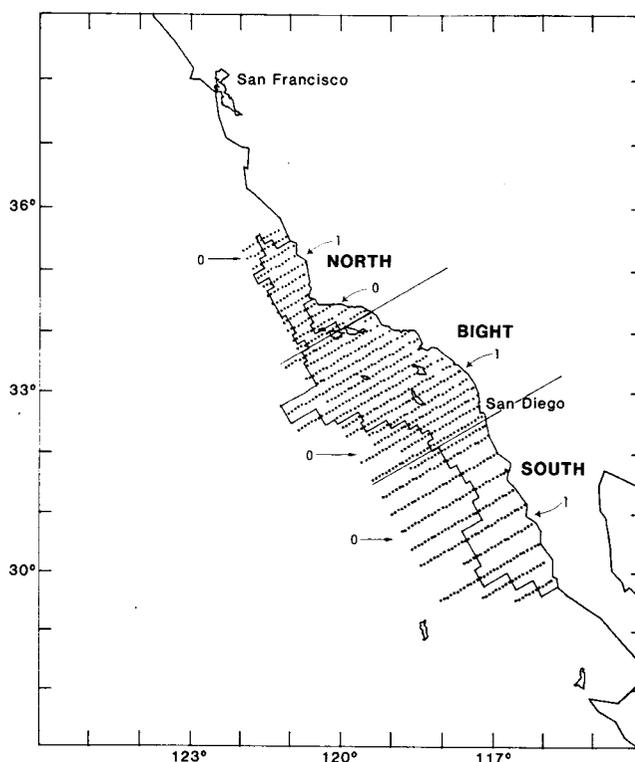
Figure 3. Subdivision of CalVET survey into strata (0—beyond the range of anchovy spawning, 1—within the range of anchovy spawning) and regions (north, bight, and south).

decreased from north to south while spawning fraction increased.

The survey area was divided into three regions (Figure 2), within which each parameter was relatively constant. The north region was the area north of the boundary line drawn halfway between CalCOFI lines 82.5 and 83.3; it contained 150 egg samples and 10 positive trawl samples. The northern boundary for the south region corresponded roughly to the U.S.-Mexican border and was drawn halfway between Cal-COFI lines 95.0 and 95.8; this region contained 263 egg samples and 11 positive trawl samples. The bight region, everything between the north and south regions, contained 437 egg samples and 30 positive trawl samples (Figures 2 and 3). We estimated the spawning biomass separately for each region. The total estimated spawning biomass is the sum of the three regional biomasses, and the total variance is the sum of the three regional variances.

Daily Production of Eggs in the Sea

The parameter $P_o A$, the daily production of eggs in the sea, is the total area multiplied by the number of eggs spawned per night, per unit area, averaged over the range and duration of the survey, or in this case, region. The plankton samples provide counts of eggs

of each age for each station (Figure 1). We estimated egg production by fitting an exponential mortality function to the egg data and then extrapolating back to the number of eggs at the time of spawning.

We analyzed the egg counts using a two-stage systematic sampling scheme (see Picquelle and Hewitt 1983, for a complete description of the sample design). First, we gave each station a weight proportional to the area the station represents. Second, we stratified the stations by location to decrease the variance. Many of the stations were beyond the spawning range of the anchovy and contributed a large number of zero counts to the egg data set, thus inflating the variance. This effect was minimized by defining a stratum to contain those stations that were determined after the survey to be located beyond the geographic area of spawning; this was called stratum 0. Stratum 1 was the geographic area that included all stations where anchovy eggs were found. These two strata were created for each region (Figure 3); the area (nm^2) and number of samples (n) for each stratum within each region were:

| Stratum | | Region | | | |
		North	Bight	South	Total
1	area	3,480	14,800	9,340	27,620
	n	86	351	126	563
0	area	2,640	4,600	10,420	17,660
	n	64	86	137	287
Total	area	6,120	19,400	19,760	45,280
	n	150	437	263	850

The mortality function is fit to the egg data by regressing egg counts on age. The eggs for each sample are assigned an age that is determined by the developmental stage, water temperature, and the time the sample was collected. It is assumed that all eggs are spawned and fertilized each night at time 2200 (Stauffer and Picquelle 1980). Water temperatures range from 14° to 17°C; at these temperatures hatching begins at the age of 2.5 days, hence only eggs up to 2.5 days old are used in the regression. The data are then tabulated by age for each station, with each station contributing up to three observations (one count for each age). The exponential mortality model

$$P_{ijk} = P_{oi}e^{-Zt_{ijk}} + \varepsilon_{ijk} \qquad (3)$$

was then fit to the data by a weighted nonlinear least squares regression (Dixon and Brown 1979),

where P_{ijk} is the number of eggs in the kth day age category from the jth station in the ith stratum,

t_{ijk} is the age in days measured as the elapsed time from the time of spawn for the kth day category eggs to the time of sampling of the jth station in the ith stratum,

P_{oi} is the daily production of eggs per unit area $(0.05m^2)$ in stratum i,

Z is the daily rate of instantaneous egg mortality, and

ε_{ijk} is the additive error term.

Egg mortality, Z, is difficult to estimate precisely, so we pooled the data from stratum 1 for all regions to produce a single estimate of Z. This value was 0.1836/day with standard error 0.1302/day. Next, we fit the model to the data from stratum 1 for each region separately, where Z was fixed at 0.1836/day. This produced an estimate of P_{o1} for each region (Figure 4). The stratified estimate of P_o for each region was calculated as the weighted average of P_{o1} and P_{oo}, where P_{oo} is zero by definition, and the weights are the relative areas of the two strata. Thus

$$P_o = \frac{A_1}{A}P_{o1} + \frac{A_o}{A}P_{oo} \qquad (4)$$

and the variance, adjusted for postsurvey stratification (Jessen 1978), is

$$(5)$$

$$\text{Var}(P_o) = \left(1 + \frac{1}{h}\right)\left[\left(\frac{A_1}{A}\right)^2 \text{Var}(P_{o1}) + \left(\frac{A_o}{A}\right)^2 \text{Var}(P_{oo})\right]$$

where A_i is the area of stratum i for each region,

n is the total number of observations by region,

Var (P_{o1}) is estimated for each region from the regression (3), and

Var (P_{oo}) = 0 by definition.

The estimates for P_{o1} and P_o, their standard errors, and total production A_iP_o for the three regions were:

	North	Bight	South
P_{o1} (eggs/0.05m²)	2.85	9.54	10.71
Standard error	1.44	0.625	2.43
P_o(eggs/0.05m²)	1.62	7.28	5.06
Standard error	1.09	0.547	1.68
A_iP_o ($\times 10^{12}$ eggs)	0.682	9.70	6.87

The egg densities, P_{o1}, of the bight and south regions were similar, but the eggs were much less dense in the north region. The variance of egg densities was very small in the bight region; the large variance for the north region was partially due to the small number of positive egg samples; the large variance for the south region was due to a few samples with extremely large egg counts.
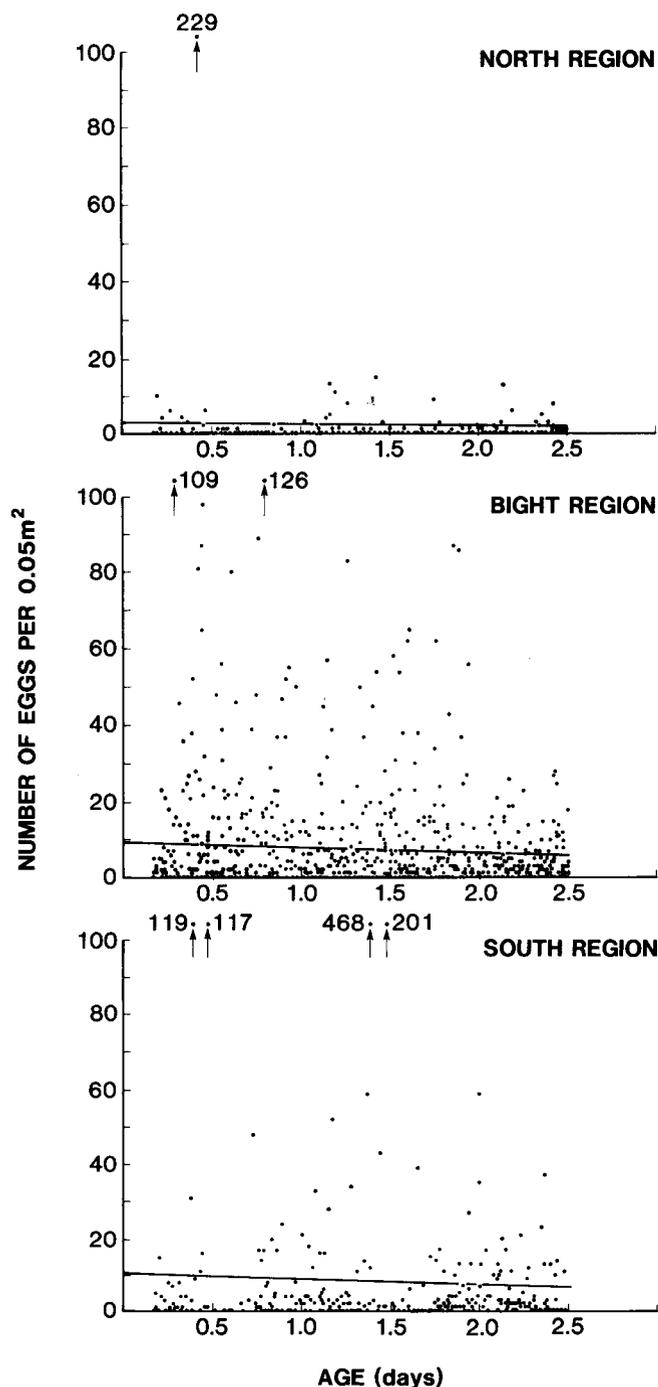
Figure 4. Exponential mortality model for estimating P_{o1}, daily egg production for stratum 1, plotted with egg abundances for each region.

Adult Parameters W,F,S, and R

The parameters W, F, S, and R were estimated from samples of adult anchovies collected by the midwater trawl survey (Figure 2). The sample design consisted of three stages: (1) selection of trawl stations, (2) sample of fish at the station using the midwater trawl, and (3) subsample of fish from the trawl catch. (See Picquelle and Hewitt 1983, for a complete description of the sample design.)

We estimated each parameter for each region by a weighted sample mean ($\bar{\bar{y}}$) and with a weighted variance (Cochran 1963):

$$\bar{\bar{y}} = \sum_{i=1}^{n} \left(\frac{m_i}{mn}\right) \bar{y}_i \qquad (6)$$

$$\text{Var}(\bar{\bar{y}}) = \frac{\sum_{i=1}^{n} \left[\left(\frac{m_i}{m}\right)^2 (\bar{y}_i - \bar{\bar{y}})^2\right]}{n(n-1)} \qquad (7)$$

where m_i is the number of fish subsampled from the ith trawl,

$\bar{m}$ is the average number of fish subsampled per trawl,

n is the number of positive trawls,

y_{ij} is the observed value for the jth fish in the ith trawl, and

$\bar{y}_i = \sum_{j=1}^{m_i} y_{ij}/m_i$ is the average for the ith trawl.

Average Female Weight

The average female weight, W, was calculated for each region using equations (6) and (7), where $\bar{y}_i$ was the average female weight for the ith trawl within the region. The desired subsample size was $m_i = 25$ mature females from each trawl; however, this was not always attainable for small trawl catches or for catches composed mostly of immature fish.

The weight of females with hydrated eggs in their ovaries is inflated because of water retention in their ovaries. To correct for this, we adjusted their weight using the regression of whole body weight on ovary-free weight. We estimated this regression using mature females without hydrated eggs from the entire survey,

$$\hat{W}_{ij} = 0.0972 + 1.05 \ W_{ij}^* \qquad (8)$$

where $\hat{W}_{ij}$ is the estimated whole body weight in grams, and

W_{ij}^* is the ovary-free weight in grams; the regression had an $r^2 = 0.998$.
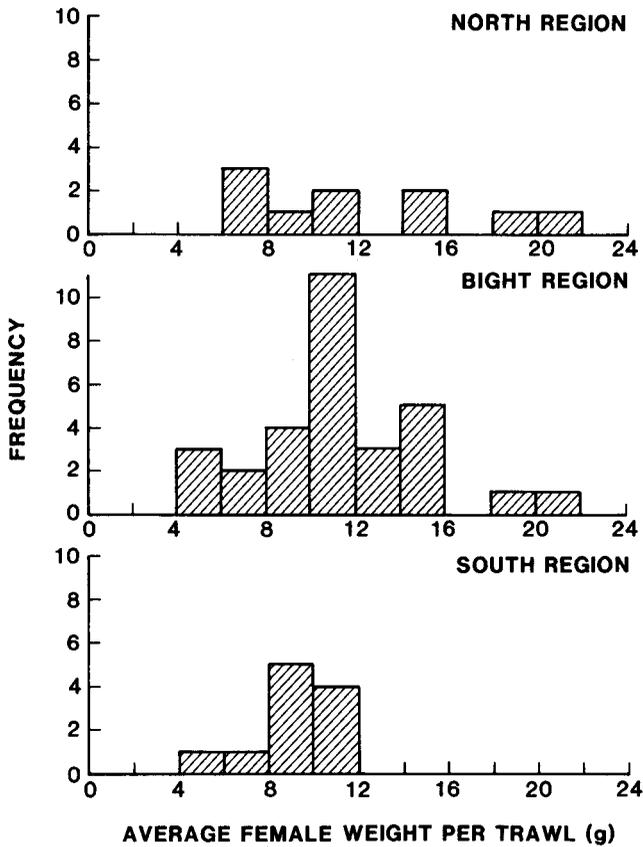
Figure 5. Frequency distribution for average whole-body weight (in grams) of mature females for each region.

The estimated average female weights and standard deviations for each region were:

	North	Bight	South
$\overline{\overline{W}}$ (grams)	12.9	11.2	9.63
Standard error	1.56	0.790	0.371
n	10	30	11

The frequency distributions of average weight per trawl were quite different among regions (Figure 5). The weights for the north region had the same range as the weights for the bight region, but there was no clear mode, and a high standard error. The distribution of the weights for the bight region was symmetrical, with both mean and mode at 11 grams. The distribution of fish in the south region was truncated, with no average weights greater than 12 grams; the average southern weight was significantly smaller than both the bight and northern average weights (one-tailed test, p = 0.10).

Batch Fecundity

Fecundity for each mature female was estimated by the regression of fecundity on ovary-free weight esti-

mated from a sample of 83 females with hydrated eggs that were collected over the duration of the survey. This sample was selected so that its weight distribution was similar to the weight distribution of females for the whole cruise (Figure 6). The fitted linear regression is

$$\hat{F}_{ij} = -942 + 582 \ W_{ij}^* \qquad (9)$$

where $\hat{F}_{ij}$ is the estimated fecundity for a female with W_{ij}^* ovary-free weight; r^2 = 0.83 (Figure 7).

Batch fecundity is then estimated for each region using equation (6) where the $y_{ij} = \hat{F}_{ij}$ are estimated using equation (9). Again, the desired m_i was 25 mature females. The variance estimate (equation [7]) is modified to include the extra source of variance resulting from trawl averages being estimated rather than observed directly (Draper and Smith 1966):

$$\text{Var}(\overline{\overline{F}}) = \frac{\sum\limits_{i=1}^{n} \left\{ \left(\frac{m_i}{m}\right)^2 \left[\frac{(\overline{F}_i - \overline{\overline{F}})^2}{n-1} + \frac{S_h^2}{83} + (\overline{W}_i^* - W_h^*)^2 \ \text{Var}(b) \right] \right\}}{n} \qquad (10)$$
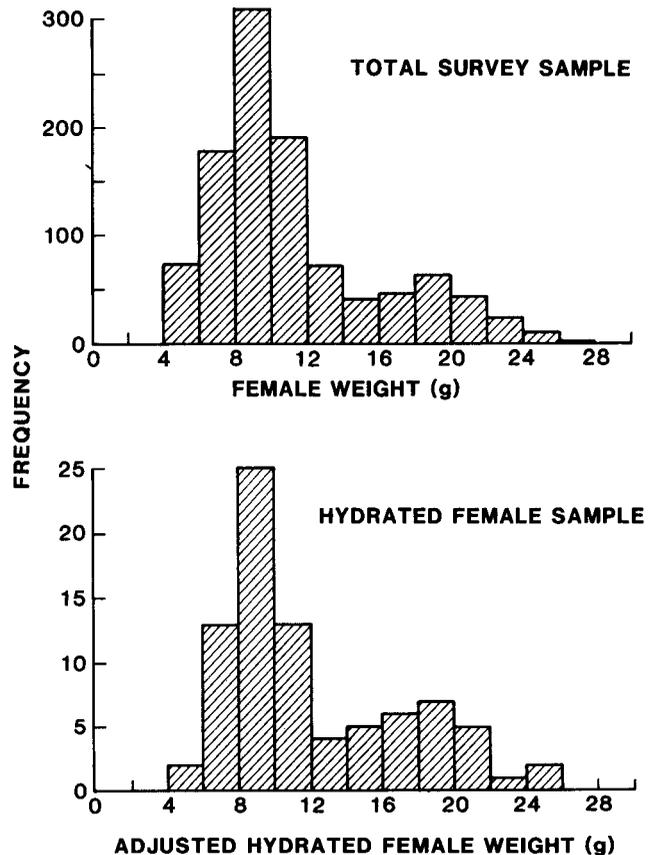
Figure 6. Frequency distribution for whole-body weight (in grams) of mature females. The top histogram is for all mature females; the bottom histogram is for those females used to estimate the fecundity regression.

Figure 7. The linear regression of batch fecundity on ovary-free weight fit to 83 females with hydrated eggs.

Year	1980	1981	1981	1982	1983
Survey	8003/4	8102	8104	8202	8302
Mean weight (g)	17.4	13.4	16.2	18.8	11.2
Eggs/gram	444	623	546	576	473

Spawning Fraction

To estimate spawning fraction, S, for each region, we again used equation (6), where $\bar{y}_i = S_i$ was the proportion of mature females in the ith trawl that spawned one night prior to capture (day-1 spawners). (See Hunter and Macewicz 1980, for histological definition of day-1 and day-0 spawners.) The desired m_i was again 25 mature females.

The proportion of day-0 spawners (females that spawn on the night of capture) can also be used to estimate spawning fraction. However, it was suspected that these females are overrepresented in the trawl catches, thus biasing the proportion of day-1 spawners. Hence, the value of m_i in equations (6) and (7) is adjusted by deleting day-0 spawners from the sample and equating the number of day-0 spawners to the number of day-1 spawners, thus reducing the average subsample size, $\bar{m}$.

The adjusted estimates of spawning fraction for each region are:

	North	Bight	South
$\bar{\bar{S}}$	0.0346	0.103	0.126
Standard error	0.0195	0.0178	0.0299
n	10	30	11

Spawning fraction varied greatly among regions (Figure 8), violating the assumption of the egg production model that all parameters were constant. This observation necessitated regionalizing the survey so that the parameters within each region were constant. Spawning fraction to the north region was significantly smaller than that for the bight and south regions (two-tailed test, $p = < 0.10$). The estimated mean spawning fractions for the bight and south regions were similar, although their observed distributions were quite different (Figure 8).

Sex Ratio

The parameter sex ratio, R, was measured as the fraction of females in the population based on fish weight. We again used equations (6) and (7) by setting $\bar{y}_i = R_i$ where R_i is the estimated total weight of females in the first 50 fish subsampled divided by the estimated total weight of the 50 fish; and m_i is the estimated total weight of the first 50 fish (Picquelle and Hewitt 1983). The average weights for each sex for each trawl were estimated from 5 males and from 25 females; again the weight of any females with hydrated eggs was adjusted using equation (8).

where $S_h{}^2 = 867,000$ is the variance about the regression (9),

$\bar{W}_i{}^*$ is the average ovary-free weight for the ith trawl,

$\bar{W}_h{}^* = 11.6$ grams is the average ovary-free weight for the 83 hydrated females used in regression (9),

$\text{Var}(b) = 1040$ is the variance of the slope of regression (9), and

n is the number of positive trawls.

The resulting means and standard errors for fecundity for each region were:

	North	Bight	South
$\bar{\bar{F}}$ (eggs per batch)	6285	5295	4423
Standard error	879	467	252
n	10	30	11

Fecundity follows the same pattern over regions as weight because it was positively correlated with weight.

Specific fecundity, expressed as eggs per gram of whole body weight, was calculated for the entire survey without regionalization to allow for easy comparison to previous years (these values were not used to estimate biomass):

The estimated sex ratios for the three regions were similar (Figure 9).

	North	Bight	South
$\bar{\bar{R}}$	0.523	0.559	0.549
Standard error	0.0496	0.0411	0.0703
n	10	30	11

Biomass Estimate and Variance

The parameter estimates and their coefficients of variation are summarized by region in Table 1. The biomass estimates for each region were calculated using equation (1), and approximate variances were calculated using equation (2). The sample covariance terms in equation (2) were calculated only for adult parameters; P_o was derived from a separate survey than that for the adult parameters (the plankton survey

vs the trawl survey), hence the sample covariances between P_o and the adult parameters were assumed to be zero.

The sample correlations among the adult parameters that were significantly different from zero are (by region):

North $-\, \text{corr}(WF) = 0.978$, $\text{corr}(WS) = 0.735$, corr $(FS) = 0.714$
Bight $-\, \text{corr}(WF) = 0.930$, $\text{corr}(WR) = 0.473$, corr $(FR) = 0.439$
South $-\, \text{corr}(WF) = 0.824$

The correlation between weight and fecundity was high for each region because fecundity was estimated by a linear regression on weight. Weight and spawning fraction were highly correlated for the north region, implying that the larger females spawned more
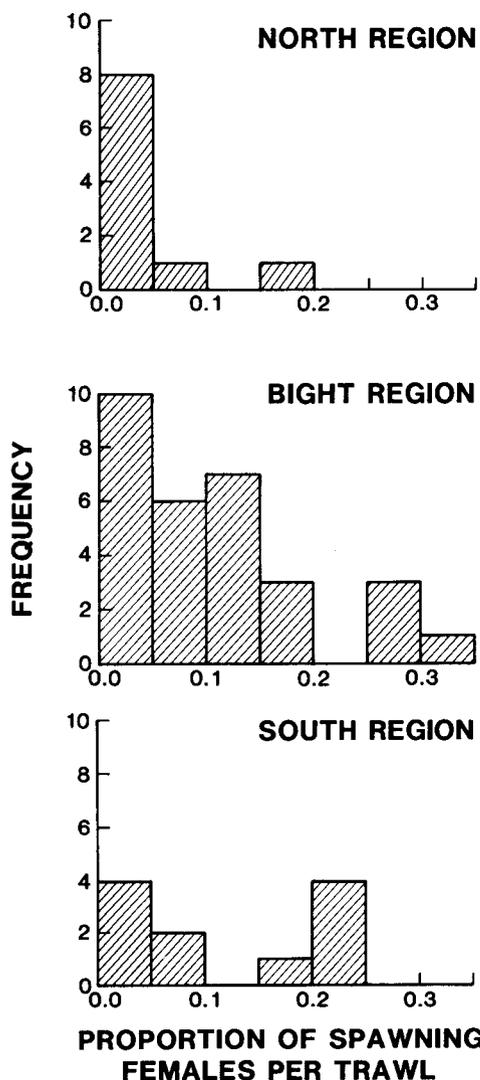
Figure 8. Frequency distributions of spawning fractions for each region.
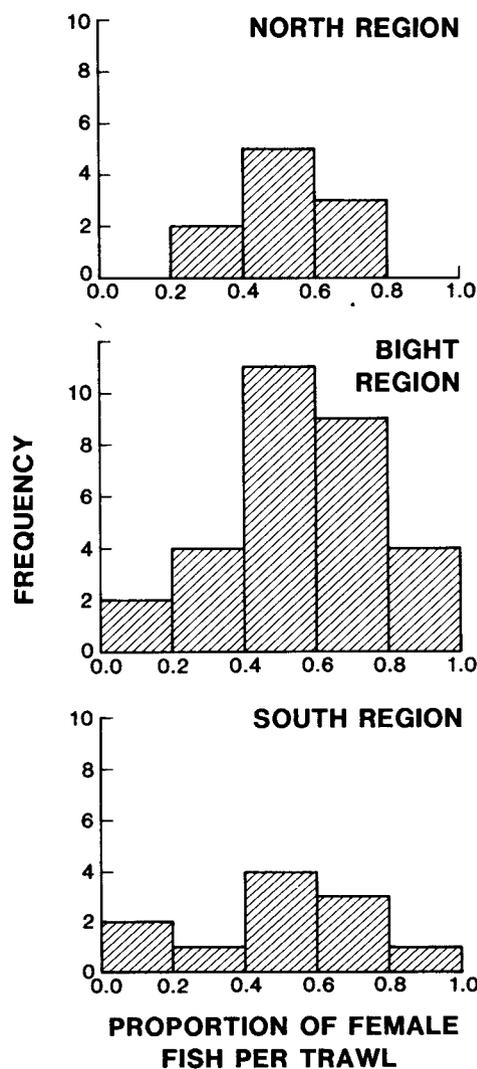
Figure 9. Frequency distributions of sex ratio for each region.

23

TABLE 1
Estimates of Egg Production Parameters and Spawning
Biomass by Region for 1983

Parameters		North	Bight	South	Total
Egg production	P_o	1.62	7.28	5.06	
(eggs/0.05m²-day)		(0.671)	(0.0751)	(0.332)	
Area of survey	A	0.420	1.33	1.36	
(*10¹² 0.05m²)					
Average female weight	W	12.9	11.2	9.63	
(grams)		(0.121)	(0.0705)	(0.0385)	
Batch fecundity	F	6285	5295	4423	
(eggs per batch per		(0.140)	(0.0882)	(0.0570)	
mature female)					
Spawning fraction	S	0.0346	0.103	0.126	
(spawning females/		(0.563)	(0.174)	(0.237)	
total females)					
Sex ratio	R	0.523	0.559	0.549	
(females/total)		(0.0949)	(0.0736)	(0.128)	
Spawning biomass	B	77,500	358,000	216,000	652,000
(metric tons)		(0.897)	(0.214)	(0.419)	(0.211)

Coefficient of variation indicated by ( ).

frequently or that the smaller females had a much shorter spawning season. The partial correlation of fecundity and spawning fraction would be negligible if adjusted for weight.

The total biomass is estimated by the sum of the regional biomasses. The variance of the total biomass is the sum of the regional variances. These are:

	North	Bight	South	Total
B (MT)	77,500	358,000	216,000	652,000
Standard error	69,500	76,800	90,500	137,000
Coefficient of variation	0.897	0.214	0.419	0.211

The 1983 biomass estimate increased substantially from 1982 and is approximately midway between the 1980 biomass and the first 1981 biomass estimate (Stauffer and Picquelle 1980; Picquelle and Hewitt 1983). In 1983 the mesh size of the plankton net used to sample eggs was reduced from 0.333 mm to 0.150 mm. Experimentation has shown that the previously used larger mesh net retains 91% of the eggs caught by the smaller mesh net (Lo 1983). The previous spawning biomass estimate should be corrected for net retention, giving the second series of biomasses in the table below:

Year	1980	1981	1981	1982	1983
Cruise	8003/4	8102	8104	8202	8302
Reported B (MT)	792,000	577,000	339,000	378,000	652,000
Coefficient of variation	0.262	0.216	0.187	0.057	0.211
Retention-corrected B (MT)	870,000	635,000	372,000	415,000	652,000

The increase in biomass was probably due to a very large 1982 year class. This conclusion is supported by

a shift in the weight distribution towards much smaller fish. In 1982 the modal mature female weight was 19 grams; in 1983 it was 11 grams. The 1982 year class constituted the major portion (75%) of a trawl survey conducted by the California Department of Fish and Game in February, 1983 (K. Mais, Cruise Report 83-X-1, dated March 21, 1983, Calif. Dept. of Fish and Game, Long Beach CA).

EQUIVALENT LARVAL CENSUS ESTIMATE BIOMASS

The best estimate of the 1983 anchovy spawning biomass is the quotient of the production of eggs and the adult fecundity by weight as described above. However, the Anchovy Management Plan requires that the biomass estimate be based on the larval census method, which assumes that spawning biomass is simply proportional to the annual census of larvae.

The larval census method defines the spawning biomass as proportional to the average standing stock of larvae summed over four quarters of the year, and assumes constant reproductive output by the adults and constant survival of the young. The proportionality constant was defined from a regression of sardine biomass on sardine larvae and extended to the anchovy by assuming a constant relative fecundity between the two species (Smith 1972).

During the 1983 biomass survey, 850 vertical tows for eggs (CalVET) and 78 oblique tows for larvae (CalBOBL) were conducted during the anchovy spawning season. These samples are adequate to determine the daily production of eggs and larvae during the sampling period, but not adequate to *measure* the annual census of larvae. Instead, the annual census of larvae may be *estimated* by integrating the larval production curve and extrapolating the resulting estimate of standing stock to an annual census using historical proportions of quarterly abundances.

In order to correctly use Smith's (1972) proportionality constant, the estimate of standing stock of larvae must be reduced to that portion which would have been retained by a standard plankton net. Thus:

$$\hat{B}_1 = N(2.12) \ (r)(k) \quad \text{(Picquelle and Hewitt 1983)} \quad (11)$$

where $\hat{B}_1$ is the equivalent larval census estimate of spawning biomass (MT),

N is the average standing stock of larvae during the spawning season estimated as the integral of the larval production curve over the age period which is vulnerable to capture (larvae),

2.12 is the average factor by which the annual census has exceeded the standing stock of lar-

vae during the spawning season, (Picquelle and Hewitt 1983)

r is the retention of larvae in the net (Picquelle and Hewitt 1983), estimated as the ratio of the raw catch and the catch adjusted for extrusion and avoidance (size-specific retention from Lo 1983, weighted by abundance at size), r = 0.30,

k is Smith's (1972) proportionality constant = 8.9×10^{-8} (MT/larva).

The distributions of anchovy eggs and larvae describe the same general geographic pattern (Figure 10): extensive spawning throughout the Southern California Bight with the exception of the Santa Barbara Channel, spawning along a narrower coastal band adjacent to the northern Baja California coast inside of Guadalupe Island, and measurable but reduced spawning adjacent to the coast north of Point Conception. Larvae were distributed more extensively over the survey area than were eggs. Both eggs and larvae were distributed farther offshore in 1983 than in 1982.

We used the CalVET sample to estimate the egg production curve, as described earlier and shown in Figures 4 and 11. We used the CalBOBL sample to estimate the larval production curve (Figure 11). The larvae were grouped into twelve size categories (yolk-
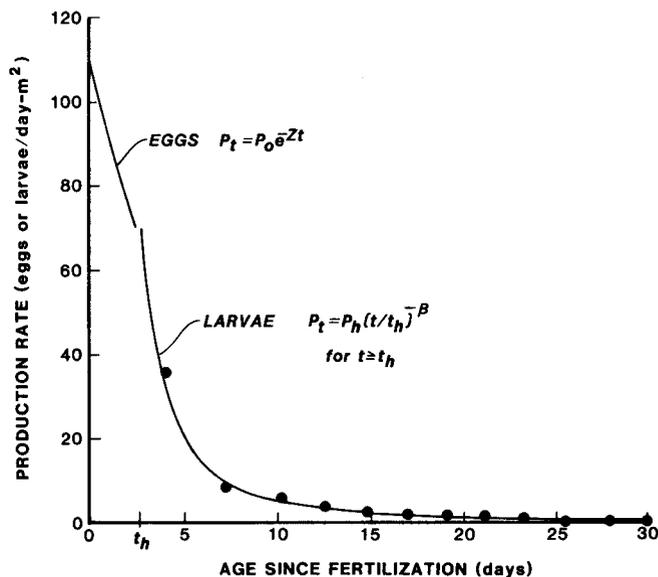
Figure 11. Production rate of anchovy eggs and larvae as a function of age since fertilization. The egg production curve was fit to the CalVET samples (Figure 4); the larval production curve was fit to the CalBOBL samples.

sac to 15 mm), and catches were adjusted for variations in the volume of water filtered per m of depth. Bias corrections were also applied for extrusion of small larvae through the meshes of the net and avoidance of the net by large larvae. The adjusted catches
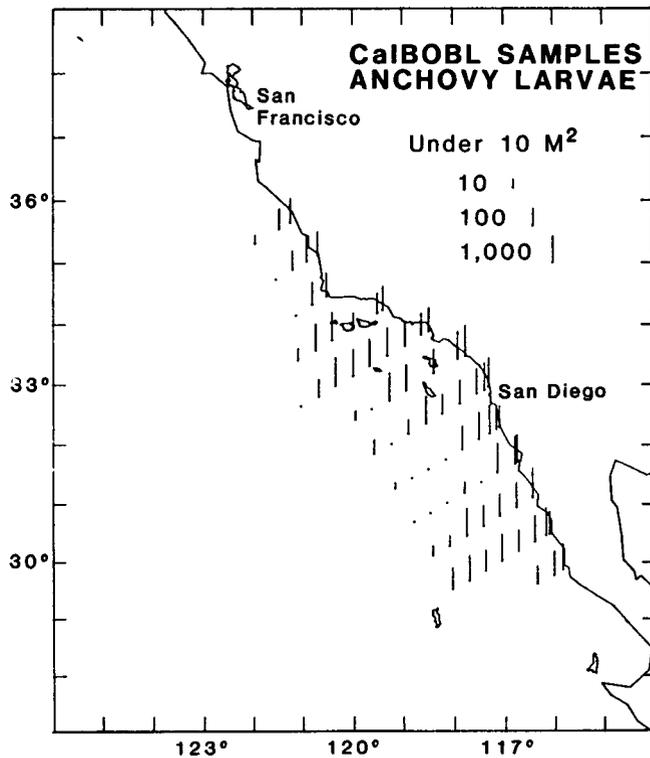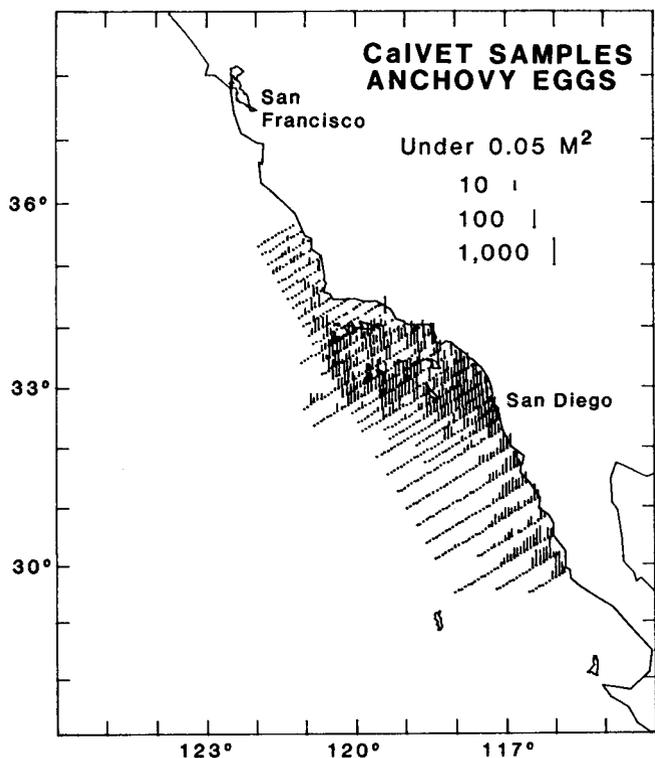
Figure 10. The distributions of anchovy eggs from CalVET samples and anchovy larvae from CalBOBL samples. The distributions of eggs and larvae describe the same general geographic pattern, with the larvae distributed more extensively over the survey area.

were divided by the duration of growth, through each size class, to estimate the age-specific production of larvae (P_t). The adjustments were accomplished by fitting a weighted negative binomial model to the sample frequency distributions of each size class. Each observation is weighted by a factor that is the product of the various adjustments, and the means of the final distributions are unbiased estimates of production (P_t). The procedure was developed in a series of papers: Bissel 1972; Zweifel and Smith 1981; Hewitt 1981, 1982; Hewitt and Methot 1982; Hewitt and Brewer 1983; Picquelle and Hewitt 1983.

Estimates of larval production (P_t) decline at a decreasing rate with age (t) (Figure 11). An unweighted nonlinear least squares method was used to fit the following two-parameter function to the data:

$$P_t = P_h \left(\frac{t}{t_h}\right)^{-\beta} \text{ for } t \geqslant t_h. \qquad (12)$$

where t_h is the age (since fertilization) at hatch, and P_h is the production of hatching larvae. (This form results from expressing the mortality rate as continually decreasing with age: $dP/Pdt = -\beta/t$; Lo, in press.) The average standing stock of larvae (N) is the integral of the production curve from the age at hatch to 30 days, multiplied by the area of the survey:

$$N = \frac{AP_h t_h}{\beta - 1} \left(1 - \left(\frac{t_h}{30}\right)^{\beta - 1}\right) \qquad (13)$$

where A = the area of the survey.

Because the egg production curve is derived from more observations than the larval production curve, the former may be expected to yield a more precise estimate of production at age of hatch. For this reason we used the CalBOBL data to determine the *shape* of the larval production curve and the CalVET data to *scale* the curve. To do this, we substituted $P_o s$ for P_h in the above expression for N, where P_o is the initial production of eggs and s is the fraction surviving to hatch.[2] As it turned out, the two production curves lined up reasonably well (Figure 11) with $P_h = 81/m^2$ and $P_o s = 69/m^2$ (see also Table 2). In constraining the larval production curve to be consistent with the egg production curve, we improve the precision of the estimate of the larval standing stock (time integral of the larval production curve).

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[2]The fraction surviving to hatch, s, is estimated by applying the egg mortality rate over the incubation period. The incubation period (time to hatch in Table 2) is calculated using Lo's (1983) expression and the mean temperature at 10 m depth weighted by egg abundance (15.9°C).

TABLE 2
Parameters Used to Estimate Larval Census Equivalent Spawning Biomass

Parameters		Estimates
Area of survey	A	$155.5*10^9$ m^2
Initial production of eggs	P_o	110.95 eggs/m^2
Egg mortality rate	Z	0.18356
Time to hatch	t_h	2.56 days
Survival to hatch	$s = e^{-Z t_h}$	0.6251
Production of eggs surviving to hatch	$P_o s$	69.35 eggs/m^2-day
Retention factor	r	0.30
Larval mortality coefficient	β	2.0229
Production of hatching larvae	P_h	80.49 larvae/m^2-day
Standing stock of larvae	N	$24,813*10^9$ larvae
Equivalent larval census		$15,800*10^9$ larvae
Estimate of spawning biomass	B_t	$1.405*10^6$ mt

Parameter values are listed in Table 2. The 1983 equivalent larval census estimate of anchovy spawning biomass is 1.405×10^6 MT; the equivalent annual larval census is $15,800 \times 10^9$ larvae. The observations were not stratified; rather, all were treated in an equal manner regardless of their geographic position. The retention factor, r, was lower in 1983 because larval population was composed of a relatively large number of small larvae, which are more easily extruded through the net meshes.

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Part II

SCIENTIFIC CONTRIBUTIONS

LAGRANGIAN OBSERVATIONS OF NEAR-SURFACE CURRENTS IN CANAL DE BALLENAS

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ABSTRACT
Radio buoys tracked at depths of 0 and 50 m in the northern portion of Canal de Ballenas, Gulf of California, in June 1982, show a current dominated by alongchannel oscillations, on which are superimposed smaller-scale turbulent eddies. Maximum displacements and velocities of the motions recorded alongchannel are 0(15 km; 3 m sec^{-1}), and crosschannel they are 0(5 km; 0.5 m sec^{-1}). The mean velocity was generally towards the southeast along the channel and close to two orders of magnitude smaller than the maximum instantaneous velocities observed. The eddy-like motions, which had no preferred sense of rotation, had typical scales similar to those of the crosschannel excursions and appeared to trap the buoys after these had traveled southeastward for a few hours. This suggests a spatial variation of the flow, which might be associated with the rough configuration of the channel's coastline and bottom topography. Spectral analysis of the drogue excursions about their mean positions indicated that the motions were probably related to the semidiurnal tide and, at the surface, to the strong winds that blew from the mountain passes in Baja California, and also showed a large spatial variability. Logistics and weather conditions made longer and more precise measurements impossible, and it is difficult to conclude here on the dynamics of the flow in Canal de Ballenas. These measurements, to our knowledge, represent the first direct measurements of circulation reported for this area.

RESUMEN
Un grupo de radioboyas en superficie y a 50 m, rastreadas en la parte norte de Canal de Ballenas, Golfo de California, en Junio de 1982, muestra corrientes dominadas por oscilaciones longitudinales sobre las cuales se superponen vórtices de menor escala. Los desplazamientos y velocidades máximas registradas son de 0(15 km; 3 m sec^{-1}) en la dirección longitudinal y 0(5 km; 0.5 m sec^{-1}) en la dirección transversal al canal, respectivamente. La velocidad media fue generalmente hacia el sureste a lo largo del canal y

aproximadamente dos órdenes de magnitud menor que las velocidades instantáneas máximas observadas. Los giros turbulentos se observaron carentes de sentido preferente de rotación y con escalas típicas comparables a la de los desplazamientos transversales al canal. En apariencia, dichos giros atraparon a las boyas después de que éstas se desplazaron hacia el sureste por algunas horas. Esto sugiere una variación espacial del flujo, asociada posiblemente con la configuración irregular de la costa y del fondo del canal. El análisis espectral de la excursión de las boyas con respecto a su posición media indica una relación probable con la marea semidiurna y, en superficie, con los vientos fuertes provenientes de los pasos de las montañas de Baja California, los cuales presentaron asimismo una marcada estructura espacial. Las condiciones atmosféricas locales y logísticas no permitieron efectuar observaciones más prolongadas y precisas, por lo que es difícil concluir aquí sobre la dinámica de la corriente en Canal de Ballenas. El principal interés de nuestros resultados reside en que representan las primeras observaciones directas de la circulación dentro del canal.

INTRODUCTION
Canal de Ballenas is a complex stretch of water that, together with the eastern Tiburon Basin, connects the northern Gulf of California to its central Guaymas Basin. It is bounded on the west by the peninsula of Baja California and on the east by a long, continuous submarine ridge from which rise Angel de la Guarda, San Lorenzo, and other smaller islands (Figure 1). The bathymetry of Canal de Ballenas is poorly known, but its main depression is the Salsipuedes Basin, where depths exceed 1,600 m. The channel is about 125 km long and is bounded by sills at both ends. In the area of our study, the width varies from 15 to 25 km.

The purpose of this note is to report on drogue measurements of the near-surface currents in the northern end of Canal de Ballenas, during the Pichicuco I expedition in June 1982. No extensive analysis can be done of these series, which are fewer and shorter than could be wished in a study of such a complicated system. But they are, to our knowledge,

among the first direct measurements made of the circulation in this region.

Early reports of the flow in Canal de Ballenas indicated the currents can reach speeds of 3 m sec^{-1} (Hubbs and Roden 1964). Studies of the base of the shelf in Salsipuedes Basin showed exposed bedrock, suggesting that currents at depth are strong enough to scour or inhibit the deposition of sediments (Rusnak et al. 1964). On the other hand, Brown's (1965) drogue measurements of less than a day at the southern end of Salsipuedes Basin showed slow currents with a net drift to the south along the channel, believed to be the result of the combined driving influences of tides and wind.

Currents in Canal de Ballenas have been attributed mainly to the large tidal range in the northern gulf and to the narrow configuration of the channel. These motions appear to produce intense vertical mixing that brings cool water to the sea surface during most of the year (Robinson 1973; Badan-Dangon et al. in press) and generate packets of internal waves that radiate away from the sill regions, particularly during spring tides (Fu and Holt 1984). The mixing above sill depth probably causes the weakly stratified water column found beneath the thermocline in Canal de Ballenas (Roden 1964; Alvarez-Borrego 1983).

THE EXPERIMENT

Our measurements were made near the northern end of Canal de Ballenas, with drogues consisting of a window-shade-type drag element, with a 9-m^2 effective surface, hanging either directly beneath a surface float of 40 cm in diameter, or attached to it with a line that set the sail 50 m beneath the surface. Attached to this drogue was a radio buoy that transmitted at frequencies close to 4 MHz. The drogues, numbered consecutively, were launched in two sets from R/V *El Puma*, at positions shown in Figure 1. The first set, consisting of three surface drogues, was launched on the evening of June 17. Of these, two buoys were tracked for 14 and 27 hours, respectively. The second set, consisting of three surface and three 50-m drogues, was released near noon on June 24. Of these, two drogues transmitted for 7 and 19 hours and two others provided data for up to 74 hours. None of the drogues launched were recovered; they probably collapsed because of the extreme sea conditions that prevailed at the time.

The tracking was done from two radio direction finder (RDF) stations located 39 km apart on the western side of the channel (Figure 1). These positions
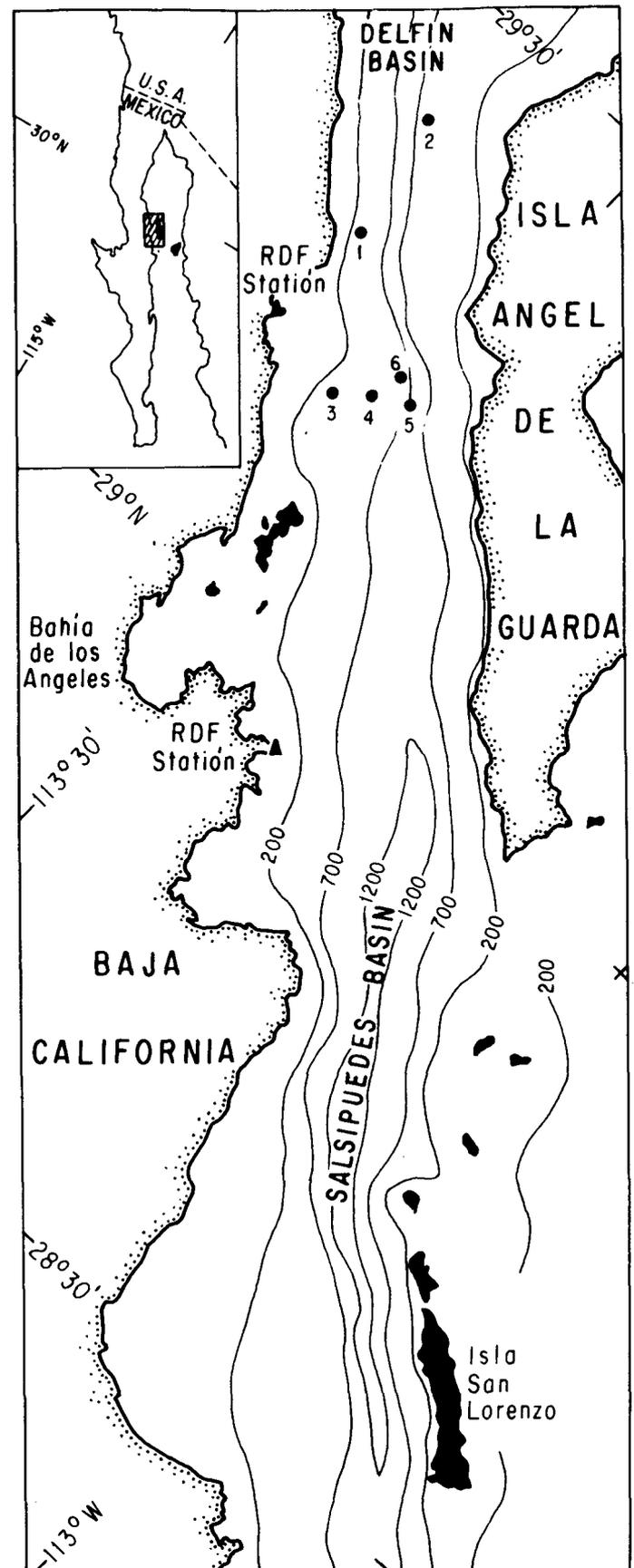
Figure 1. Location of the drogue experiment, showing the sites of the two RDF stations and the launching positions of the drogues. Depth contours are in meters and known to be approximate.

were chosen because we expected more southerly excursions of the drogues than were in fact observed. The successive positions of the buoys were obtained between every half hour to one hour by averaging twelve readings with respect to true north, to the nearest half degree, from each RDF station.

The manufacturer of the equipment (Telecommunications Enterprises Co.) reports the accuracy of each reading to be better than one degree, which is supported by the studies of Murray et al. (1975) and of Wiseman et al. (1977). In our study we found that the readings from the southern tracking station, farthest from the group of buoys, had a standard deviation close to one degree, whereas that of the northern station was closer to 2.5 degrees. Added difficulties appeared to be the echoing of the signals by the elevated terrain surrounding the channel, and radio interference that often obscured the readings, principally

during the hours close to dawn. Our estimate of the average positional accuracy is reported graphically below for each drogue.

In addition to positioning the drogues, we measured winds with recording anemometers at the sites of both RDF stations for the entire period of the experiment (Figure 2). Predicted tidal elevations were obtained for Bahía de los Angeles (Figure 3). Standard hydrographic measurements with bottles were made from R/V *El Puma* (Figure 4).

RESULTS

The conditions that prevailed during the experiment are illustrated by the wind series obtained at the sites of the tracking stations (Figure 2). They show a strong sea breeze regime superimposed on a trend of weakening northerly winds as the experiment progressed. Winds were strong, often peaking above 25 m sec^{-1} at
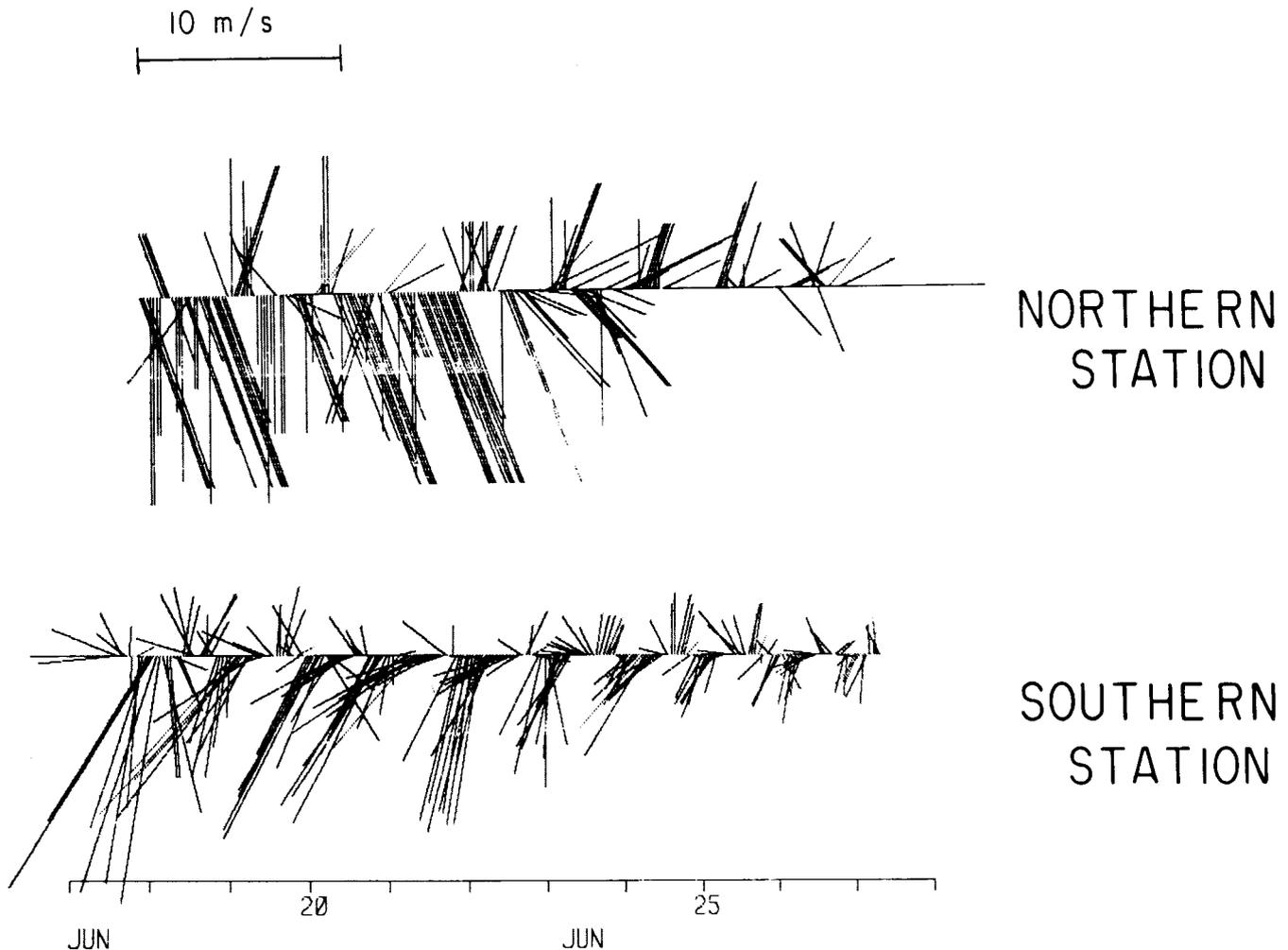
Figure 2. Wind vectors measured at the two RDF stations, rotated so the general orientation of the channel is vertical on the page.

DROGUES 1, 2

DROGUES 3, 4, 5, 6
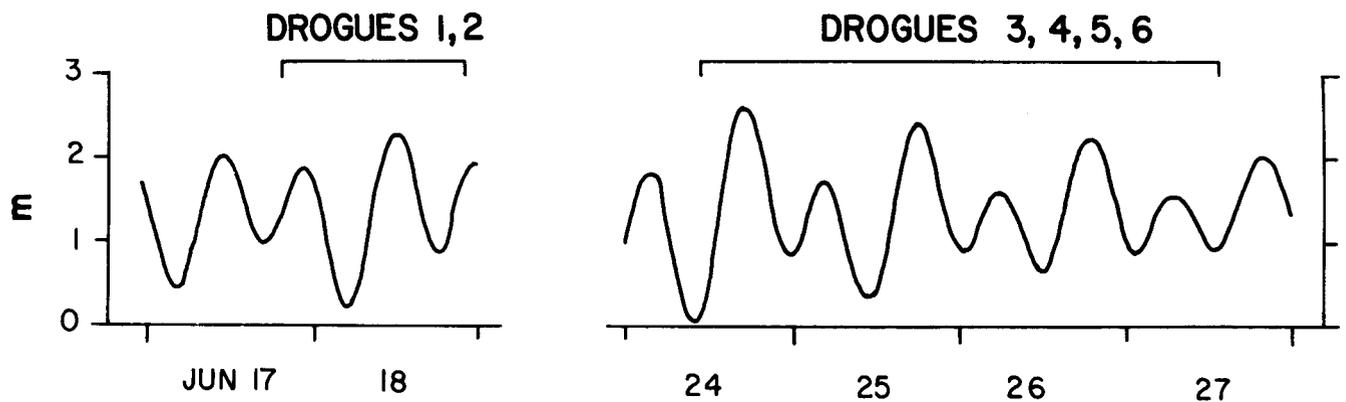
Figure 3. Predicted tidal elevations at Bahía de los Angeles for the duration of each set of measurements.

the beginning of the experiment, and caused heavy
local seas that made tracking the buoys difficult and
caused several of them to fail. The series confirm the
marked spatial variability of winds that may be ex-
pected in the region. This variability was manifested

during the experiment by widely differing local sea
states.

Figure 3 shows the predicted sea-surface elevations
at Bahía de los Angeles for the time of the two sets of
measurements. The character of the tide is dominated

STATIONS

STATIONS
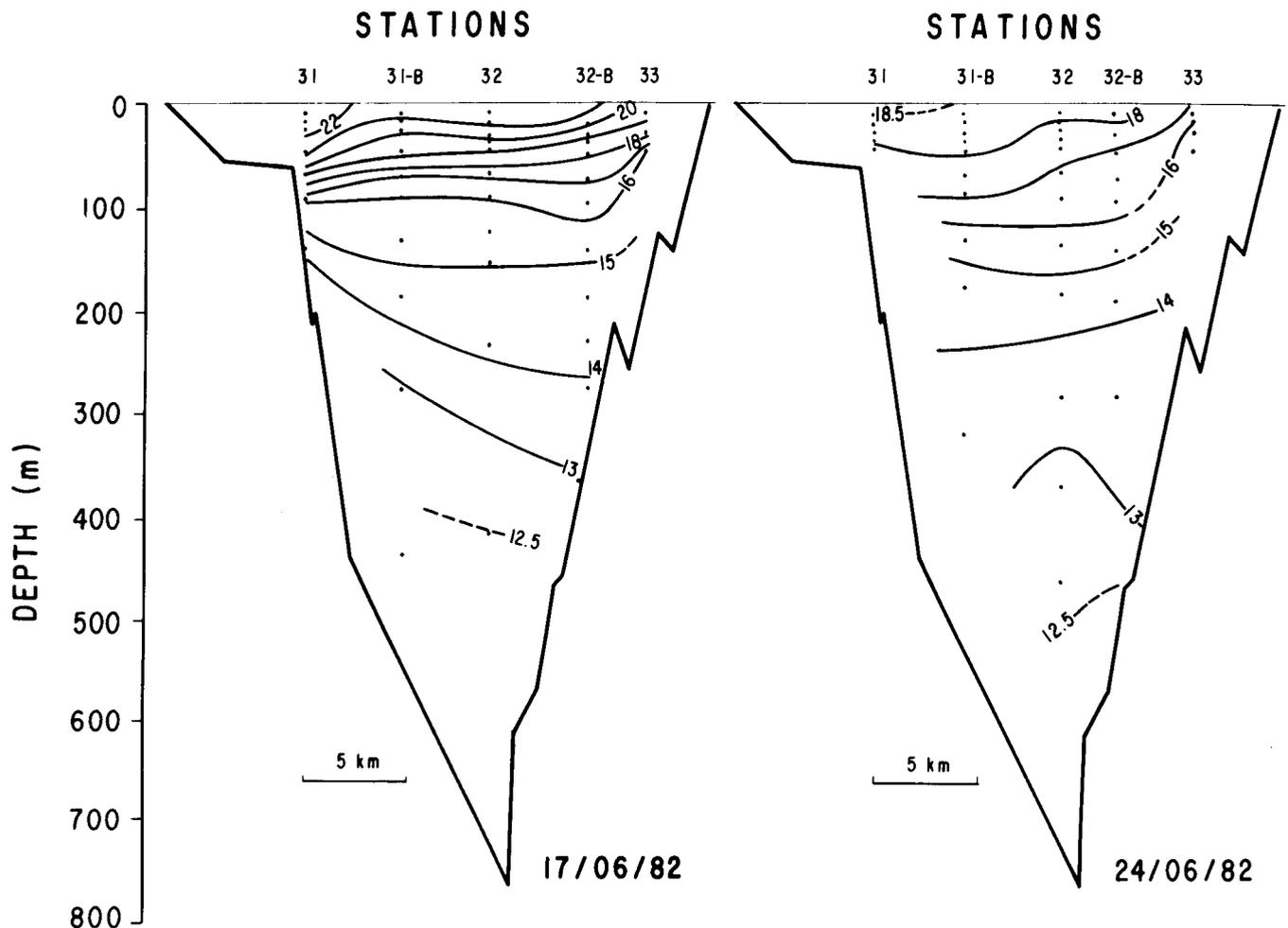
Figure 4. Temperature sections (in degrees C) made across the wider, central portion of Canal de Ballenas at the times the drogues were launched.
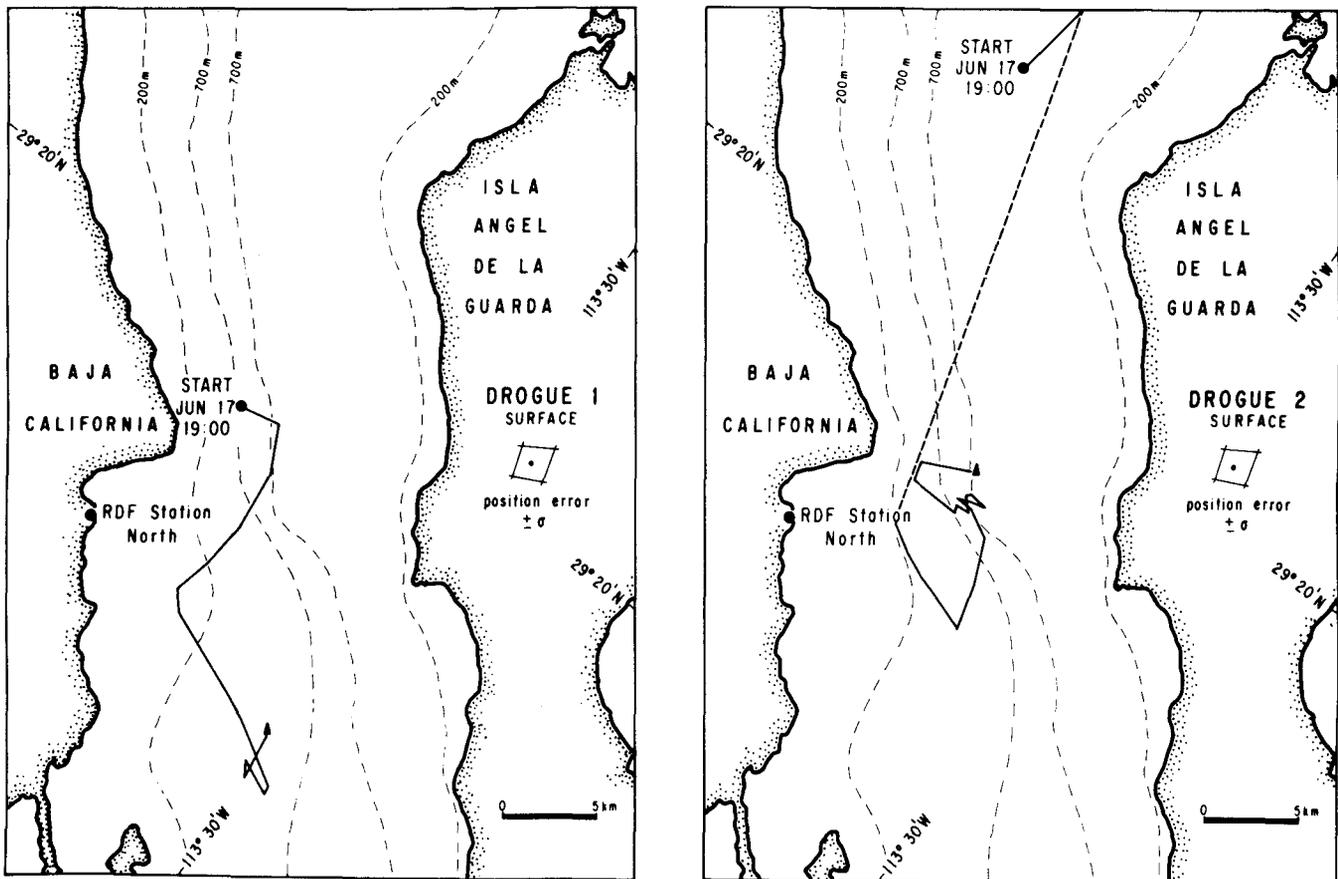
Figure 5. Tracks of the drogues launched in the first set. Launching time, depth of drogue, and estimated average position error is indicated.

by the semidiurnal components, with maximum ranges close to 3 m. Unfortunately, logistics prevented us from launching buoys during the peak of the spring tides that occurred between the two sets of measurements and probably would have resulted in more rapid displacements of the drogues than documented here. Two hydrographic lines were made across the wide section of the channel after launching the two sets of drogues (Figure 4). They show the water column consisting of an initially well-stratified, 100-m-thick near-surface layer overlying the weakly stratified water typical of this region. Although the hydrographic structure in the channel is known to be extremely variable in short time scales, all of our drogue measurements were clearly made within the near-surface layer, as defined by the 16°C isotherm.

The first set of drogues was released in the northern end of the channel, close to where its narrowest cross section (4.5 km²) separates the Salsipuedes Basin from the southern extension of the Delfin Basin. The second set was released 10 km farther south, where the channel widens to 9.7 km² (Figure 1). Trajectories of interpolated hourly positions were obtained for each

drogue by fitting a cubic spline to the original series of averaged positions (Figures 5 and 6). All drogues, with the exception of drogue 3, show large alongchannel excursions, apparently in response to reversals of the tidal flow through the channel. These alongchannel displacements appear larger in the narrow northern end of the channel than in the wider central portion. This is shown more clearly in Figure 7, where successive alongchannel departures from their mean positions were computed for drogues 3 and 4. Drogue 3, a surface buoy, remained in the southern part of the study area and had limited excursions of less than 5 km for all 74 hours. During the first 24 hours of that same period, drogue 4, a 50-m buoy, showed excursions close to 15 km as it traveled in the narrow section of the channel. It then moved south, where it had excursions comparable to those of buoy 3 for the remaining 48 hours. The qualitative impression provided by the trajectories is that the buoys moved rapidly alongchannel until they were caught in complicated eddylike motions in the wider part of the channel. As a result, it appears that motions are more rapid alongchannel in the narrow northern channel than in

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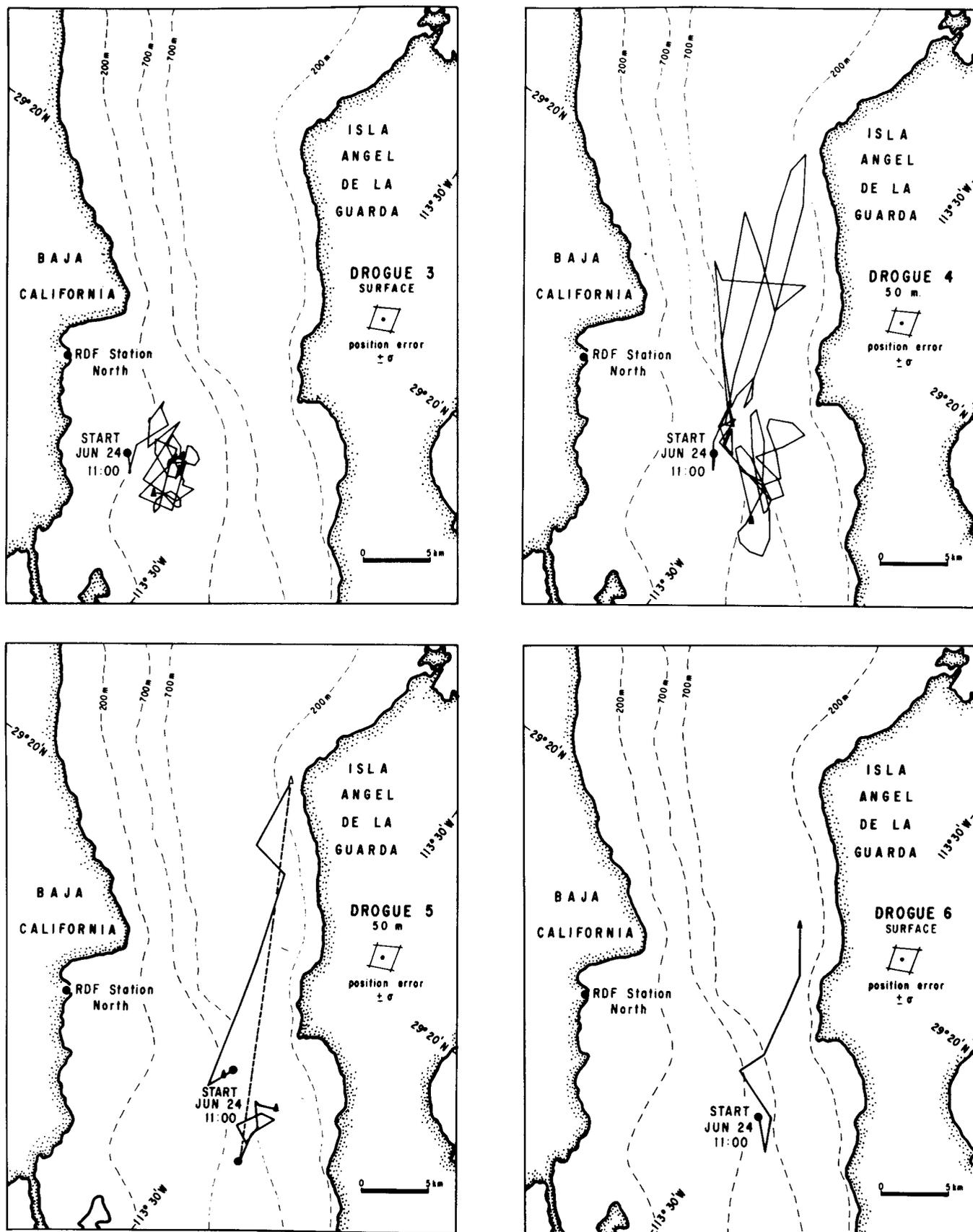
Figure 6. Same as Figure 4, for the second set.

TABLE 1
Basic Statistics of the Velocity Components Computed from Hourly Positions of the Drogues

Drogue Number Tracking time		1 (sfc.) 14 hrs	2 (sfc.) 27 hrs	3 (sfc.) 74 hrs	4 (50 m) 73 hrs	5 (50 m) 19 hrs	6 (sfc.) 7 hrs
	Mean	−0.34	−0.19	−0.01	−0.02	−0.39	0.57
Alongchannel	St. dev.	0.45	0.63	0.28	0.71	0.72	0.69
velocity (m·s^{-1})	Max.	0.57	0.84	0.72	2.76	2.35	1.26
	Min.	−0.97	−1.94	−0.96	−2.03	−0.39	−0.68
	Mean	0.03	0.04	0.00	0.00	0.04	0.08
Crosschannel	St. dev.	0.36	0.50	0.24	0.45	0.56	0.53
velocity (m·s^{-1})	Max.	0.49	1.25	0.79	1.56	1.15	0.74
	Min.	−0.51	−1.48	−0.84	−1.28	−0.82	−0.74

its central part, by a factor close to the inverse proportion of the corresponding cross-sectional areas. This suggests that the rough configuration of the channel's coastline and bottom topography is important in determining spatial variations of the flow. In contrast, transverse excursions were everywhere of the same magnitude, about two to three times smaller than the alongchannel excursions in the narrow part of the channel.

The net flow, inferred from buoys 3 and 4 after six tidal cycles, appears to be towards the southeast along the channel and about two orders of magnitude smaller than the maximum velocities observed. The remaining drogues, with the exception of drogue 6, also had net southward displacements, but their series were too short to suppose this to be a real indication of net flow.

In the same way, buoy 6 suggests a flow to the north close to Angel de la Guarda Island, where less violent winds were observed and the surface layer is also less deep (Figure 4). However, this northward flow was also observed with other buoys that later returned southward (e.g., buoy 5), and buoy 6 was lost after only 7 hours of measurements, so it is difficult to attach much significance to a possible counterflow on that side of the channel.

Table 1 summarizes some basic statistics of the velocity components computed from the successive positions of the drogues. In all cases the mean is only a few centimeters per second and smaller than the standard deviations, suggesting that the net flow through the channel is much smaller than the instantaneous transports. The mean alongchannel velocities are generally larger than the mean crosschannel velocities. However, the standard deviations of both components are comparable, with the alongchannel only slightly higher than the crosschannel. The maximum velocities reach between 2 and 3 m sec^{-1}, confirming the estimates reported by Hubbs and Roden (1964). The largest velocities in both components were shown by buoy 4, generally located closer to the center of the channel and at 50-m depth. Hence, during this experiment, the flow in the channel had large oscillations and a smaller net flow, generally to the south, except possibly very close to the eastern edge of the channel. Since the buoys stayed for the most part in the wider part of the channel, the standard deviation of the two horizontal velocity components is similar, suggesting a dominance in this region of turbulent eddy motions with typical horizontal scales of about 5 to 7 km.

In an attempt to investigate the character of the alongchannel motions, we computed maximum entropy spectra of the two longest series, provided by buoys 3 and 4. These show rather different compositions (Figure 8). The spectrum for the surface drogue shows peaks close to the semidiurnal and diurnal frequencies and smaller peaks at higher frequencies. The spectrum for the 50-m drogue shows a well-defined peak at the semidiurnal frequency and a smaller sec-
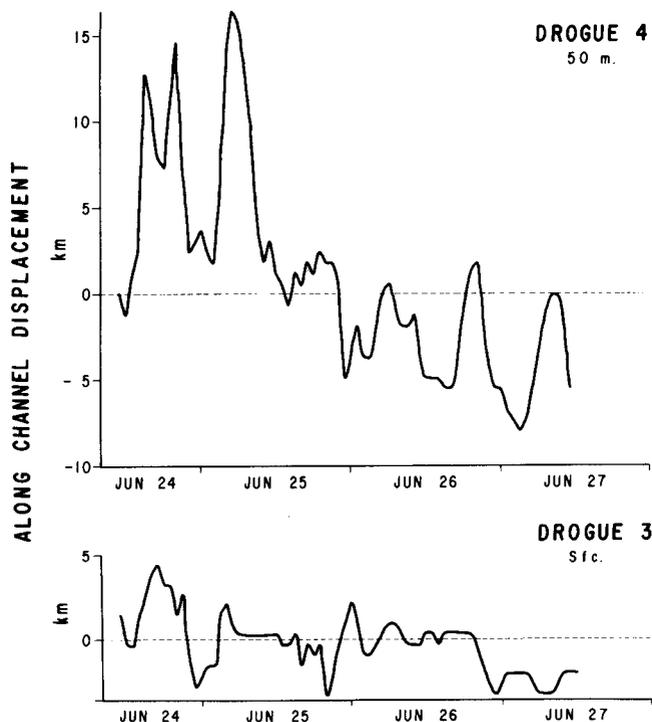
Figure 7. Hourly alongchannel displacements about their mean positions for drogues 3 and 4.
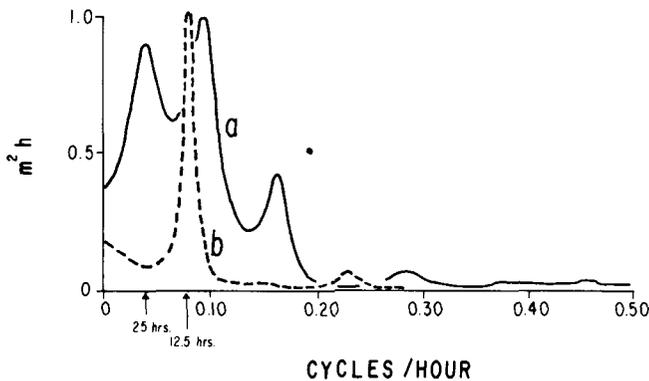
Figure 8. Normalized MEM spectra of alongchannel displacement for surface drogue 3 (a) and 50-m drogue 4 (b). These were computed from series of 73 hourly data points, with a 15-element predictor error filter.

ondary peak. The diurnal peak is absent from the 50-m spectrum. The peak at the semidiurnal frequency is probably associated with the strong tidal forcing by the M2 component, which is prominent in the gulf (Filloux 1973), whereas the diurnal peak exhibited by the spectrum of the surface drogue might be associated with the diurnal sea breeze, which we have shown to be very strong during the experiment. We have no satisfactory explanation for the smaller peaks at higher frequencies, since they do not correspond to any of the higher-order tidal components. If real, these may represent the frequencies of the turbulent eddies that appear dominant in the central part of the channel, or they could have been induced by our sampling and interpolating schemes.

CONCLUSIONS

The extreme conditions that prevailed in Ballenas Channel during our field experiment made it impossible to obtain longer and more accurate series of measurements with the drogues. It is therefore difficult to provide more quantitative results about the kinematics, or strong conclusions about the dynamics of the flow through the channel. Qualitatively, the data support the notion that the flow is forced by the semidiurnal tide. At the surface, the intense winds can play an important role, and thus their strong spatial variability contributes to the complexity of the flow patterns. The flow is predominantly in the alongchannel direction, with typical excursions of about 15 km. Nonetheless, crosschannel motions are not negligible, and in the wider, central part of the channel, motions appear dominated by eddylike patterns with typical scales close to 5 km. Thus, spatial variability of the flow is large, and it is to be expected that the dynamics of the flow are strongly nonlinear in this region.

Because the tidal range in the channel can account for but a fraction of the instantaneous volume trans-

port, and the motion is turbulent, it appears that although no large net flow takes place through the channel, a considerable amount of water may be exchanged through eddy processes over several tidal cycles. Moreover, the magnitude of the velocities observed and the general configuration of the flow support the idea that the region is able to sustain the efficient mixing suggested by other investigators. More extensive conclusions about the net flow through the channel should await longer series of measurements, which must include a sampling of the motions of the deeper, weakly stratified layer beneath the thermocline.

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SPAWNING FREQUENCY AND SEX RATIO IN THE PERUVIAN ANCHOVY, *ENGRAULIS RINGENS*[1]

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ABSTRACT

Spawning frequency was determined for the first time for the Peruvian anchovy, *Engraulis ringens*, using the incidence of postovulatory follicles. The agreement between two independent frequency estimates, one for females taken one day after spawning and another for females taken two days after spawning, demonstrated the reliability of this method. In August-September, the main period of annual spawning, 16.04% of the female population of the central and northern anchovy stock off Peru spawned per day: i.e., every 6.23 days the average female spawned a new batch of eggs. Hydration of ovaries began as early as 0700 hours in the morning. Spawning occurred at night between 1800 and 0200 hours, reaching a maximum at about 2200 hours. Sex ratio was 57.9% females by weight. The vulnerability of females to the purse seine changed with their reproductive state. Females with hydrated ovaries who were ready to spawn seemed to attract males and to form male-dominated "spawning schools" by segregating from "normal" schools at night.

RESUMEN

La frecuencia de puesta en la anchoveta peruana *Engraulis ringens* ha sido determinada por primera vez, tomando como base la incidencia de folículos post-ovulatorios. La concordancia entre dos estimaciones independientes de esta frecuencia, obtenidas de hembras un y dos días después de la puesta, demuestran la fiabilidad de esta método. Anualmente, el período principal de la puesta abarca de Agosto a Septiembre, cuando la puesta diaria comprendió el 16.04% de las hembras de las poblaciones del norte y centro de la región peruana; es decir, cada 6.23 días una hembra promedio pone una nueva remesa de huevos. La hidratación de los ovarios se inició temprano, a eso de las 0700 de la mañana. La puesta se produjo entre las 1800 y 0200 horas, alcanzando un máximo a las 2200 horas aproximadamente.

La proporción de sexos calculada en peso fue de 57.9% de hembras. La vulnerabilidad de las hembras a la pesca con redes de jareta varía con la fase reproductora enque se encuentran. Hembras con ovarios hidratados, que estaban dispuestas para la puesta parecian atraer a los machos y formar cardúmenes de puesta dominados por machos separándose de los cardúmenes normales durante la noche.

INTRODUCTION

In the past, estimating the spawning biomass of multiple-spawning pelagic fish species like anchovies and sardines posed serious problems because no adequate methods were available to determine the spawning frequency, i.e., the fraction of the female population spawning per unit time. Recently, Hunter and Goldberg (1980) solved this problem for the northern anchovy, *Engraulis mordax*, by an ingenious technique. They followed up the suggestion of Yamamoto and Yoshioka (1964) that spawning frequency could be determined by incidence of postovulatory follicles— the remnants of ovulated follicles.

Follicles are the layers of cells surrounding developing oocytes in the ovaries. After ovulation, they immediately begin to deteriorate and are then called postovulatory follicles (Hunter and Goldberg 1980). Hunter and Goldberg identified postovulatory follicles in histological sections of northern anchovy ovaries and classified the females into three groups: those spawning on the night of capture (new, or day-0 postovulatory follicles), those spawning on the night previous to capture (day-1 postovulatory follicles), and those showing no evidence of recent spawning. Hunter and Goldberg then used the frequency of day-1 postovulatory follicles as a measure of spawning frequency. They used anchovy spawned in the laboratory to develop this technique (Leong 1971). Because the time of induced spawning was known, they could de-

scribe histological criteria for aging postovulatory follicles. These criteria were then applied to field populations.

Hunter and Goldberg collected their field samples with a small trawler, which could catch adult anchovy only at night. They were therefore not able to obtain complete 24-hour time series of females with postovulatory follicles. This could have resulted in a bias in the estimation of spawning frequency, since Hunter and Goldberg (1980) had already shown that females captured on the night of spawning were oversampled.

It is well known that prior to ovulation the ovaries of teleost fish take up fluid, a process called hydration (Fulton 1898). Hunter and Macewicz (1980) suggested that if anchovies could be sampled during the day, it might be possible to use the incidence of females with hydrated ovaries ("hydrated females") to determine spawning frequency. The advantage would be that time and money could be saved because histological examination would no longer be required.

In this paper we estimate the spawning frequency of the Peruvian anchovy, *Engraulis ringens*, using Hunter and Goldberg's (1980) method. We can answer some of the questions posed by Hunter and Goldberg and Hunter and Macewicz (1980) because we used a different technique to sample anchovy. In Peru, anchovy were collected with a purse seiner and could therefore be sampled in the day as well as at night. Thus, females with postovulatory follicles and females in the hydrated, prespawning stage could be obtained for an entire 24-hour cycle. Any time-related bias in the incidence of females with postovulatory follicles would become obvious when a series of samples taken at regular intervals over 24 hours was examined. Thus, the use of a purse seine for the Peruvian anchovy gave new insights into bias in estimating spawning frequency. Because hydrated females were sampled during the day, the alternative approach of using incidence of hydrated females to estimate spawning frequency could also be evaluated. Thus the objectives of this paper are to evaluate Hunter and Goldberg's (1980) method for estimating spawning frequency by using a 24-hour sampling scheme and to determine the effect of different sampling gear (trawl versus purse seine) on the estimates of spawning frequency and sex ratio of Peruvian anchovy schools.

The findings of Hunter and Goldberg (1980) enabled the Southwest Fisheries Center, La Jolla, to develop the "egg production method" (Parker 1980; Stauffer and Picquelle 1980) for estimating spawning biomass of the northern anchovy off California. Two of the five parameters required for this method are spawning frequency and sex ratio. The data presented here were used to estimate the spawning biomass of

the Peruvian anchovy using the egg production method (Santander et al., in press).

METHODS

Adult anchovies were collected with a purse seiner. The cruise was run from August 25 to September 17, 1981. It began in the south and proceeded northwards. The purse seine stations were usually located within 20 miles of the shore because of adverse weather conditions and the scarcity of anchovy schools farther offshore. Most of the collections came from the southern part of the investigation area because weather conditions in the north prohibited use of the purse seine (Figure 1). The total number of collections was 49.

Immediately after capture, the anchovy's body cavity was opened from the anus to the ventral fins. Only live specimens were processed because of the rapid degeneration of the postovulatory follicles. The fish were preserved in a 4% buffered formaldehyde solution. Seawater was not used to dilute the formaldehyde solution because it causes a white precipitate that makes reading the histological sections difficult.

Twenty mature females were collected at random
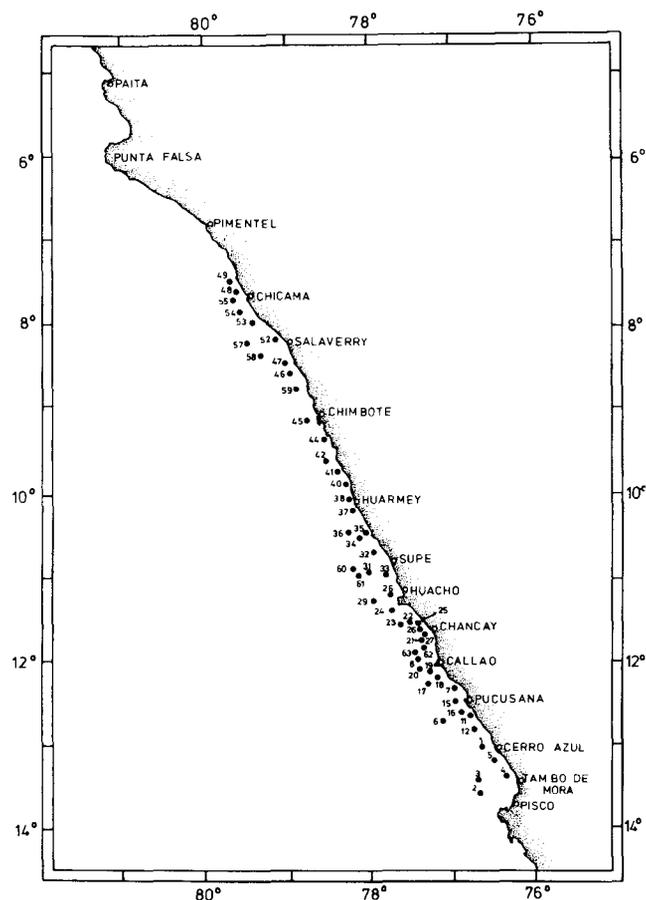
Figure 1. Map of surveyed area and location of samples of anchovies.

for histological analysis. Standard methods were used to process the ovaries. A small cube of about 0.125 cm^3 was cut from the center of the ovary. It was dehydrated in a series of alcohol solutions and embedded in paraplast. The histological sections were cut at 6 μm and stained with hematoxylin/eosin. A detailed account of the procedure is given in Alarcón et al. (in press). The criteria developed by Hunter and Goldberg (1980) for aging postovulatory follicles are based on the stages of degeneration through which they pass. Because postovulatory follicles degenerate rapidly, their age can only be determined up to 50 hours after spawning. The age classes for postovulatory follicles used here are somewhat different from those described by Hunter and Goldberg (1980).

The fraction of females (sex ratio) was estimated for each collection from a subsample consisting of the first 800 g of fish. The total body weight was used, because the gonad-free weight of males was not measured. The total body weight of hydrated females was adjusted (Santander et al., in press) for the excess weight of the hydrated ovary (Stauffer and Picquelle 1980). Immature fish were included because it was not possible to distinguish between mature and immature males. In order to attain exactly 800 g of fish it was necessary to use only that fraction of the weight of the last fish in the collection that completed the 800 g. Sample mean and variance were estimated according to Stauffer and Picquelle (1980):

$$\bar{\bar{R}} = \frac{\sum \bar{R}_i}{n}$$

and
$$V(\bar{\bar{R}}) = \frac{\sum (\bar{R}_i - \bar{\bar{R}})^2}{n(n-1)}$$

where
$\bar{R}_i$ = fraction of females by weight in percent in collection i

$\bar{\bar{R}}$ = average fraction of females by weight in percent from all collections.

For estimating the spawning frequency (fraction of mature females spawning per day) we used only postovulatory females taken at least 9 hours after peak spawning (2200 hours), to prevent bias arising from sampling females during the time of day when they are actually spawning. Two independent 24-hour sets of postovulatory follicles could be separated: one set of postovulatory follicles with an age between 9 and 32 hours after spawning and another set of postovulatory follicles with an age between 33 and 56 hours. Henceforth females with ovaries containing postovulatory follicles of 9-32 hours will be called day-1 females;

those having ovaries containing postovulatory follicles of 33-56 hours will be called day-2 females.

Assuming that sampling of females with hydrated ovaries, day-1 females, or day-2 females is unbiased, then the spawning fraction for collection i is estimated by:

$$F_i = \frac{m_{hi}}{m_i} \text{ or } \frac{m_{1i}}{m_i} \text{ or } \frac{m_{2i}}{m_i}$$

where
$$m_i = m_{hi} + m_{1i} + m_{2i} + m_{ai}$$

and where
m_{hi} = number of hydrated females in collection i
m_{1i} = number of day-1 females in collection i
m_{2i} = number of day-2 females in collection i
m_{ai} = number of females that have not spawned within the past 9 to 56 hours (includes females with postovulatory follicles of an age of less than 9 hours)
m_i = number of mature females in collection i
F_i = spawning fraction in collection i

The results for the Peruvian anchovy were similar to results for the northern anchovy (Stauffer and Picquelle 1980); they indicated that hydrated females were oversampled. To correct for this apparent oversampling, under the assumption that the true fraction of hydrated females is the same as the fraction of day-1 or day-2 females, m_{hi} is replaced by $\frac{m_{1i} + m_{2i}}{2}$ such that

$$\hat{F}_i = \frac{m_{1i}}{\frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}}$$

or
$$\frac{m_{2i}}{\frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}}$$

where
$\hat{F}_i$ = corrected fraction of day-1 or day-2 females in collection i.

The estimates for mean and variance are given by:

$$\bar{F} = \frac{\sum m_{1i} + m_{2i}}{2 \sum \frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}} = \frac{\sum m_{1i} + m_{2i}}{2 \sum m_{yi}}$$

and

$$V_{(\bar{F})} = \frac{1}{n(n-1)} \sum \left(\frac{m_{yi}}{\bar{m}}\right)^2 (\hat{F}_i - \bar{F})^2$$

45

where

$\bar{F}$ = average fraction of females spawning per day from all collections

$$m_{yi} = \frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai} = \text{corrected}$$

number of mature females in collection i

$\bar{m}$ = average number of mature females corrected per collection i

$$= \frac{\sum m_{yi}}{n}$$

n = number of collections.

RESULTS

Peak Spawning Time

To age postovulatory follicles, one must determine the duration of the daily spawning period and its midpoint. This goal can be reached in three ways: (1) by recording time of incidence and frequencies of new postovulatory follicles from samples of adult anchovy females; (2) by recording the decline of occurrence of hydrated females; and (3) by recording time of occurrence and frequencies of newly spawned eggs from ichthyoplankton samples. Hunter and Macewicz (1980) demonstrated clearly that the percentage of northern anchovy females with hydrated oocytes declined steadily from 10% to 14% at 1800 hours to 0% at 2400 hours, and concluded that 2200 to 2300 hours was the period of maximum spawning.

The data from the Peruvian anchovy did not provide as clear a picture, for two reasons. Hunter and Macewicz (1980) collected all their samples at night between 1800 and 0500 hours, whereas only 40% of the Peruvian samples were collected between 1800 and 2300 hours, and only one sample was obtained between 2300 and 0700 hours. In the Peruvian samples, females with new postovulatory follicles were recorded for the first time at 1800 hours, but their numbers were very low (Table 1). The numbers of females with hydrated oocytes ranged between 7.5% and 51.7% from 0700 to 2030 hours and declined sharply to 3.3% and 5% at 2130 to 2230 hours, respectively (Figure 2). The best data for estimating the midpoint of the nightly spawning period was that provided by the ichthyoplankton survey. The occurrence of newly spawned eggs in the water column demonstrated that peak spawning time of the Peruvian anchovy is between 2200 and 2300 hours (Santander et al., in press).

Combining all these data leads to the conclusion that Peruvian anchovy spawning starts at sunset,

TABLE 1
**Collections Containing Female Peruvian Anchovy
with New Postovulatory Follicles**

Collection no.	Time of day	No. of new postovulatory follicles
46	1800	1
4	1930	1
12	1930	2
41	2015	1
25	2100	1
21	2230	2
1	0315	1

around 1800 hours, and that the period of maximum spawning is between 2200 and 2300 hours. It was not possible to estimate the time when nightly spawning ceases, but by analogy to the northern anchovy, spawning probably ceases around 0200 hours. For convenience, 2200 hours is taken as the midpoint of the daily spawning period in the following analysis.

Spawning Frequency

The spawning frequency is the fraction of mature females that spawns per day. In theory, one should get three independent estimates of this parameter: (1) the percentage of females with hydrated oocytes, (2) the percentage of females with day-1 postovulatory follicles, and (3) the percentage of females with day-2 postovulatory follicles. Because females with hydrated oocytes tend to be oversampled, they cannot be used for this purpose. The age of postovulatory follicles can only be determined up to about 50 hours after spawning, because older postovulatory follicles may be confused with other structures, such as atretic follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980).

Because the northern anchovy were sampled only at night (Hunter and Goldberg 1980; Hunter and Mace-
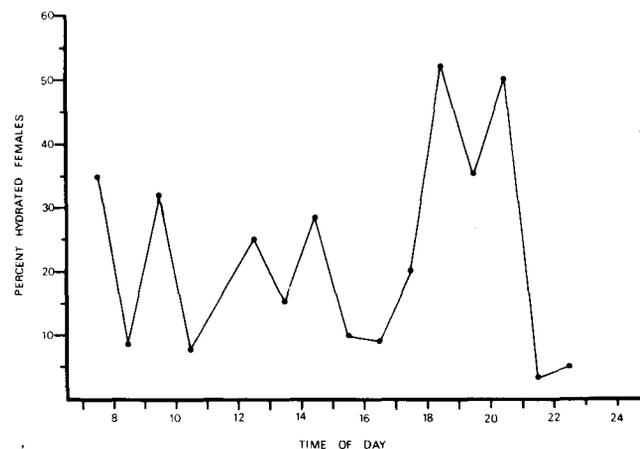
Figure 2. Change of percentage of hydrated females in collections with time of day.

wicz 1980; Stauffer and Picquelle 1980), investigators could use only day-1 postovulatory follicles to estimate spawning frequency. Our use of a purse seiner for sampling the Peruvian anchovy permitted collection of samples at any time of day. Consequently, we obtained two independent sets of data for estimating spawning frequency (day-1 and day-2 females) and compared them.

The way in which these two sets of data were obtained is demonstrated in Table 2. It was assumed that all anchovy females spawn at 2200 hours. Because the earliest sample was collected at 0700 hours, we considered that time the beginning of the day-1 and the day-2 periods. Postovulatory follicles found at this time are, according to their structure, assigned to one of the following three groups: day-1, day-2, or older postovulatory follicles. They are given ages of 9, 33, or more than 56 hours, respectively. Table 3 contains the summary of all data: (1) date and time of each collection, (2) numbers of hydrated, day-1, and day-2 females, (3) hours past spawning of each collection, (4) values corrected for oversampling hydrated females, and (5) percentage of hydrated, day-1, and day-2 females per collection.

Stauffer and Picquelle (1980) suggested that females with new postovulatory follicles may also be oversampled, but lacked data with which to test this
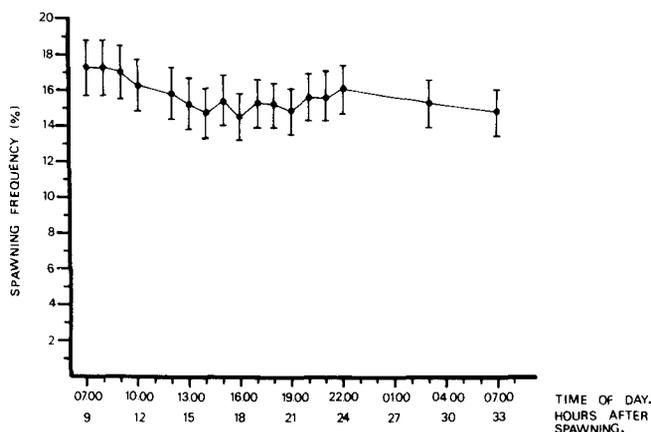
Figure 3. Spawning frequencies calculated from consecutive 24-hour periods. The time of day indicates at what time each 24-hour period begins. The corresponding hours after mean spawning time (2200 hours) are also indicated. Standard deviations are added.

hypothesis. To test it, we calculated the mean spawning frequencies for consecutive 24-hour periods. First, we calculated the mean spawning frequency for the first 24-hour period starting at 0700 hours—9 hours after mean spawning time. Only postovulatory follicles within the age range from 9 to 32 hours were included (Figure 3). Then we calculated the spawning frequency for the second 24-hour period, beginning at 0800 hours and including postovulatory follicles with

TABLE 2
Time of Collection of Females and the Age of Postovulatory Follicles

	Time of day	Age of postovulatory follicles (hours past spawning)	
		Day-1	Day-2
Night of spawning	22.00 (Peak spawning)		
1st day following spawning	07.00-07.59	9	33
	08.00-08.59	10	34
	09.00-09.59	11	35
	10.00-10.59	12	36
	11.00-11.59	13	37
	12.00-12.59	14	38
	13.00-13.59	15	39
	14.00-14.59	16	40
	15.00-15.59	17	41
	16.00-16.59	18	42
	17.00-17.59	19	43
	18.00-18.59	20	44
	19.00-19.59	21	45
	20.00-20.59	22	46
	21.00-21.59	23	47
	22.00-22.59	24	48
	23.00-23.59	25	49
2nd day following spawning	00.00-00.59	26	50
	01.00-01.59	27	51
	02.00-02.59	28	52
	03.00-03.59	29	53
	04.00-04.59	30	54
	05.00-05.59	31	55
	06.00-06.59	32	56

an age from 10 to 33 hours. We repeated these calculations for a total interval of 48 hours, always advancing by one hour, so that the last 24-hour period starts again at 0700 hours—33 hours after mean spawning time and includes postovulatory follicles with an age from 33 to 56 hours. Theoretically, there should have been 25 different 24-hour periods. However, because no collections were taken at 1100 hours and only one between midnight and 0700 hours (Table 3), only 17 consecutive 24-hour periods are included in Figure 3.

The spawning frequencies calculated from these 17 consecutive 24-hour periods showed no strong trend over the observed 48-hour interval, and ranged from 14.70% to 17.26%. We conclude that females with postovulatory follicles of 9 hours and older are equally available to the purse seine.

If spawning frequency data for day-1 females and for day-2 females are independent of each other and identically distributed, they could be combined. Their combined total would double the sample size and

TABLE 3

Data Summary

Time of day	Collection No.	Date	Sex ratio (% females)	Hydrated females No. (m_{hi})	Hydrated females %	Day-1 females Hours past spawning	Day-1 females No. (m_{1i})	Day-2 females Hours past spawning	Day-2 females No. (m_{2i})	$\frac{m_{1i}+m_{2i}}{2}$	m_{ai}	m_{yi}	$\hat{F}_1$ Day-1 (m_{1i}/m_{yi})	$\hat{F}_2$ Day-2 (m_{2i}/m_{yi})
07.15	28	5.9.	52.76	11	55	9	0	33	0	0	9	9.0	0	0
07.25	38	8.9.	55.30	3	15	9	3	33	3	3.0	11	20.0	.1500	.1500
08.00	33	6.9.	83.01	0	0	10	2	34	1	1.5	17	21.5	.0930	.0465
08.30	26	2.9.	68.74	0	0	10	2	34	4	3.0	14	23.0	.0870	.1739
08.45	48	12.9.	45.32	5	25	10	6	34	3	4.5	6	19.5	.3077	.1538
09.00	5	26.8.	44.96	11	55	11	2	35	1	1.5	6	10.5	.1905	.0952
09.00	10	28.8.	31.51	7	35	11	6	35	1	3.5	6	16.5	.3636	.0606
09.00	42	9.9.	33.38	2	10	11	0	35	0	0	18	18.0	0	0
09.15	29	5.9.	90.50	2	10	11	2	35	3	2.5	13	20.5	.0976	.1463
09.30	17	30.8.	54.44	10	50	11	2	35	0	1.0	8	11.0	.1818	0
10.00	22	1.9.	67.33	0	0	12	2	36	1	1.5	17	21.5	.0930	.0465
10.10	52	16.9.	45.80	3	15	12	6	36	3	4.5	8	21.5	.2791	.1395
12.00	2	25.8.	68.95	2	10	14	5	38	3	4.0	10	22.0	.2273	.1364
12.00	57	17.9.	63.62	2	10	14	6	38	5	5.5	7	23.5	.2553	.2128
12.10	34	7.9.	70.96	10	50	14	3	38	0	1.5	7	11.5	.2609	0
12.30	27	2.9.	49.89	6	30	14	1	38	2	1.5	11	15.5	.0645	.1290
13.00	18	30.8.	55.32	3	15	15	2	39	2	2.0	13	19.0	.1053	.1053
13.10	53	16.9.	62.04	4	20	15	6	39	3	4.5	7	20.5	.2927	.1463
13.15	49	12.9.	59.29	2	10	15	4	39	2	3.0	12	21.0	.1905	.0952
14.15	11	28.8.	47.43	3	15	16	4	40	4	4.0	9	21.0	.1905	.1905
14.15	58	17.9.	28.18	11	55	16	1	40	1	1.0	7	10.0	.1000	.1000
14.45	35	7.9.	70.51	3	15	16	0	40	6	3.0	11	20.0	0	.3000
15.30	6	28.8.	81.27	2	10	17	9	41	1	5.0	8	23.0	.3913	.0435
16.00	15	29.8.	32.57	5	25	18	1	42	3	2.0	11	17.0	.0588	.1765
16.10	40	8.9.	60.38	1	5	18	3	42	5	4.0	11	23.0	.1304	.2174
16.15	20	31.8.	26.36	3	15	18	4	42	6	5.0	7	22.0	.1818	.2727
16.30	3	25.8.	74.42	0	0	18	4	42	7	5.5	9	25.5	.1569	.2745
16.45	23	1.9.	78.73	0	0	18	6	42	4	5.0	10	25.0	.2400	.1600
17.10	44	9.9.	62.12	2	10	19	1	43	3	2.0	14	20.0	.0500	.1500
17.35	54	16.9.	71.94	6	30	19	7	43	4	5.5	3	19.5	.3590	.2051
18.00	8	27.8.	45.21	1	5	20	1	44	1	1.0	17	20.0	.0500	.0500
18.00	36	7.9.	36.11	13	65	20	2	44	4	3.0	1	10.0	.2000	.4000
18.00	46	11.9.	29.90	16	80	20	1	44	0	0.5	3	4.5	.2222	0
18.15	31	5.9.	67.15	2	10	20	5	44	1	3.0	12	21.0	.2381	.0476
19.00	24	1.9.	60.38	3	15	21	1	45	2	1.5	14	18.5	.0541	.1081
19.15	19	30.8.	46.13	4	20	21	4	45	7	5.5	5	21.5	.1860	.3256
19.30	4	25.8.	55.33	13	65	21	3	45	0	1.5	4	8.5	.3529	0
19.30	7	26.8.	58.28	2	10	21	2	45	4	3.0	12	21.0	.0952	.1905
19.30	12	28.8.	12.62	17	85	21	0	45	0	0	3	3.0	0	0
19.30	16	29.8.	43.93	8	40	21	3	45	3	3.0	6	15.0	.2000	.2000
19.40	55	16.9.	65.52	2	10	21	1	45	5	3.0	12	21.0	.0476	.2381
20.10	45	9.9.	73.93	1	5	22	5	46	6	5.5	8	24.5	.2041	.2449
20.15	41	8.9.	15.86	19	95	22	0	46	0	0	1	1.0	0	0
21.00	25	2.9.	78.68	2	10	23	4	47	7	5.5	7	23.5	.1702	.2979
21.00	47	11.9.	79.20	0	0	23	4	47	4	4.0	12	24.0	.1667	.1667
21.15	32	5.9.	64.18	0	0	23	2	47	2	2.0	16	22.0	.0909	.0909
22.30	21	31.8.	79.68	1	5	24	3	48	4	3.5	12	22.5	.1333	.1778
22.55	37	7.9.	64.36	1	5	24	9	48	1	5.0	9	24.0	.3750	.0417
03.15	1	25.8.	51.42	2	10	29	5	53	3	3.0	12	21.0	.2381	.0476

TABLE 4
Arithmetic Means and Probability Values p and q of the Binomial Distributions of Hydrated, Day-1, and Day-2 Females

Reproductive stage of females	$\bar{x}$	p	q
Hydrated	4.6122	.2306	.7694
Day-1	3.1633	.1726	.8274
Day-2	2.7143	.1481	.8519

thereby reduce the variance of the estimate of spawning frequency. If their occurrence were random, the observed frequencies of day-1 and day-2 females should follow a positive binomial distribution. To test this assumption, we applied the Kolmogorov/Smirnov test (Siegel 1956). The frequencies of all three groups of females in different reproductive stages are listed in Table 3. Table 4 gives arithmetic means and the probability values p and q of the binomial distribution. The term k of the positive binomial distribution, the maximum number of individuals in a collection, was 20; in other words, 20 females per collection were included in the estimate of the frequency of hydrated, day-1, and day-2 females. The 5% significance level (D) for the Kolmogorov/Smirnov test is 0.1943, and the estimated maximum differences $(\hat{D})$ were 0.3628 (hydrated), 0.1656 (day-1), and 0.1859 (day-2). These results demonstrate that the frequencies of day-1 and day-2 females were not significantly different from the positive binomial distribution at the 5% level, whereas the hydrated females do not correspond to the positive binomial distribution. This becomes more obvious when the cumulative percentages of the observed and expected class frequencies of all three groups of females are plotted (Figure 4).

If the spawning frequencies of day-1 and day-2 females are to be combined, they must not be statistically different. To establish this we used a test of the difference between paired independent samples
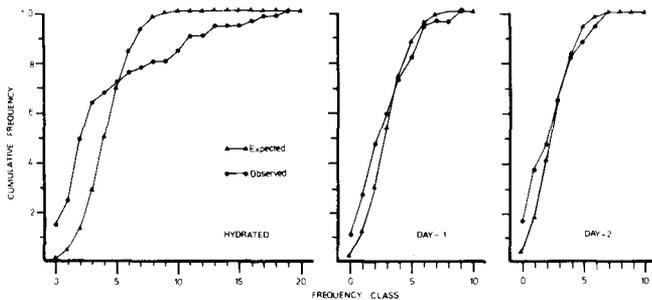
Figure 4. Cumulative frequencies of observed and expected (positive binomial distribution) class frequencies of females in different reproductive stages. The 49 collections of mature female anchovies are distributed into frequency classes according to the number of females they have in a particular reproductive stage (hydrated, day-1, or day-2); for example, in the left panel, frequency class 0 contains all collections having 0 hydrated females.

TABLE 5
Mean Percentage of Hydrated, Day-1, and Day-2 Females with Variance (V), Standard Deviation (SD), and Coefficient of Variation (CV)

Reproductive stage of females	Mean	V	SD	CV
Hydrated	.2306	1.2198×10^{-3}	.0349	.1515
Day-1	.1726	2.3248×10^{-4}	.0152	.0883
Day-2	.1481	1.7224×10^{-4}	.0131	.0886
Day-1 & day-2 (combined)	.1604	1.0175×10^{-4}	.0101	.0629

(Snedecor and Cochran 1967). The paired samples were the spawning frequency values of day-1 $(\hat{F}_1)$ and day-2 $(\hat{F}_2)$ females from each collection (Table 3). The null hypothesis was that the mean difference $(\bar{D})$ between $\hat{F}_1$ and $\hat{F}_2$ equals zero. $\bar{D}$ was 0.032. The t-test gave a value of 1.526 with $n-1 = 48$ degrees of freedom. This shows that the null hypothesis cannot be rejected at the 5% level of significance. Therefore, the two estimates can be combined, thus doubling the sample size.

The spawning frequency of the day-1 females was 0.1726 with a variance of 2.3248 $\times$ 10^{-4}, a standard deviation of 0.0152, and a coefficient of variation of 0.0883 (Table 5). The spawning frequency of the day-2 females was 0.1481 with a variance of 1.7224 $\times$ 10^{-4}, a standard deviation of 0.0131, and a coefficient of variation of 0.0886. When these two data sets were combined, the estimate of spawning frequency was 0.1604 with a variance of 1.0175 $\times$ 10^{-4}, a standard deviation of 0.0101, and a coefficient of variation of 0.0629 (Table 5). By combining the data we have reduced the coefficient of variation by nearly a third. This would be important when the estimate of spawning frequency is used to calculate spawning biomass using the egg production method (Parker 1980; Stauffer and Picquelle 1980), because by reducing the coefficient of variation for spawning frequency one reduces the coefficient of variation for the biomass estimate (Santander et al., in press).

A spawning frequency of 16.04% (Table 5) means that in August/September 1981 the average mature Peruvian anchovy female spawned a new batch of eggs every 6.23 days. The high daily incidence of hydrated females (23.06%; Table 5) clearly indicates that hydrated females were oversampled. Comparing the coefficient of variation for the incidence of hydrated females with that of the day-1 and day-2 females indicates that the number of hydrated females per sample was much more variable than were the numbers of day-1 or day-2 females per sample.

Hydrated females also seem to be more vulnerable to the purse seine than other females. In order to test
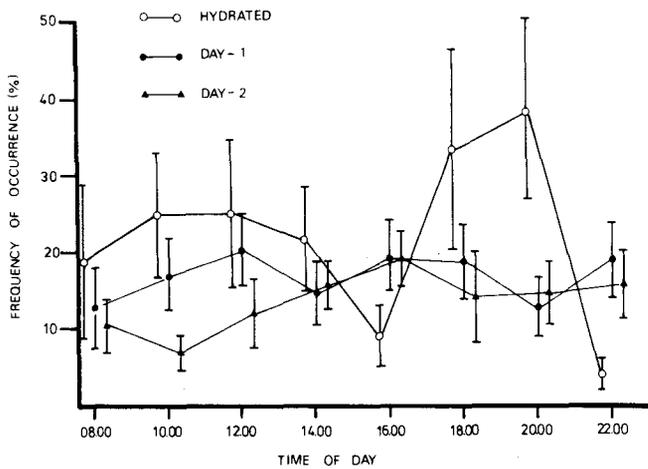
Figure 5. Change of percentage of frequency of occurrence of hydrated, day-1, and day-2 females in collections with time of day.

whether the three groups of females (hydrated, day-1, and day-2) show a diel change in their vulnerability to purse seining, the percentage of females in each group was calculated for 2-hour intervals and plotted at the midpoints of the 2-hour interval (Figure 5). The hydrated females had the highest percentage except for collections taken at about 1600 and at 2200 hours. The value at 2200 hours (4%) is low because most of the fish had completed spawning at that time. The very high values at 1800 hours (33%) and at 2000 hours (38%) indicate that hydrated females are particularly vulnerable at that time of day. At these hours, hydration of the ovaries has reached its maximum, and the ovaries are extremely heavy—in some cases up to 25% to 30% of the female's gonad-free body weight. The percentages of day-1 and day-2 females, on the other hand, remain relatively constant throughout the period, indicating that their vulnerability to capture does not change significantly with time of day.

Sex Ratio

The sex ratios (percentage of females on a weight basis) of all 49 collections showed large variations ranging from 12.62% to 90.50% females (Table 3). The average sex ratio was 56.43%, with a variance of 0.0007, a standard deviation of 0.0259, and a coefficient of variation of 0.0459. Similar variability in sex

ratio of the northern anchovy has been reported by Klingbeil (1978), Hunter and Goldberg (1980), and Stauffer and Picquelle (1980). Klingbeil demonstrated that the greatest variability in the sex ratio occurs in the months of peak spawning. Hunter and Goldberg showed that sex ratio varied with spawning activity. We carried out the same analysis for the Peruvian anchovy.

We grouped all 49 collections into three classes based on their sex ratio. For each of these three classes we calculated the percentage of females in the following four spawning groups: (1) spawning on the night of capture (includes hydrated females and females with new postovulatory follicles), (2) day-1 females, (3) day-2 females, (4) females with no evidence of recent or imminent spawning (Table 6). In the male-dominated collections, which contained only 10% to 39% females, 54% of the females had spawned on the night of capture. On the other hand, in the female-dominated collections, where 70% to 99% of the fish were females, only 13% of the females had spawned on the night of capture. Correlation coefficients for sex ratio and (1) number of hydrated females, (2) number of day-1 females, and (3) number of day-2 females were −0.66, 0.35, and 0.34, respectively. Only the correlation coefficient of −0.66 for the hydrated females was significant at the 5% level. This shows that as the proportion of males in a collection increases, so does the proportion of hydrated females.

In addition, sex ratio also seemed to change with time of day. Most samples taken between 0700 and 1800 hours had 50% to 70% females, whereas after sunset (1800-2100 hours) the average ratio of females in the collections dropped below 50%. A similar pattern is described for the northern anchovy by Stauffer and Picquelle (1980). Average sex ratios (including all collections) computed for morning, afternoon, and night periods were 56.80%, 59.11%, and 54.25%, respectively (Table 7). These data show that the average sex ratio (56.43% females, $N = 49$) is probably biased by including those collections that have more than 30% hydrated females and were sampled at night. A more realistic sex ratio is computed by excluding all night collections sampled between 1800 and 2300

TABLE 6
Sex Ratio and Percentage of Females in Different Reproductive Stages

Sex ratio class (% females)	Number of collections	% Females				No. of females classified
		Spawning on day of capture	Day-1	Day-2	No evidence of spawning	
10-39	9	54	8	8	29	180
40-69	28	19	16	13	52	560
70-99	12	13	20	20	48	240

TABLE 7
Sex Ratios at Different Times of Day

Time of day	All collections		Excluding collections with >50% hydrated females		Excluding collections with >30% hydrated females	
	No. of collections	% of females	No. of collections	% of females	No. of collections	% of females
07.00-12.00	12	56.80	9	56.44	8	59.56
12.00-18.00	18	59.11	16	60.30	14	60.22
18.00-23.00	18	54.25	13	63.59	12	65.23

hours, the time of peak variability in sex ratio. From the remaining 30 collections we calculated a sex ratio of 57.90% with a variance of 0.0010, a standard deviation of 0.0311, and a coefficient of variation of 0.0536.

DISCUSSION

The spawning frequency of the Peruvian anchovy was found to be 16.04% in August-September 1981. This means that during the peak spawning period, Peruvian female anchovy spawn a new batch of eggs about once every six days. The spawning frequencies reported for the northern anchovy off California are somewhat lower: 14.5% in March-April 1980 (Stauffer and Picquelle 1980), 10.6% in February 1981 and 12.5% in April 1981 (Stauffer and Picquelle[2]), and 12.0% in January-March 1982 (Picquelle and Hewitt 1982). Hunter and Leong (1981) estimated that the northern anchovy spawns about 20 times per year; however, this has yet to be proven by an annual sampling program. These data on northern and Peruvian anchovy clearly contradict earlier assumptions that these two and other multiple-spawning pelagic species spawn only two or three times a year. Consequently, spawning biomass of such fishes has been considerably overestimated because of a severe underestimate of total fecundity (batch fecundity times spawning frequency).

Sex ratio is an important parameter for the application of the egg production method (Parker 1980), because of possible biases. The midwater trawl is reported to be a biased sampler with respect to sex ratio and hydrated females (Hunter and Goldberg 1980; Stauffer and Picquelle 1980). A higher-than-expected number of trawl samples had a high or a low number of females. In addition, hydrated females were twice as numerous as day-1 females. Stauffer and Picquelle[3] suggest that males and hydrated females segregate from other females at the hours of

peak spawning at a depth where they are more vulnerable to the trawl.

The purse seine samples also appear to be biased in respect to sex ratio and numbers of hydrated females. In our study, oversampling of hydrated females occurred in the early morning hours, when the onset of hydration could be determined only by recording the migration of the oocyte nucleus to the pole. At this time, the oocytes have not increased perceptibly in size, and the ovary is only a small fraction of the total female weight. Three different explanations are possible for the oversampling of hydrated females in purse seines:

1. Hydration decreases the ability of female anchovies to avoid nets.

2. Females segregate vertically (by depth), and those with hydrated oocytes are more accessible to the purse seine than other females.

3. Females segregate horizontally (by area), and those with hydrated oocytes occur in different areas than those without hydrated oocytes.

In any case, using the incidence of hydrated females to estimate spawning frequency for anchovy (suggested by Hunter and Macewicz 1980) seems an inaccurate procedure, even if day samples of anchovies can be obtained.

The sex ratio in the 49 collections ranges from 12.62% to 90.50% females, with an average of 56.43% (Table 3). Night purse seine collections with a high percentage of hydrated females (with respect to the female fraction) also contain a high percentage of males. Hydrated females are oversampled both day and night, but the co-occurrence of high percentages of hydrated females and of males is recorded only at night. It might be hypothesized that the high male ratio in these night collections is because hydrated females, which are about to spawn, are attractive to and surrounded by a high number of males (Hunter and Goldberg 1980). If the hypothesis is correct that hydrated females are caught more often (than expected) because their vulnerability to the net increases, then only the hydrated females should be

[2]Stauffer, G.D., and S.J. Picquelle. The 1981 egg production estimates of anchovy spawning biomass. Unpublished manuscript, 29 p. NMFS, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.
[3]Ibid.

oversampled and not the males as well. Thus it seems more likely that the hydrated females segregate, either by depth or by area, from the "normal" school, taking a high percentage of males with them and forming "spawning schools" dominated by males.

The average sex ratio is biased because the night collections contain a high percentage of hydrated females. When these collections are omitted, the average sex ratio rises to 57.90%. If the true sex ratio of the population is 50% female, the purse seine clearly oversamples females, whereas the trawl seems to undersample them slightly (Stauffer and Picquelle 1980; Picquelle and Hewitt 1982). Klingbeil (1978) reported similar findings when he compared the sex ratios of anchovy obtained from commercial purse seiners (females:males = 1.60:1) and from research trawlers (females:males = 1.09:1). He suggested that the male-dominated schools may not form the large dense aggregations required for effective purse seining. This might also explain the difference in sex ratios between the northern and the Peruvian anchovy collections. The large Peruvian purse seiner (270 tons) may have shot the seine when the echo sounder indicated a relatively large, dense, female-dominated school, whereas each California trawl sample collected fish from a much larger area. Thus the trawl samples included more male-dominated spawning schools, which presumably are less dense and extend over a much larger area. Therefore, if spawning schools are segregated horizontally from normal schools, the trawl may be a more suitable tool for determining the sex ratio of anchovies than a purse seine.

Interpreting the different effects of trawling and seining on sampling of hydrated females is difficult. They were oversampled by the Peruvian purse seiner in 1981 and by the California trawler in 1980 and 1981 (Stauffer and Picquelle 1980; Stauffer and Picquelle[4]). However, hydrated females were not oversampled by the California trawler in 1982, possibly because the trawl may have fished a shallower depth (Picquelle and Hewitt 1982). The oversampling of hydrated females might be solved by a comparative study be-

tween a purse seiner and a larger midwater trawler, which allows fishing in depths not reached by a purse seine.

ACKNOWLEDGMENTS

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[4]See footnote 2 on page 51.

SOME EFFECTS OF EL NIÑO 1983 ON THE NORTHERN ANCHOVY

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ABSTRACT

A major California El Niño began in late 1982, bringing unusually large positive anomalies in sea-surface temperature and sea-level height. Analysis of historical records reveals a weak positive relationship between northern anchovy population growth and interannual variations in these parameters, except in the second year of major El Niño events. 1983 spawning activity was marked by an extended spawning range, dominance of small, year-old females, and faster egg maturation caused by warm water. El Niño 1983 appears to have been unfavorable for the growth of larvae, juveniles, and adults, possibly because of reduced food availability.

RESUMEN

A finales de 1982 se inició en California un fenómeno similar a El Niño, el cual originó altas anomalías positivas en las temperaturas superficiales y en el nivel del mar. El análisis de los datos históricos señala una débil relación positiva entre el incremento de la población de la anchoveta del norte, *Engraulis mordax*, y las variaciones interanuales en esos parámetros, excepto durante el segundo año de aquellos El Niño de mayor intensidad. La actividad de puesta de la anchoveta durante 1983 se caracterizó por cubrir un área más extensa, la dominancia de hembras pequeñas, de un año, y la rápida madurez de los óvulos ocasionada por la influencia de las aquas cálidas. El Niño de 1983 resultó al paracer desfavorable para el crecimiento de larvas, juveniles y adultos, debido posiblemente a una escasez de alimento.

INTRODUCTION

El Niño events have contributed to catastrophic declines in populations of seabirds and pelagic fish in the normally highly productive coastal upwelling system off Peru (Idyll 1973). An unusually strong El Niño began to affect the eastern tropical Pacific in mid-1982 (Cane 1983). Sea-surface temperature anomalies greater than +2°C were observed off California beginning in November (Auer 1982). During peak northern anchovy spawning in January-April 1983, very unusual oceanographic conditions prevailed off southern California: sea-surface temperatures were up

to 3°C warmer than normal; the mixed-layer depth increased by 50 m; and unprecedented sea-level heights were recorded (Simpson 1983, Lynn 1983). This paper is a brief discussion of some consequences of El Niño for the anchovy central subpopulation between Point Conception, California, and Punta Baja, Baja California.

HISTORICAL RELATIONSHIP BETWEEN ANCHOVY AND EL NIÑO

One of the best biological time series available to relate to interannual oceanographic variability off California was recently developed by MacCall and Methot (1983, Table 3-1 therein). This 1951-82 series of annual estimates of anchovy central subpopulation spawning biomass was constructed from four separate data sets: (1) CalCOFI ichthyoplankton surveys, (2) California Department of Fish and Game acoustic surveys, (3) commercial aerial spotter logbooks, and (4) CalCOFI egg production method surveys. MacCall (MacCall and Methot 1983) fit the following population growth model to this time series:

$$B_{t+1} = aB_t^b - \delta C_t + r_t$$

where B_t is spawning biomass in year t,
C_t is total catch discounted by a factor δ,
r_t is a random error term including both measurement error and the effects of environmental anomalies,
a and b are constants.

The term δC_t represents spawners that would have survived natural mortality had they not been caught by the fishery. Parameters a and b can be related to more meaningful parameters—maximum net productivity (MNP) and the spawning biomass at which MNP occurs (BMNP)—as follows:

$$MNP = \max(aB^b - B)$$

$$BMNP = (ab)^{1/(1-b)}$$

If the model describes the *true* influence of the population on itself, then r_t would be the added effect of the environment. I solved the above equation for $ln(r_t)$, $t = 1954$ to 1982, using the log-transformed
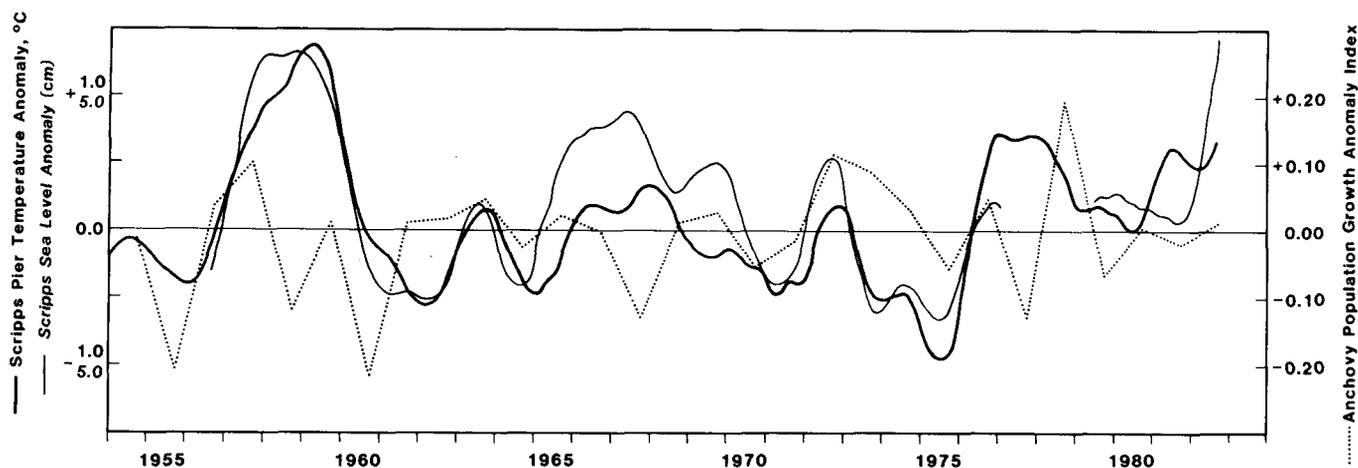
Figure 1. Time series of yearly anchovy population growth anomaly index and monthly anomalies of surface temperature and sea level at Scripps Pier.

biomass time series and MacCall's parameter values ($a = 7.164$, $b = 0.742$, $\delta = 0.82$). The anchovy population growth anomaly index, $ln(r_t)/ln(aB_t^b)$, represents the relative deviation of annual recruitment and adult survival from what would be expected for a stock of a given size. I assume it reflects influences of interannual environmental changes, compounded by errors in the biomass estimates.

Interannual variability in the California Current is closely associated with El Niño (Chelton et al. 1982). Time series of anomalies of monthly mean surface temperature[1] and sea level[2] at Scripps Pier in La Jolla were used as indicators of environmental variability off southern California. Both series were smoothed twice by a 13-month running mean, which serves as a low-pass filter to isolate interannual variability. Coastal sea level is strongly related to seasonal and interannual variations in geostrophic flow of the California Current, with high sea levels corresponding to anomalous northward flow (Chelton et al. 1982). A linear trend of $+0.21$ cm yr^{-1} was removed from the sea-level data.

The monthly records of surface temperature and sea level are strongly correlated, although there was a notable exception to this relationship in 1981 (Figure 1). The maximum correlation ($r = +0.85$, $P < < .001$) occurs when the sea-level record is lagged by one month. In comparison, Enfield and Allen (1980) found that temperature lagged sea level by 2-6 months, at interannual frequencies, in an analysis of 1950-74 records from four California shore stations. I used the smoothed Scripps Pier temperature record as an index of environmental variability associated with El Niño. Changes at La Jolla, however, may not always repre-

sent changes over the entire range of the central subpopulation.

There is no significant correlation between anomalies in anchovy population growth and surface temperature ($r = +0.04$ using December surface temperature values). However, there are large negative population growth anomalies associated with the 1957-59, 1966-68, and 1976-78 California El Niño events. The two largest anomalies, in 1955 and 1960, occur during cold or cooling years before and after the 1957-59 event. A more interesting pattern emerges when the large anomalies in 1958, 1967, and 1977 are considered: the anchovy population growth anomaly index drops well below zero in the second year of each of the three multiyear warm events observed prior to 1980.

If 1958, 1967, and 1977 are excluded from the time series, a weak positive correlation between anomalies in anchovy population growth and temperature is observed ($r = +0.32$, $0.10 > p > 0.05$). This implies that the relationship is nonlinear: i.e., relatively warm or warming years tend to be favorable for population growth, but prolonged warming is unfavorable.

SPAWNING ANOMALIES IN 1983

Spawning activity has been monitored once or twice yearly since 1980 by month-long CalCOFI egg and trawl surveys during the height of the spawning season (February-April). The 1983 spawning range, indicated by the distribution of first-day eggs, extended beyond Point Conception at the northwest edge of the Southern California Bight (Figure 2). In contrast, spawning during 1980-82 was apparently excluded from this region by a plume of cold California Current water to the south of Point Conception (Lasker et al. 1981; Fiedler 1983). The February 21, 1981, satellite image

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[1]E. Stewart, Scripps Institution of Oceanography.

[2]D. Brown, Scripps Institution of Oceanography.
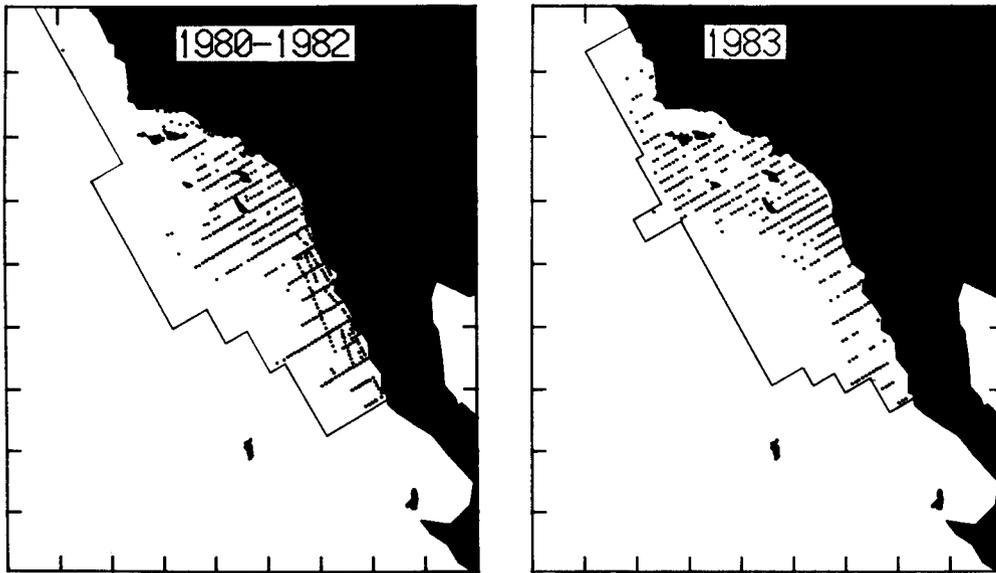
Figure 2. Distribution of CalVET tows with first-day eggs on CalCOFI cruises: *left*, 8003, 8102, and 8202; *right*, 8302. Boundaries mark limit of sampling effort.

in Figure 3a shows the influence of this cold-water boundary (the six lines of stations south of Point Conception were occupied on February 15-20). The boundary corresponded approximately to the 14°C isotherm.

Sea-surface temperatures (SSTs) off southern California were 1°-3°C warmer than the 1942-69 means during the first few months of 1983 (Auer 1983). Figure 3b illustrates the unusual SST pattern present in the Southern California Bight during CalCOFI cruise

8302: there was no cold-water plume south of Point Conception. In fact, the 14°C isotherm remained north of Morro Bay at lat. 35°20'N from February until the middle of March, when it moved south to Point Conception[3]. No SSTs colder than 14°C were measured on this cruise, although the warmest temperatures did not exceed the extreme of 17.7°C recorded on cruise 8003

[3]Weekly GOSSTCOMP sea-surface temperature maps distributed by NOAA, National Environmental Satellite Data and Information Service, Washington, D.C.
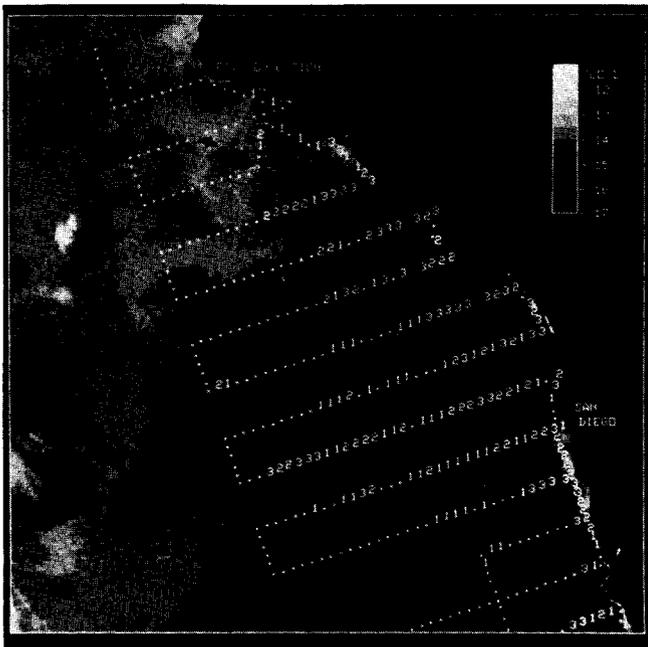
Figure 3a. CalCOFI 8102 A-day anchovy egg distribution. February 12-March 10, 1981. · = 0, 1 = 1 − 4, 2 = 5 − 15, 3 = 16 − 157 eggs/0.05 m². Sea-surface temperature from NOAA-6 AVHRR, channel 4, February 21, 1981.
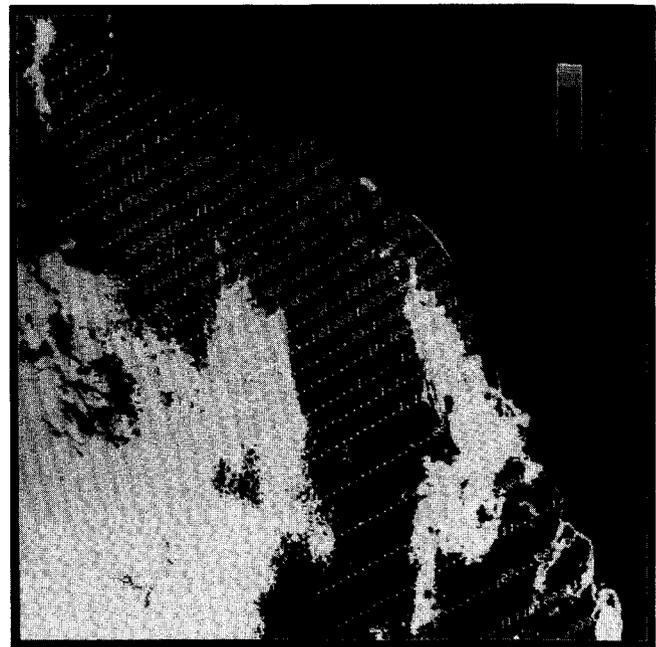
Figure 3b. CalCOFI 8302 A-day anchovy egg distribution, February 9-March 29, 1983. · = 0, 1 = 1 − 3, 2 = 4 − 12, 3 = 13 − 229 eggs/0.05 m². Sea-surface temperature from NOAA-7 AVHRR, channels 4 and 5, March 15, 1983.

TABLE 1
Egg Production Estimates of Anchovy Spawning Parameters

	1980[a]	1981[a]	1982[a]	1983[b]
Spawning biomass (x10^3 metric tons)	870	635	415	625
Average female weight (g)	17.4	13.4	18.8	11.2
Sex ratio by weight (females/total)	0.48	0.50	0.47	0.55
Spawning frequency of mature females (1/day)	0.14	0.11	0.12	0.09
Batch fecundity (eggs/batch)	7750	8330	10840	5300
Population production of spawned eggs (x10^{12} eggs/day)	26.3	21.0	13.5	17.2
Incubation period (days)	2.71	2.75	2.91	2.56
Egg mortality rate (1/day)	0.45	0.14	0.16	0.18
Population production of hatching eggs (x10^{12} eggs/day)	7.7	14.3	8.5	10.8

[a]Picquelle and Hewitt (1983). Original estimates of egg production and spawning biomass were elevated by a factor of 1/0.91 to correct for 91% retention of eggs by nets on 1980-82 surveys (R. Hewitt, NMFS/Southwest Fisheries Center, pers. comm.).
[b]Picquelle and Hewitt (1984).
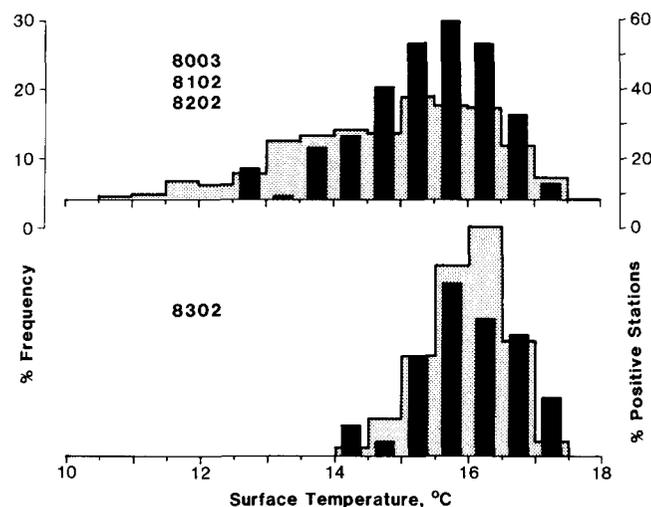
Figure 4. Frequency distributions of CalCOFI stations by surface temperature (stippled), with frequency of positive A-day anchovy egg catches within each temperature interval (solid bars), for 1980-82 (3 cruises, 2036 stations) and 1983 (850 stations).

(Figure 4). Spawning success, measured by frequency of positive egg stations in a temperature interval, was shifted slightly to warmer temperatures in 1983. Several factors associated with El Niño contributed to changes in the SST field off southern California at this time: diminished wind-driven flow of the California Current (Simpson 1983), an anomalously strong poleward countercurrent (Lynn 1983), and weakened coastal upwelling. Monthly upwelling indices between lat. 30° and 36°N averaged 70% (range 8%-309%) below the 1948-69 means during January-April 1983.[4]

Several 1983 spawning parameters appear to have been anomalous (Table 1), although the limited history of egg production surveys, beginning in 1980, precludes statistical evaluation of departures from "normal." Estimated spawning biomass increased for the

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[4]Monthly analyses of North Pacific wind-driven surface transport, from surface marine weather observations, distributed by NMFS/Pacific Environmental Group, Monterey, California 93942. See also Bakun (1973).

first time since 1979. However, females were young and of low body weight, resulting in subnormal spawning frequency and fecundity. A slightly increased egg maturation rate, probably related to warmer water temperatures, was not sufficient to reduce egg mortality to less than normal. El Niño seems to have had no net effect on the total production of hatching eggs in 1983.

GROWTH AND SURVIVAL DURING EL NIÑO

Three environmental processes have received much attention as potential regulators of recruitment of pelagic fish and, in particular, northern anchovy. Fluctuations in primary productivity associated with upwelling are important in the California Current as in other major upwelling regions (Bakun and Parrish 1980). Availability of appropriate food organisms in dense, subsurface layers is critical for survival of first-feeding anchovy larvae (Lasker 1978). Finally, offshore transport of larvae by wind-induced Ekman flow may be especially important where seasonally strong flow occurs over a narrow continental shelf, as in central and northern California (Parrish et al. 1981). We know less about factors affecting the survival of juvenile anchovy, after metamorphosis at the age of ~50 days, but it is likely that food availability continues to be important. Unusual conditions off southern California during the first few months of 1983 may have affected food availability:

1. Coastal upwelling was weak from January through April.
2. The thermocline was up to 50 m deeper than the long-term mean (Simpson 1983). The chlorophyll maximum layer, which often indicates a subsurface accumulation of phytoplankton, was also 10 to 50 m deeper than normal (McGowan 1983).
3. Phytoplankton pigment levels estimated from satellite data were relatively low in March (Fiedler,

1984). Vertically integrated chlorophyll concentrations along CalCOFI line 90 steadily declined from March to August, when they were about one-quarter the normal value. (J. A. McGowan, Scripps Institution of Oceanography, pers. comm.).

4. The coast was hit by violent storms in late January and in late February and early March because of an equatorward shift of the normal storm track.

This evidence, although indirect, indicates reduced phytoplankton productivity in the spawning habitat of the northern anchovy. Turbulent mixing by the winter storms could have dispersed any near-surface layers of phytoplankton that would normally support first-feeding larvae.

The California Department of Fish and Game has conducted trawl surveys of pelagic fish off California and Baja California since 1966. Preliminary data are available from two surveys in late 1983: September 23-October 12 from Blanca Bay (lat. 28°50'N) to Point Conception; and November 2-21 in the Southern California Bight[5]. The catch rate for 1983 year-class anchovy was not unusual: among eight annual surveys since 1976, the 1983 rate ranked fourth by weight and third by number of fish. However, these fish were remarkably small, with a mode of 65-75 mm, compared to 85-95 mm for young-of-the-year in 1976-82.

Adult fish were also abnormally small, with a mode of 100-105 mm, compared to an expected 115-120 mm. Yet these fish were still much larger than southern subpopulation fish (south of lat. 29°N), which averaged 87 mm in 1966-73, with only 10% exceeding 106 mm (Mais 1974). The small size of central subpopulation anchovy in 1983 cannot be explained simply by transport or migration of smaller southern subpopulation fish: very few or no anchovies were caught south of Punta Baja (lat. 30°N) on the trawl surveys. The anomaly more likely reflects reduced growth during El Niño 1983. The 1982 year-class fish appeared to have grown by only 10 mm since a survey in February 1983, compared to a normal growth increment of 15 mm for year-old fish from February to November (Mallicoate and Parrish 1981).

CONCLUSIONS

Anchovy population growth since 1954 has shown a weak positive correlation with interannual sea-surface temperature variations. This relationship has broken down, however, in the second year of major California El Niño events in 1957-59, 1966-68, and 1976-78. The 1983 California El Niño brought large and, in some cases, unprecedented oceanographic anomalies begin-

ning just before the peak northern anchovy spawning season. Several aspects of 1983 spawning were unusual: an extended spawning range, relatively young and small-sized spawners, and rapid egg maturation. The resultant production of hatching eggs was not unusually large or small, and no marked effect on the size of the 1983 year class could be detected by the end of the year. However, both juveniles and adults appeared to be abnormally small, possibly because of reduced food availability throughout the year.

As 1983 ended, the consensus of meteorologists and oceanographers was that El Niño was well into its final, decay phase at the equator (Rasmusson and Wallace 1983; Cane 1983). However, the California El Niño lingered: sea-surface temperature anomalies > 1°C and subsurface anomalies > 2°C were observed up to 400 km offshore between Point Reyes and Santa Monica on CalCOFI cruise 8401 (R. Lynn, NMFS/ Southwest Fisheries Center, pers. comm.; see also Auer 1984). The ultimate effect of the 1983 California El Niño may yet be manifested in the size of the 1984 year class of northern anchovy.

ACKNOWLEDGMENTS

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COASTAL FRONT OBSERVATIONS WITH
AN INFRARED SCANNER

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ABSTRACT

Thermal infrared (IR) images from NOAA environmental satellites and from a helicopter-borne thermal IR scanner were used to study water-mass dynamics in the vicinity of San Onofre Nuclear Generating Station (SONGS). The approach consists of using the satellite images to establish the identity and spatial distribution of oceanographic phenomena and using the helicopter-borne IR scanning equipment jointly with ground truth measurements to obtain increased resolution.

Coastal fronts, ubiquitous yet not readily visible to earthbound observers, were recognized on the satellite thermal IR images as having an elongated shape and being located within a few to several kilometers from the coast. A front emanating from Dana Point, California, divided cool coastal water from warmer water on the offshore side. Thermal IR images obtained from a helicopter revealed the details of two additional front-like structures, or plumes, near SONGS. The fronts are important because they are typically regions of high biological productivity; they also affect dispersion of floatables and buoyant effluent.

The existence of the coastal fronts appears to be linked to coastal upwelling processes occurring in the lee of coastal headlands. This characteristic location suggested that the phenomenon was associated with a raised thermocline at the center of a cyclonic gyre driven by the predominant northwesterly wind. The cool water from the upwelling pockets formed a plume, which advected downwind, displacing the warmer water seaward and creating a coastal front. During the lull in upwelling activity, the front appeared to decrease in size and even disappear entirely.

RESUMEN

Imágenes térmicas IR de satélites NOAA así como de un rastreador termal IR a bordo de un helicóptero fueron usadas para estudiar la dinámica de cuerpos de agua en las cercanías de la Planta Generadora Nuclear de San Onofre (SONGS). El procedimiento consiste en, através de imágenes transmitidas por satélite, establecer la identidad y la distribución espacial de fenómenos oceanográficos usando el equipo de rastreo IR a bordo de helicóptero, unido a mediciones en tierra, para proveer un aumento en la resolución del fenómeno así identificado.

Los frentes costeros, siempre presentes pero no fácilmente visibles, fueron identificados en las imágenes térmicas IR presentando una forma alargada y situados de unos cuantos, a varios kilómetros de la costa. Un frente empezando en Dana Pt., California dividía aguas frías hacia la costa, de aguas templadas del lado opuesto a la costa. Las imágenes termales IR obtenidas desde un helicóptero revelaron los detalles de otras dos estructuras tipo frentes, o plumas, cercanas a SONGS. La importancia de los frentes para SONGS es que las zonas frontales son típicamente regiones de alta productividad biológica; también afectan la dispersión de elementos flotantes y emanaciones más livianas que el agua.

La existencia de los frentes costeros parece ligada a los procesos de surgencia costera que ocurren a sotavento de las tierras costeras. Esta localización característica surgiere que el fenómeno estaba asociado con una termoclina elevada ubicada en el centro de un giro ciclónico generado por el viento predominante del norte. El agua más fría proveniente de los bolsones de surgencia se desplazó en la dirección del viento, en forma de pluma, desplazando el agua más cálida mar adentro, creando así un frente costero. Por otra parte, durante un relajamíento del proceso de surgencia, el frente disminuyó en tamaño, llegando a desaparecer completamente.

INTRODUCTION

A coastal front frequently appears in the vicinity of San Clemente, California (Figure 1). The coastal front, marked by a discontinuity in the sea-surface temperatures, has been recognized repeatedly on thermal IR images from NOAA satellites collected since 1980 (SCE 1982; SCE 1983). The front extends southeast from Dana Point, passing beyond San Clemente and the San Onofre Nuclear Generating Station (SONGS), dividing a cool water mass adjacent to shore from warmer water offshore. The width of the cool-water band on the shore side of the front varies from 1 to 15 km, with occasional periods during which the front is not observed (Grove and Sonu 1983).

The front's downcurrent range of influence is on the order of 10^1 km or less, thus implying that the front is
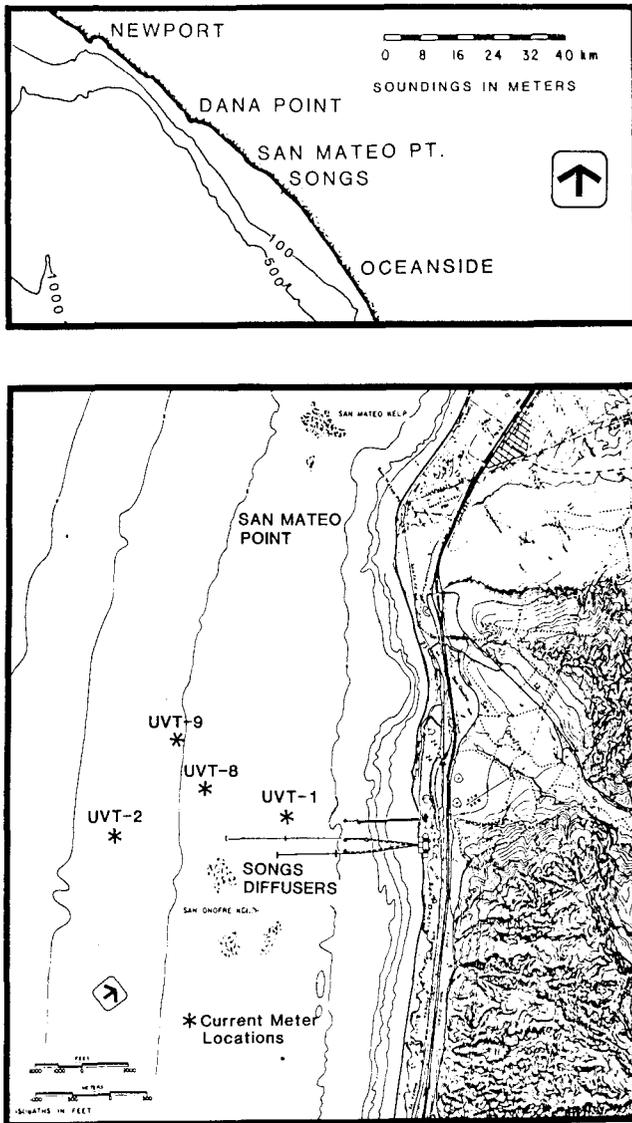
Figure 1. Study location.

submesoscale in size. The processes contributing to the front's characteristics are also submesoscale, since the front appears to be an independent system in the region (Grove and Sonu 1983). The fronts discussed in this paper will be termed microfronts to distinguish them from mesoscale fronts as described by Mooers et al. (1977) and Simpson and Pingree (1977). Although the satellite IR images have been useful for identifying the existence of microfronts, the 1.1-km spatial resolution of the images precluded a detailed description of their characteristics.

The coastal front's importance lies in the fact that there are increased nutrient concentrations as a result of upwelling activity near the front, and consequently increased primary productivity (Mooers et al. 1977). The microfront phenomenon is being studied in the

Dana Point to San Onofre region because of the similarities between the biological influences of the localized front and those influences predicted to occur as a consequence of operating the SONGS thermal diffuser system.

Murdoch et al. (1980) predict that on the order of 84,000 tons of additional phytoplankton might be produced per year as a result of diffuser-induced upwelling. However, in this prediction no consideration was given to the interaction of the diffuser-induced upwelling with the San Clemente nearshore microfronts. Further, the biological and physical processes at San Onofre may be caused by this regional microscale frontal system. This study characterizes these regional microfronts in greater detail than previously reported (Grove and Sonu 1983).

To study the front more closely, we augmented satellite IR images with a low-altitude, helicopterborne thermal infrared scanning system and with in situ profiling of water temperature from a surface vessel. We sought the following specific objectives:

1. To demonstrate the applicability of low-altitude thermal IR sensing for monitoring coastal fronts,
2. To identify the features associated with the coastal microfront in the vicinity of SONGS,
3. To assess the interaction of the microfronts with the nearshore waters near SONGS.

METHODS

Satellite thermal IR images were obtained for the survey days from the Scripps Institution of Oceanography Remote Sensing Facility.

The equipment for the low-altitude IR scanning consisted of a thermal imaging system (Flir Systems, Inc. model 1000B) mounted on a Hughes 500 helicopter. This IR scanning system is sensitive to temperature variations on the order of 0.2°C, but is reliable and easy to use. Its ability to instantaneously produce sea-surface temperature patterns on a video monitor aboard the helicopter permits coordination with a surface vessel for concurrent water temperature measurements.

The detector used in the thermal imaging sensor is mercury cadmium telluride, which has a spectral response range of 8 to 12 microns. The spectral peak of the detector at 10.6 microns is optimal for measuring sea-surface radiant emittance. The sensor is contained in a spherical case mounted in a remotely controlled gimbal fastened to the bottom of the helicopter. A video monitor and control panel is inside the helicopter.

The thermal imaging system provides a 17° (vertical) by 28° (horizontal) field of view. It displays a real-time video image of the temperature field by

showing gray-scale levels on the video monitor corresponding to temperature bands.

After collecting the video IR images in the field, we chose several portions of the video tape for enhancement with a digital image enhancement system. We used the image processing system at the Remote Sensing Facility of Scripps Institution of Oceanography to digitally filter the video noise in the images and enhance the gray-scale contrast.

During the IR scanning flight, vertical temperature profiles were taken from a surface vessel along several transects, as directed by the observer in the helicopter. Ocean currents were measured by continuously recording current meters permanently moored near SONGS.

FIELD PROGRAM

A total of four low-altitude IR scanning flights were conducted: August 26, September 27, October 11, and October 12, 1983. Each flight was begun at approximately 0800 hours, because in the early morning there was minimal IR interference from solar and land reflection. We empirically determined that a satisfactory resolution of the thermal imaging system was retained at altitudes as high as 9,000 ft. Since this altitude also provided a large area coverage, we conducted the remaining flights as close to this altitude as permitted by weather conditions. The flights covered the area between Dana Point and a few miles south of

SONGS, and as far as several miles offshore on a few occasions.

The prevailing environmental conditions during the IR flights are summarized in Tables 1 and 2. The wind data given in Table 1 are based on measurements made at SONGS meteorological station (SCE unpublished data). The ocean currents shown in Table 2 were measured near SONGS at four stations (Figure 1) and at two depths. The currents are given as hourly averages of the longshore component of the current between 0800 and 1300 hours.

DISCUSSION

The principle behind the IR scanner is that a sensor measures the amount of radiant flux emitted by a substance, in this case the ocean water, in the 8-to-12-micron wavelength band. Each substance emits radiant flux in proportion to its temperature, thus permitting a measurement of temperature by comparing the magnitude of the radiant flux. The radiant flux emitted from water is limited to the top few microns of the water surface in the 8-to-12-micron wavelengths; thus the temperatures measured are limited to the ocean surface. The radiant flux of a substance as measured by a remotely located IR sensor can be affected by several mechanisms such as atmospheric reflection and scattering of the emitted energy, absorption of the emitted energy by atmospheric moisture, and, in the case of a water surface, nonhomogeneous reflection

TABLE 1
Environmental Conditions during IR Overflights

Date	Weather	Flight altitudes	Concurrent satellite images	Ground truth	Comments
8/26 1983	Clear, winds from west @ 5-7 mph	5,000 ft. 9,000 ft.	NOAA-7, 8/25 NOAA-7, 8/28 NIMBUS-7, 8/26	None	Coastal front from Dana Point identifiable: strong front emanating from San Mateo Point
9/27 1983	Overcast at 5,000 ft., winds from north @ 8-10 mph	4,500 ft.	NOAA-7, 9/27	2 temperature transects	Thermal features in vicinity of San Mateo Point
10/11 1983	Clear, winds southwest @ 1-5 mph	5,000 ft. 9,000 ft.	NOAA-7, 10/12 NIMBUS-7, 10/12	4 temperature transects	Layered fronts near San Mateo Point; coastal front in vicinity of Dana Point
10/12 1983	Clear, winds from west @ 2-5 mph	5,000 ft. 9,000 ft.	NOAA-7, 10/12 NIMBUS-7, 10/12	4 temperature transects	Coastal front in vicinity of Dana Point

TABLE 2
Longshore Currents during IR Flights

Station UVT-1, 3-m depth					Station UVT-1, 9-m depth			
Time	8/26	9/27	10/11	10/12	Time	8/26	9/27	10/11	10/12
8-9	—	−11.3	−5.1	2.0	8-9	−7.4	−4.8	−12.2	−7.5
9-10	—	−8.3	−5.3	2.3	9-10	−5.8	−7.8	−11.1	−4.7
10-11	—	−7.7	−5.0	3.9	10-11	−3.0	−6.9	−9.0	−4.7
11-12	—	−6.6	−5.2	2.3	11-12	−0.4	−6.5	−8.1	−5.4
12-13	—	−2.7	−6.1	0.8	12-13	—	−6.9	−4.6	−4.8

Station UVT-2, 3-m depth				
Time	8/26	9/27	10/11	10/12
8-9	−31.4	5.2	−29.7	−27.3
9-10	−36.6	2.4	−27.2	−27.8
10-11	−37.3	−6.8	−26.4	−26.9
11-12	−34.5	−10.3	−26.3	−27.0
12-13	−27.7	−13.5	−26.9	−27.2

Station UVT-8, 3-m depth					Station UVT-8, 9-m depth			
Time	8/26	9/27	10/11	10/12	Time	8/26	9/27	10/11	10/12
8-9	—	−6.8	−30.3	−26.2	8-9	−16.8	−7.0	−30.9	−21.5
9-10	—	−1.0	−32.0	−30.9	9-10	−11.4	−4.9	−28.8	−24.4
10-11	—	−1.8	−30.3	−31.8	10-11	−11.6	−6.9	−20.8	−17.9
11-12	—	−4.1	−32.8	−30.7	11-12	−12.9	−6.0	−34.7	−16.5
12-13	—	−8.9	−33.7	−32.3	12-13	−15.4	−3.9	−35.3	−20.8

Station UVT-9, 3-m depth					Station UVT-9 9-m depth			
Time	8/26	9/27	10/11	10/12	Time	8/26	9/27	10/11	10/12
8-9	−14.1	—	—	−23.0	8-9	−2.4	−10.3	−9.8	−26.0
9-10	−15.0	—	—	−31.1	9-10	1.0	−12.1	−16.1	−21.9
10-11	−11.2	—	—	−34.6	10-11	1.7	−13.1	—	−19.0
11-12	−7.9	—	−45.9	−35.0	11-12	3.7	−16.4	−24.7	−23.8
12-13	−4.5	—	−31.6	−36.7	12-13	7.4	−11.9	−31.7	−23.1

Note: Negative longshore currents are downcoast (i.e., 130 deg true). Current speeds are expressed in cm/sec.

of ambient radiance caused by surface waves. Despite these sources of interference, IR scanning has proved useful for qualitatively describing ocean surface temperature differences.

The IR images from the helicopter are shown as oblique images taken toward the northwest. The shoreline in all cases is shown along the right edge of the photos; the land is black. Warmer ocean temperatures are shown as darker shades of gray; cooler ocean temperatures are lighter shades of gray.

Front at Dana Point

During the IR scanning flight of August 26, 1983, we observed a front extending southeast from Dana Point (Figure 2). The image shows Dana Point in the upper right corner, with a cool water mass (lighter shades) extending toward the bottom of the photo. On this particular occasion, the front appeared as the offshore edge of a large cool-water plume extending from its point of origin. The plume then formed a narrow band of cool water surrounded by warm water both on its onshore and offshore sides as it streamed downcoast. Review of data indicates the existence of a southeastward flow at all the current-meter stations.

The hourly average longshore current component reached as high as 37.3 cm/sec at the farthest offshore station, station UVT-2, at a depth of 3 m.

A satellite thermal IR image, taken August 25 at 1503 hours, confirms the existence of the front emanating southeast from Dana Point. This satellite image, shown in Figure 3, does not contain the resolution necessary to identify the separation of the front from the shoreline as observed in the low-altitude image (Figure 2). However, it does show the existence of another front farther offshore. The cool-water tongue offshore is the result of a cool-water plume emanating from Palos Verdes, farther north. A second front at the edge of this plume was observed from the helicopter with the IR scanner, but the front was too extensive to adequately map.

During the IR scanning flight of September 27, 1983, we found no front emanating south or southeastward from Dana Point. A satellite thermal IR image taken at 1502 hours on September 27 confirmed these results. The satellite image, shown in Figure 4, indicates a coastal front to the northwest of Dana Point but not to the southeast. Current-meter data indicate that the southeastward flow was weaker than during the

Figure 2. Front extending to the southeast from Dana Point, August 26, 1983 (Dana Point shown on black area in upper right corner).

other flights, and in the case of station UVT-2, the farthest offshore station, the data indicate a current towards the northwest as high as 5.2 cm/sec between 0800 and 0900 hours.

A coastal front emanating from Dana Point toward the southeast was again observed on October 11 and 12. A sample IR image in the vicinity of Dana Point is shown in Figure 5. This IR image was taken from an altitude of 9,000 ft. Dana Point and Dana Point Har-

bor can be seen as the black area in the upper right corner of the photo. To the southeast of Dana Point there is a very definite cool-water mass, which is attached to the shoreline in this particular case. It is obvious that the cool surface water originates at Dana Point. Hourly average currents on this particular date were on the order of 30 cm/sec to the southeast at the

Figure 3. NOAA-7 satellite IR image of August 25, 1983, indicating existence of coastal front to southeast of Dana Point.
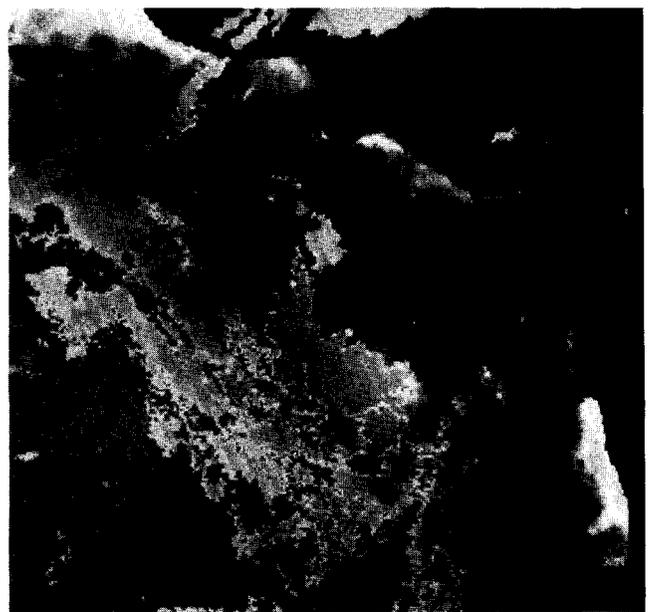
Figure 4. NOAA-7 satellite IR image of September 27, 1983, indicating the lack of a coastal front during the low-altitude IR overflight of the same date.
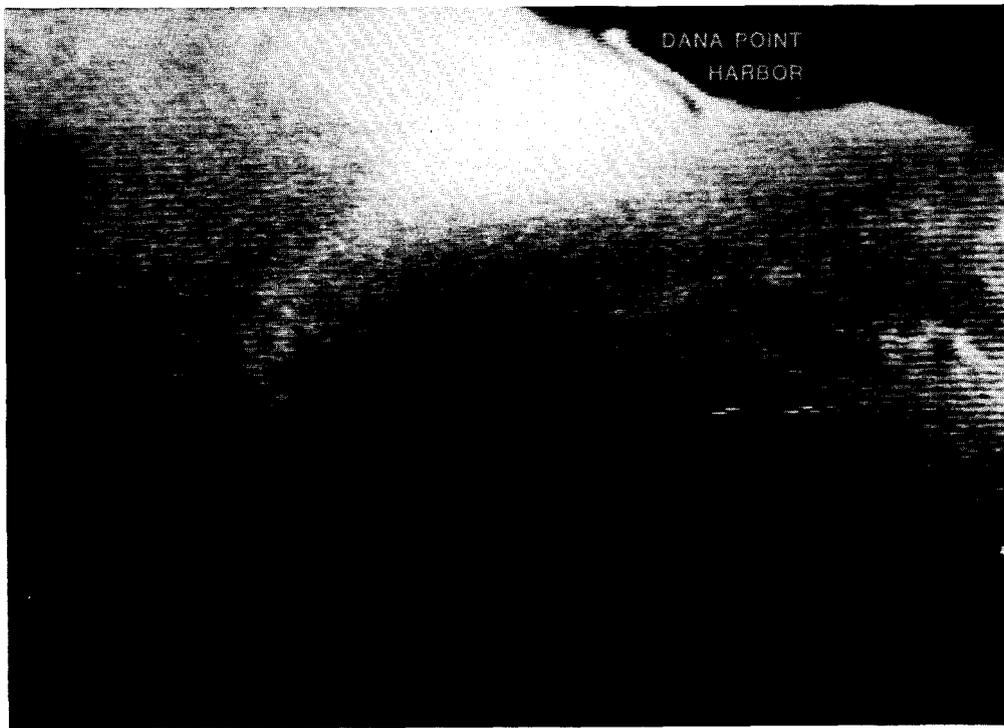
Figure 5. Oblique low-altitude IR image of coastal front emanating from Dana Point on October 12, 1983.

offshore stations at a depth of 3 m. The inshore currents, measured at station UVT-1, were actually toward the northwest at this depth, indicating the possible presence of an eddy.

The likely mechanism contributing to the upwelling in the lee of Dana Point is a cyclonic (counterclockwise) gyre, which develops at this location under a persistent northwesterly wind (Grove and Sonu 1983). Because of the cyclonic motion, the thermocline will be raised toward the surface at the center of the gyre, serving as a stationary source of cold water (Defant 1961). The cold water, upon reaching the surface, is then advected in the mean southward current, extending its plume along the downcoast shoreline. A schematic illustration of the mechanisms responsible for the front is shown in Figure 6. The mechanisms illustrated include both the conventional interpretation of upwelling as local Ekman transport offshore, and the upwelling induced by the cyclonic gyre in the lee of the headland. It is readily apparent that these two mechanisms are not exclusive but rather that they reinforce each other.

During the IR scanning flight of October 12, we visually confirmed the existence of the cyclonic gyre at Dana Point. The gyre, observed as a series of spiralling surface slicks, was estimated to be on the order of 1 km in diameter. There are also several photos of the San Mateo Point region dating back to January 22, 1973, that document a distinct turbidity pattern in

the form of a cyclonic gyre with a diameter of 1 to 4 km separating from the point (Wheeler North, pers. comm.).

Front at San Mateo Point

The front originating at San Mateo Point varied markedly from flight to flight, more so than the one at Dana Point. Two scenes of the front at this location

The upwelled water adjacent to the shoreline is the result of a raised thermocline at the center of a cyclonic gyre in the lee of the headland combined with offshore Ekman transport induced by wind.
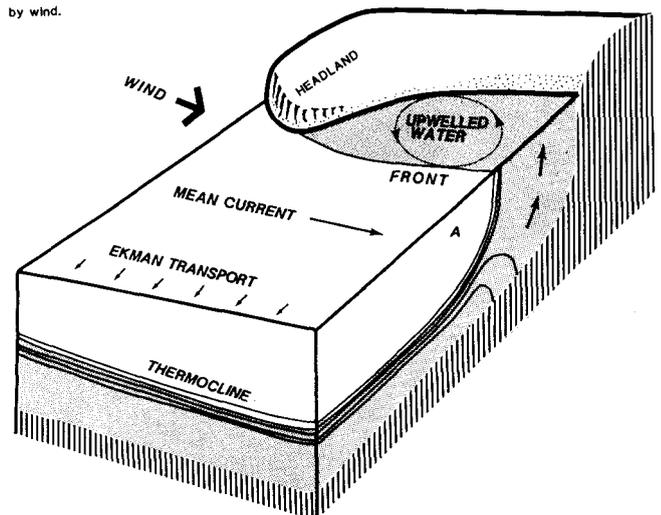
Figure 6. Schematic of the front formation in the lee of a headland.

64

Figure 7. Oblique low-altitude IR image of front at San Mateo Point September 27, 1983.

are shown in Figure 7 (September 27) and Figure 8 (October 11).

The IR image of September 27 shown in Figure 7 reveals a cool-water plume intersecting the San Mateo Point shoreline at a large angle and extending off-shore. The shape of the front on this date, coupled with a northerly displacement of the front as compared with other dates, suggests that a north-ward-flowing current has deflected a previously coast-parallel front to become a shore-perpendicular front. Current-meter data indicate that the offshore currents (station UVT-2) were toward the northwest at the 3-m depth, but the remaining stations and depths all indicate a flow to the southeast. It is likely that currents at San Mateo Point are most closely represented by the currents at station UVT-2. The fact that the 60-ft iso-bath approaches the shore at San Mateo Point from SONGS (Figure 1) reinforces this conclusion. The coastal currents would tend to follow the bathymetry and thus approach San Mateo Point.

During the IR scanning flight of October 11, we observed a multilayered front in the vicinity of San Mateo Point (Figure 8). This IR image reveals a very clear front adjacent to shore, a front shown as a streak farther offshore, and a third front, barely visible, even farther offshore. A possible linkage on this date between thermal fronts and turbidity fronts at this lo-cation is suggested by observations of turbidity coin-ciding with the thermal fronts.

Two temperature contour plots derived from the

ground truth temperature survey taken from the sur-face vessel on October 11 are shown in Figures 9 and 10. The temperature transect illustrated in Figure 9 was taken nearly normal to the shoreline, upcoast of San Mateo Point; the temperature transect shown in Figure 10 was taken normal to the shoreline just down-coast of San Mateo Point.

These temperature contour plots indicate a well-mixed layer in the top 5 m of the water column, with a thermal stratification between the bottom and 5-m-depth of as much as 2°C on both the upcoast and downcoast side of San Mateo Point. The noticeable slanting of the isotherms upward toward shore on the downcoast transect (Figure 10) may indicate a source of upwelling at this location or possibly a geostrophi-cally balanced downcoast flow. The surface temper-atures along the transect decrease as much as 1°C between the offshore and onshore limits of the tran-sects. Both temperature contour plots confirm the existence of the front at San Mateo Point and suggest that the temperature difference across the front is on the order of 1°C.

CONCLUSIONS

The helicopter-borne thermal IR scanner proved quite useful in resolving oceanographic surface fea-tures such as coastal fronts. The system's advantages are that it has high resolution and is compact, reliable, and easy to operate, qualifying it as a valuable tool for thermal surveillance operations in the coastal area. A
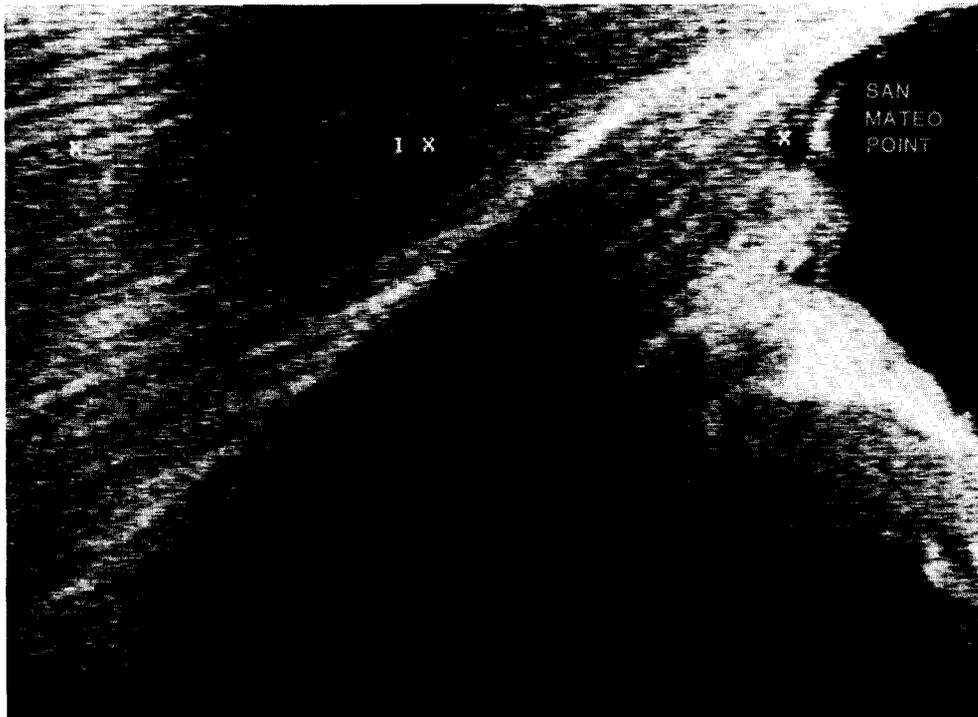
Figure 8. IR image of a multilayered front adjacent to San Mateo Point October 11, 1983 (photo taken toward northwest).

principal constraint is the system's relatively small field of view, which makes it necessary to operate the equipment at a high altitude or to aim obliquely. Although a computerized rectification procedure can be used to geographically register the video images, filter the noise, and enhance the image quality, the extra processing is of limited usefulness.

Whereas the coastal front as viewed on satellite imagery had remained somewhat blurred because of the 1.1-km spatial resolution, the low-altitude thermal IR scanning plus ground truth measurements as reported in this paper have reinforced the concept of the microfront at this location. The front forming at Dana Point did actually peel off the sharp bend of the coast at the point, suggesting a mechanism similar to the detachment of a boundary layer at a sharp corner. A cyclonic gyre, the source of the Dana Point coastal front that

had been hypothesized in the past, was seen during this study.

The coastal front forming at Dana Point, observed by the thermal IR scanner on three out of four survey days, extended southward beyond San Mateo Point and SONGS. This observation was supported by the satellite images from these days. On the fourth day the satellite image showed possible upwelling and frontal activity displaced to the north side of Dana Point, an area not covered by the helicopter IR survey.

An unexpected discovery of an additional distinct, more localized frontal system at San Mateo Point is an important result of this study. This particular microfront, not evident in satellite images, seemed to intersect the coastline at larger angles than the front at Dana Point, although its configuration appeared to depend heavily on the local current system.
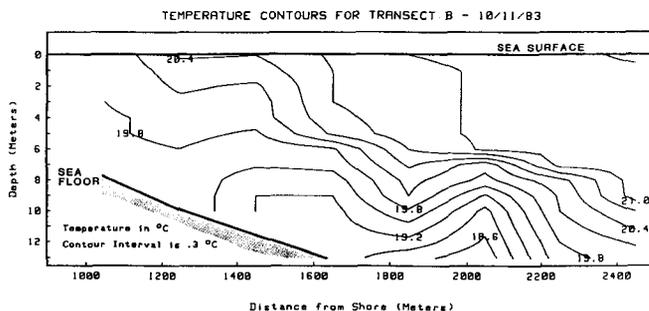
Figure 9. Temperature contours upcoast of San Mateo Point, October 11, 1983.
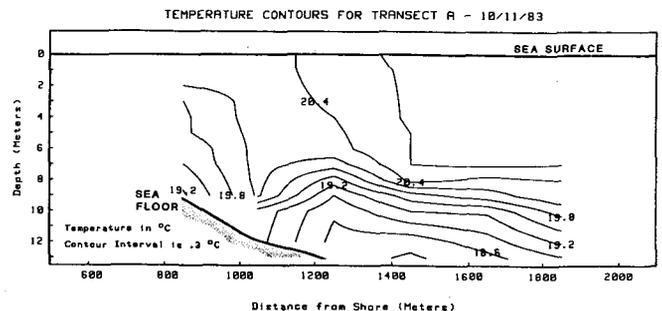
Figure 10. Temperature contours downcoast of San Mateo Point, October 11, 1983.

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DRIFT BOTTLE OBSERVATIONS OF THE NEARSHORE SURFACE CIRCULATION OFF CALIFORNIA, 1977-1983

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ABSTRACT

This report summarizes results of drift bottle studies off the California coast from June 1977 through September 1983. Approximately 2,000 bottles were released and 253 recovered. The results indicate that there are important seasonal, regional, and year-to-year variations showing a complicated pattern of nearshore surface flow off California.

North of Point Conception, a southward flow predominates, except in fall and winter when a northward flow is apparent. Anomalous summer counterflows in the vicinity of headlands occur in some years. There is also evidence of an intensified northward-flowing countercurrent in the winters of 1977-78 and 1979-80, and a strong spring reversal in 1980.

South of Point Conception, the nearshore circulation is characterized by a large variability in the direction of flow, with indications of an eddy in the area between Santa Catalina Island and the mainland.

RESUMEN

Este es el resumen de los resultados de estudios del movimiento de botellas de deriva en las corrientes costeras de California durante el período de junio de 1977 a septiembre de 1983. Se largaron aproximadamente 2.000 botellas y se recuperaron 253. Los resultados obtenidos indican que existen fluctuaciones (según la estación, la región y el año) que complican el patrón general de las corrientes superficiales de las áreas costeras de California.

Al norte de Pt. Concepción predomina una corriente con dirreción al Sur excepto durante el otoño e invierno cuando se observa una corriente hacia el norte. En algunos años, se observan contracorrientes anómalas cerca de los cabos durante el verano. También existe evidencia de una contracorriente con dirección al norte durante los inviernos de 1977-78 y 1979-80 con un fuerte cambio de dirección durante la primavera de 1980.

Al sur de Pt. Concepción, la circulación costera se caracteriza por una marcada variación en la dirección de la corriente, con indicacciones de la presencia de un remolino en el área entre la Isla de Santa Catalina y el continente.

INTRODUCTION

The circulation off the California coast is composed of a southward flow, the California Current, and a northward subsurface flow beneath it, known as the California Countercurrent or Undercurrent. North of Point Conception, a northward flow develops at the surface in fall and winter, when it is known as the Davidson Current. South of Point Conception and inshore of the Channel Islands the circulation forms a semipermanent counterclockwise eddy. Hickey (1979) reviewed the known features of these currents in detail and emphasized that the relationships between them are still unclear. Significant variations in this overall pattern are also apparent, but not yet well understood (Sverdrup et al. 1942; Reid et al. 1958; Hickey 1979).

During summer (May-August) northwesterly winds prevail, and the circulation is characterized by upwelling and offshore transport of surface waters. Southwesterly or westerly winds predominate during winter (November-February), with onshore transport of surface waters. Transitional periods between these major seasons occur during spring (March-April) and fall (September-October). Oceanic conditions often occur near the coast during the fall transitional period.

Drift bottle studies have helped to document seasonal trends and regional differences in the circulation of the California Current system (Tibby 1939; Reid 1960; Schwartzlose 1963; Hamby 1964; Burt and Wyatt 1965; Wyatt et al. 1972; Crowe and Schwartzlose 1972; Schwartzlose and Reid 1972; Crowe[1]). Drift bottle observations have also contributed to the historical record of interannual current fluctuations that are the focus of recent analysis (McLain and Thomas 1983). This report will summarize indications of seasonal, regional, and year-to-year variations in the nearshore surface circulation off California observed in drift bottle studies from June 1977 through September 1983.

METHODS

The drift bottle studies were conducted under the direction of the Extension Marine Fisheries Specialist at the University of California, Davis, by members of 4-H clubs and other educational groups. This is a contin-

[1]F. Crowe. Unpublished drift bottle data, 1971-81. Marine Life Research Group, Scripps Institution of Oceanography, La Jolla, California 92093.

TABLE 1
Drift Bottle Releases North of Point Conception, 1977-83

Season of recovery	Direction of drift	Number of recoveries	Mean minimum rate of drift (km/day)
Sep.-Oct.	North	25	4.9
Nov.-Feb.	North	9	7.1
Mar.-Apr.	North	6	15.7
	South	34	3.5
May-Aug.	North	14	10.0
	South	65	16.8

uing study with two purposes: (1) to obtain long-term drift measurements of surface currents off California, and (2) to teach youth about currents through direct study of coastal waters. Each study group selects the time, location, and size of release. Twenty release points were located north of Point Conception and 27 to the south, with releases distributed throughout the year. Most release points were within 40 km of the mainland. The drift bottles were heavy glass bottles ballasted with sand to minimize windage. Dewees and Wyatt (1977) presented details of the procedure.

Tables 1 and 2 show the direction of drift, number of recoveries, and mean minimum rate of drift by season of recovery for releases north of Point Conception (Table 1) and south of Point Conception (Table 2). Table 3 shows the number of release points with returns by season and region of recovery. Since the exact number of bottles released is not known for some of the release points, the tables include only the number of recoveries. The seasons in the tables represent the upwelling season (May-August), the Davidson Current season (November-February), and the two transitional seasons (September-October and March-April). Estimates of drift rates in the tables and text represent minimum speeds, based on the earliest recovery at a given point and an assumed straight line of travel from point of release to point of return.

TABLE 2
Drift Bottle Releases South of Point Conception, 1977-83

Season of recovery	Direction of drift	Number of recoveries	Mean minimum rate of drift (km/day)
Sep.-Oct.	North	9	5.1
	South	4	8.4
	East	3	5.5
Nov.-Feb.	North	7	2.1
	South	13	5.4
	East	3	3.0
Mar.-Apr.	South	37	7.2
	East	2	6.1
May-Aug.	North	10	7.9
	South	3	3.8
	East	3	0.4
	West	2	0.1

Recoveries from the Galapagos Islands and Hawaii not included.

TABLE 3
Drift Bottle Release Points with Returns Compared to Total Number of Release Points, 1977-83

Region	Releases	Seasons			
		Sep.-Oct.	Nov.-Feb.	Mar.-Apr.	May-Aug.
North of Pt. Conception	Release points with returns	3	5	5	4
	Total no. of release points	4	5	5	6
South of Pt. Conception	Release points with returns	5	5	8	3
	Total no. of release points	5	7	11	4

Figures 1 through 7 show the paths of drift for all recovered bottles by the year of release. Solid circles represent release points for which there were recoveries. Open circles represent release points with no recoveries. The month of release is indicated at these points. Solid lines represent the inferred path of travel for particular recoveries. A dashed line indicates a generalized direction of travel. A number in parentheses at the shore end of a line gives the total number of bottles recovered in cases where more than one bottle appeared to travel a particular route.

RESULTS

Drift Bottle Returns

About 2,000 drift bottles were released over the seven-year period (1977-83), and 253 (12.6%) were returned (Tables 1 and 2). The farthest northern return was from Pacific Beach, Washington, in March 1978. The southernmost recovery was from a May 1979 release in the San Pedro Channel that was reportedly found at Isla Santa Cruz, the Galápagos Islands, Ecuador, a month later. Since it is unlikely that this bottle could drift so quickly, we assume that someone carried it to the Galápagos. A bottle recovered in Hawaii in July 1978, a year after its June 1977 release off Point Hueneme, in Ventura County, traveled at a minimum rate of 11.2 km/day. It probably was carried south by the California Current and then west by the North Equatorial Current. Wyatt et al. (1972) reported a Hawaiian return from a July 1978 release off Newport, Oregon, with a comparable time at sea and rate of drift.

Nearshore Surface Circulation
North of Point Conception

A northward flow is evident in the majority of returns from release points north of Point Conception in fall and winter (Figures 1, 3, 4, and 7). In spring, the direction of flow reverses, and returns indicate a dom-
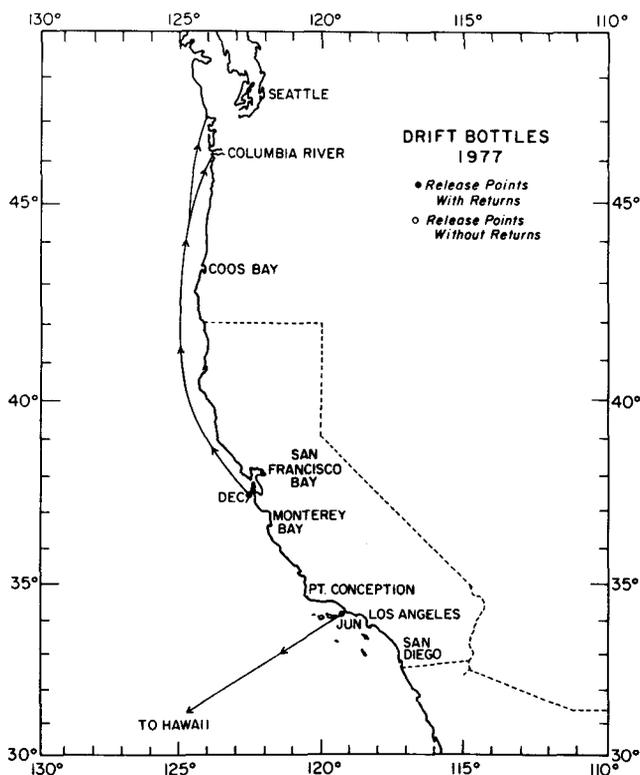
Figure 1. Drift bottle releases and recoveries for 1977.
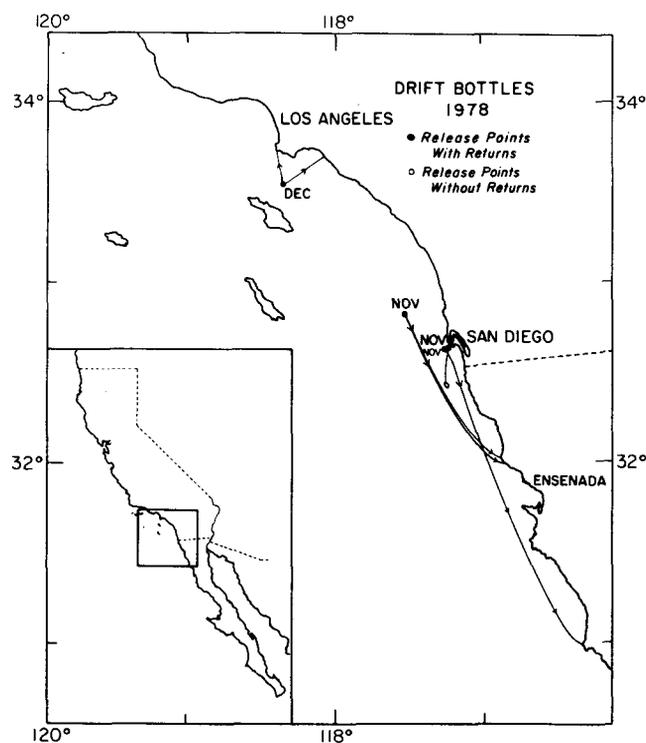
Figure 2. Drift bottle releases and recoveries for 1978.

inant southward flow from May through August (Figures 4, 5, and 7).

Returns from 1983 nearshore releases off Bodega Head indicate a reversal of flow within a three- to four-month period, with all returns from a June release showing a southward drift at a minimum rate of 22.2 km/day, whereas all those from a September release drifted north at a minimum of 6.2 km/day (Figure 7).

The strongest northward flow occurred in the winters of 1977-78 (Figure 1) and 1979-80 (Figure 3), when five bottles reached Oregon and Washington in March. This was also the greatest drift for any release north or south of Point Conception, ranging from 13-20 km/day for a distance of 1,300-1,800 km. By contrast, returns in March 1981 from releases earlier in the month traveled south an average of only 55 km at a rate of 5.3 km/day (Figure 5).

Figure 3 also shows two long-distance recoveries to the south in March 1980. These were from the same November 1979 release location at Point Conception that had long-distance northward returns.

A striking variation in the summer pattern of surface movement occurred in July 1980. All recoveries from a July 1980 nearshore release off Davenport, Santa Cruz County, flowed north and back to shore (Figure 4), counter to the usual summer offshore transport of coastal waters caused by upwelling. These

returns showed a minimum rate of drift of 11.1 km/day for an average distance of 20 km.

Nearshore Surface Circulation South of Point Conception

We observed a variability in the direction of surface circulation in the area between Santa Catalina Island and the mainland that was unlike any other area we studied (Figures 2-7). Drift both to the north and south occurred in all months except February and March, when there was a dominant southward flow. Some returns also indicated an easterly or westerly component to the drift.

Recoveries from three release points off San Diego (Figure 2) showed more uniformity in the direction of drift, with four of five returns flowing south—three as far as Baja California, apparently picked up offshore by the California Current. One bottle drifted northward into San Diego Harbor.

DISCUSSION

Our observations support the generalization that a southward flow dominates nearshore circulation off the California coast most of the year. The seasonal appearance of the Davidson Current from November through February (Figures 1, 3, and 4) is an important feature of nearshore surface circulation north of Point Conception. The comparatively low percentage of releases with returns from May through August north of
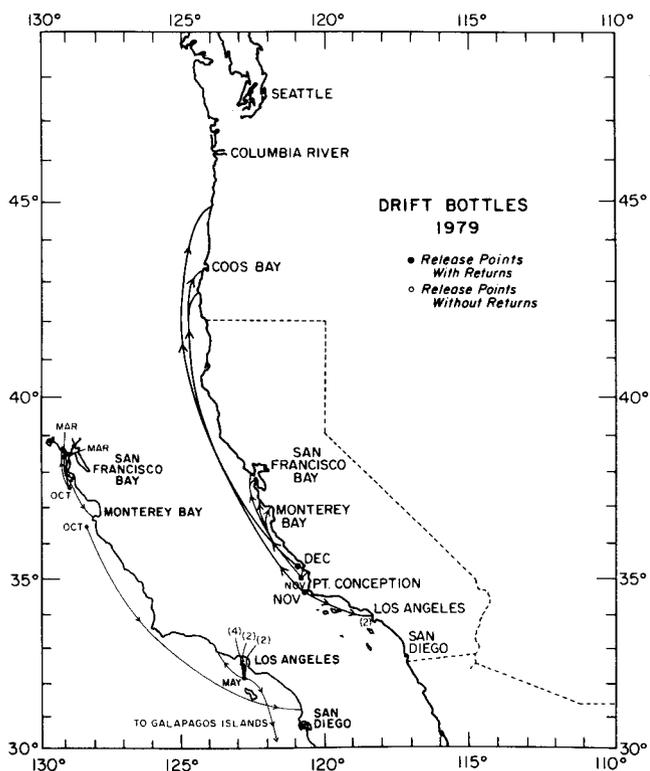
Figure 3. Drift bottle releases and recoveries for 1979.

Figure 4. Drift bottle releases and recoveries for 1980.

Point Conception (Table 3) suggests that offshore transport of drift bottles is usually significant during the upwelling season, an observation commonly made by other drift bottle investigators (Schwartzlose 1963; Burt and Wyatt 1965; and Wyatt et al. 1972). We also found evidence of local eddies and countercurrents that complicate this overall pattern and point to the importance of seasonal, regional, and interannual variations in the nearshore surface circulation off California.

The most obvious variability is that associated with the Southern California Bight (Figures 2-7). Drift bottle studies by Tibby (1939), Crowe and Schwartzlose (1972), and Crowe[2] indicate that eddies are a major factor in the circulation of the Channel Island area. Drogue measurements by Schwartzlose and Reid (1972) confirmed the presence of many small eddies inshore of the Channel Islands. We found that the nearshore waters between Santa Catalina Island and the mainland circulate in an eddy in most months except February and March, when southward flow predominates. This supports Schwartzlose's (1963) observation that eddies do not exist in the Channel Island area in March, April, and May.

In other areas, we observed countercurrents that

appeared irregularly. The reversal of flow that we observed off Bodega Head between June and September 1983 (Figure 7) was not evident in drift bottle studies by Hamby (1964), who suggested that there is a prevailing northward current throughout the year off Bodega Head. The July 1980 countercurrent off Santa Cruz (Figure 4) also appears to be unusual. No drift bottles were returned from our releases off Santa Cruz in July 1982 (Figure 6), a finding consistent with summer upwelling, but not indicated by our observations in July 1980.

Results of drift studies by other investigators also suggest that anomalous late summer and early fall countercurrents occur from time to time off certain parts of the California coast. The anomalous northward flow that we observed off Santa Cruz in July 1980 is similar to a pattern observed in Monterey Bay in 1972. Blaskovich (1973) described a counterclockwise flow in this area from June to September 1972. During the same period Griggs (1974) noted a significant northward flow, which was apparent despite northerly winds. Schwartzlose (1963) observed a shoreward movement of drift bottles between San Francisco and Monterey Bay that was occasionally to the north in summer. Some returns from a June 1981 release off San Mateo County by Crowe[3] also flowed

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[2]See footnote 1, page 68.

[3]See footnote 1, page 68.
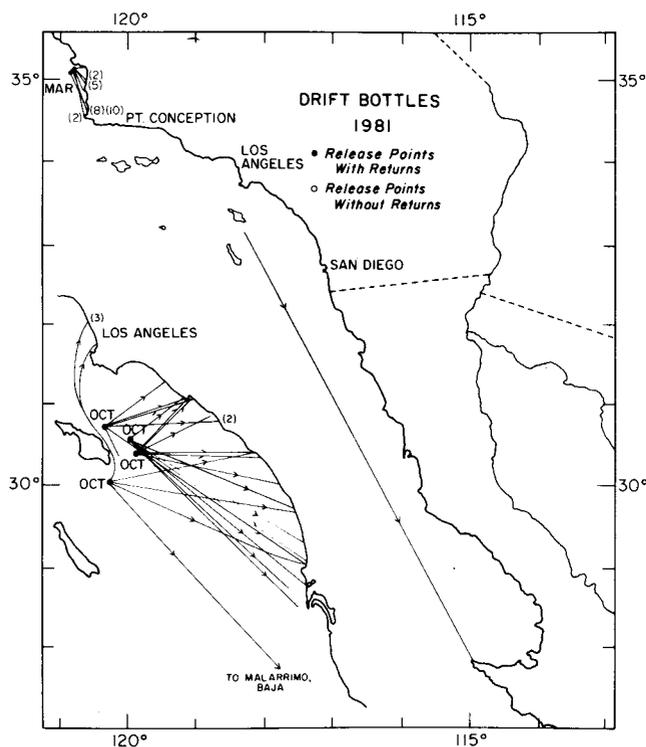
Figure 5. Drift bottle releases and recoveries for 1981.
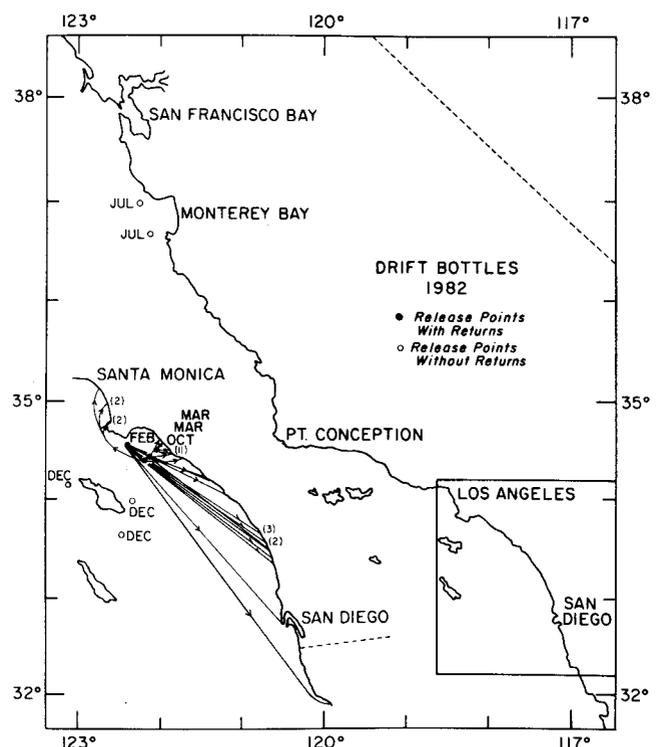
Figure 6. Drift bottle releases and recoveries for 1982.

north and shoreward, whereas his releases in the same area in other years generally had no returns.

At least two possible explanations exist for these findings and for our observations of a countercurrent off Bodega Head in September 1983 and Santa Cruz in July 1980. Sverdrup et al. (1942) suggested that as upwelling ceases toward the end of summer, the current breaks down into a number of eddies nearshore, some of which move coastal waters toward shore, particularly in areas between centers of upwelling.

An alternative explanation is suggested by recent work emphasizing the importance of interannual fluctuations in the California Current system associated with unusual oceanographic conditions. McLain and Thomas (1983) suggested that the anomalous summer counterflow observed by Blaskovich (1973) and Griggs (1974) in the Monterey area was due to an intensification of the alongshore current related to unusually high sea levels in 1972. Hickey (1979) proposed that there is a relationship between large-scale flow separations in the vicinity of headlands and unusual countercurrents that may occur in years of enhanced southward flow in the California Current. Our findings are consistent with these considerations. The summer countercurrents that we observed were in areas where headlands dominate the nearshore topography, and the summer countercurrent of 1983 was

during a year of unusual oceanic conditions associated with a strong El Niño.

The intensified Davidson Current evident in the strong poleward drift of bottles that we observed during the winters of 1977-78 and 1979-80 may also have been related to unusual oceanographic events. McLain and Thomas (1983) noted that very strong onshore Ekman transport in winter, associated with above-normal sea level and dynamic height along the coast, occurred during these years and in the winters of 1957-58 and 1969-70, when very strong northward transport of drift bottles was also observed (Schwartzlose 1963; Crowe and Schwartzlose 1972). The long-distance recoveries of drift bottles both to the north and south of a November 1979 release at Point Conception (Figure 3) may be a related phenomenon, indicating a strong and rapid current reversal in spring following the enhanced northward flow of that winter. McLain and Thomas (1983) pointed out that pronounced spring reversals do not occur every year, but tend to follow winters of unusually high sea level and dynamic height. This may also account for the northern and southern returns from a winter release off Point Conception observed by Schwartzlose and Reid (1972) during the 1963-64 El Niño, also a year of high sea level and dynamic height (McLain and Thomas 1983).

We plan future drift bottle studies to clarify the
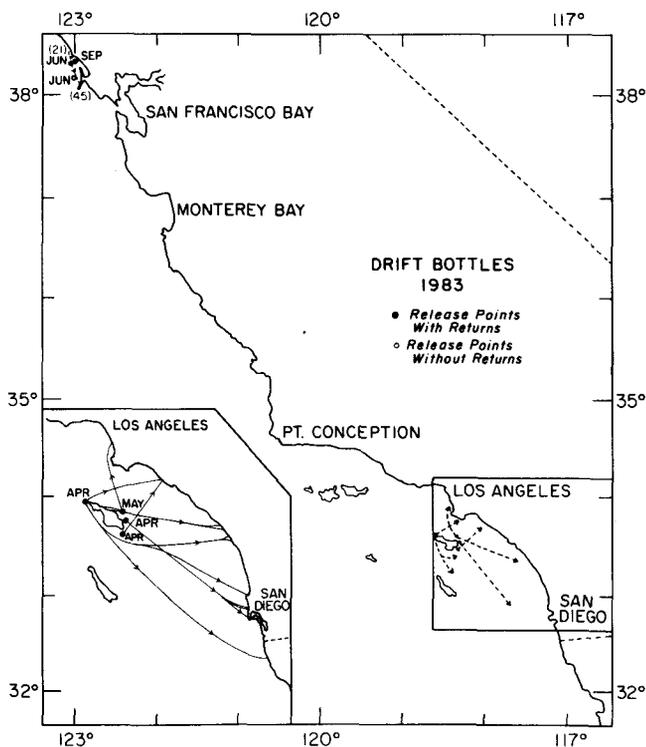
Figure 7.   Drift bottle releases and recoveries for 1983.

significance of our observations. In particular, it would be useful to have more drift bottle releases in areas near headlands. Releases made from locations offshore as well as within the immediate vicinity of headlands could indicate to what extent flow separation occurs. Additional studies throughout the Southern California Bight would help to elucidate the complex circulation in this area. Yearly studies conducted in all areas would contribute important information about interannual variations. Indications of the direction of flow derived from drift bottle observations such as these can enhance our understanding of California's nearshore surface circulation in a way not possible by indirect measurements alone.

ACKNOWLEDGMENTS

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DETERMINING CHLOROPHYLL ON THE 1984 CALCOFI SURVEYS

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ABSTRACT

Two sources of error may be relevant to the 1984 CalCOFI chlorophyll data set. These are discussed and their magnitude estimated. The first error is due to the use of GF/C glass fiber filters, which do not completely retain the smallest phytoplankters. This error is important mainly in more oligotrophic waters, where its relative bias is of the order of −15%. The second error arises from the incomplete recovery of chlorophyll from the filter when the filter is not ground in acetone but is allowed to extract in acetone for 24 hours. The relative bias introduced is about −8%. Taking into account both of these errors, the most accurate estimate of the true chlorophyll concentration falls in the range 1.1 to 1.3 times the observed concentration.

RESUMEN

Existen dos posibles fuentes de error en los datos de clorofila de CalCOFI de 1984. Sus magnitudes son discutidas y estimadas. El primer error se debe al uso de filtros de fibra de vidrio tipo GF/C los cuales no retienen completamente los fitoplanctontes más pequeños. Este error es importante principalmente en aguas oligotróficas, donde el sesgo relativo es del orden de un −15%. El segundo error proviene de la recuperación incompleta de clorofila desde el filtro cuando este filtro no es macerado sino extraído en acetona por 24 horas. El sesgo relativo que se introduce es aproximadamente −8%. Considerando ambos errores, una estimación más exacta de la concentración real de clorofila estará comprendida en un rango de 1.1-1.3 veces la concentración observada.

INTRODUCTION

The 1984 CalCOFI program includes measurements of chlorophyll a and phaeopigments in the upper 200 meters. These are made at every hydrographic station and at the noontime productivity stations. Each two-ship survey includes approximately 2,000 individual chlorophyll determinations.

Approximately 140 ml of seawater is removed from each Nansen or Niskin bottle, and is filtered through a Whatman GF/C filter to remove the particulate material. Each filter is then placed in a scintillation vial with 90% acetone and stored in the dark, under refrig-

eration, for 24 hours. The acetone is brought to room temperature, decanted into a cuvette, and the fluorescence is determined with a Turner 111 fluorometer. All fluorometers used on the survey are calibrated against a spectrophotometer using the trichromatic equations of Parsons and Strickland (Strickland and Parsons 1968). Cross-calibration of the instruments is checked at intervals during the program.

The selection of this analytical procedure involved several compromises, which are expected to reduce the accuracy of the measurements to some extent. Evaluation of the 1984 chlorophyll data set necessitates understanding the probable errors introduced by these compromises.

RESULTS

Filter Pore Size

There exists an extensive body of chlorophyll a data from the California Current based upon the material retained by the GF/C filter. This filter has a specified retention of 1.2 μ, but experimental determinations give varied results. Work by Parker (1981) suggests the average retention may be closer to 3 μ, while Eppley finds that GF/C filters will retain material that has passed through 1-μ Nuclepore filters (pers. comm.). Recent work in a variety of oceanic environments has indicated the existence of an important photosynthetic component 0.5-3 μ in diameter (the picoplankton), which is not quantitatively retained by the traditional GF/C filter. Our decision to continue using the GF/C filters, in spite of a potential negative bias, was based on the importance of maintaining long-term continuity of the data set.

On CalCOFI cruise 8105-J, comparisons were made between the chlorophyll retained on GF/C filters and on GF/F filters, which have a specified minimum retention size of 0.7 μ. Replicate subsamples from each of 71 samples were filtered, one through a GF/C filter, the other through a GF/F filter. Samples were allowed to extract for 24 hours in the dark, under refrigeration, before we determined fluorescence. Samples were collected throughout the euphotic zone and from a variety of water types. The GF/C filters did tend to underestimate the chlorophyll concentration, especially at lower chlorophyll concentrations (Figure 1). Of the 49 samples with chlorophyll concentrations less than 0.5 μ g/l, the GF/F filters retained more chlo-
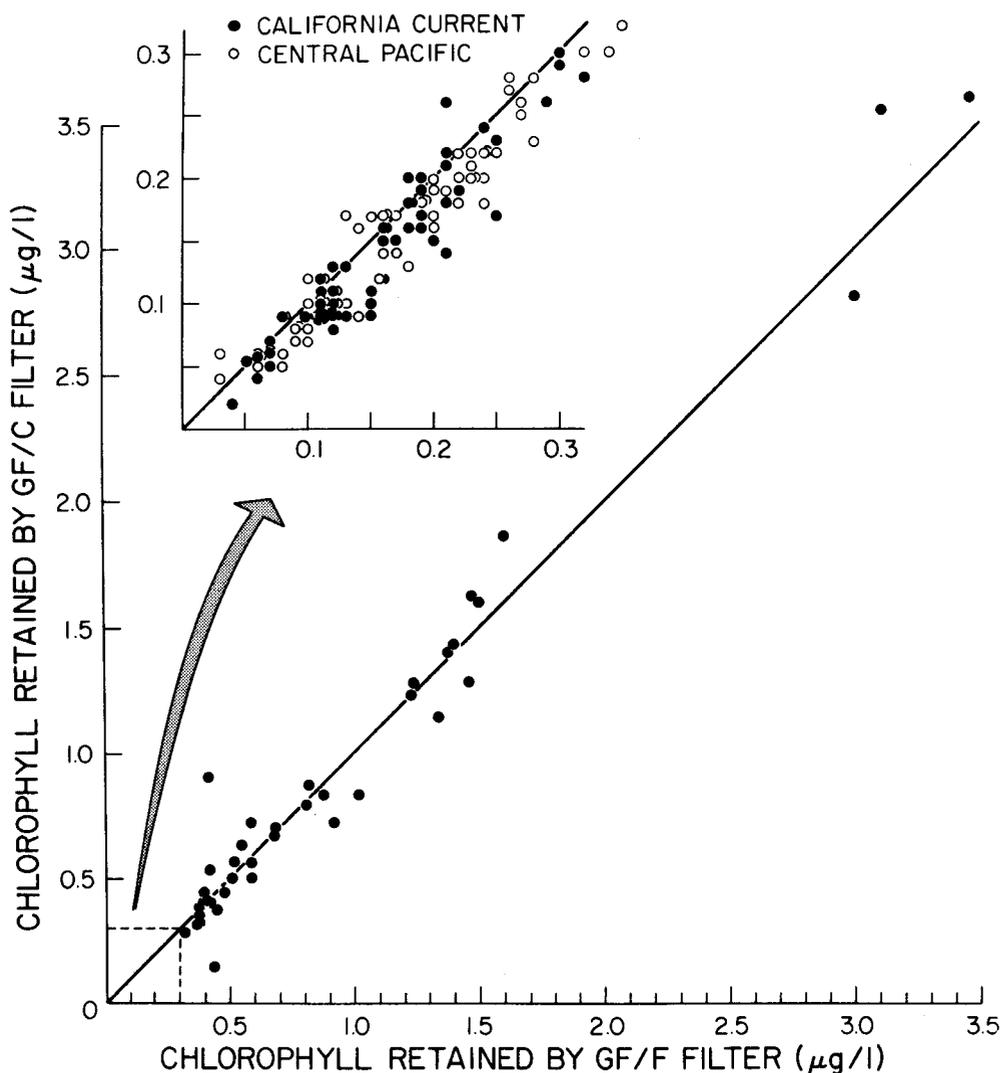
Figure 1. Comparison of the amount of chlorophyll retained by a GF/C glass fiber filter and that retained by a GF/F glass fiber filter for samples from the California Current and the Central Pacific environment. Solid line represents equal retention.

rophyll 41 times (Figure 2; $p < .01$). This pattern was similar to that observed in the Central Pacific (Figure 1, insert). However, at higher chlorophyll concentrations, this bias was not apparent. Over the entire data set the mean relative bias [(GF/C - GF/F)/GF/F] was −13%. When the 22 samples with chlorophyll concentrations in excess of 0.5 μ g/l were excluded, this bias increased to −15%. This relationship between bias and chlorophyll concentration is compatible with previous work which indicates a higher proportion of smaller phytoplankton in oligotrophic environments (e.g., Malone 1971 a,b, 1980; Li et al. 1983).

The recent quantitative work on picoplankton has been based on filters with pore sizes on the order of 0.2 to 0.4 μ (Waterbury et al. 1979; Platt et al. 1983), considerably smaller than the minimum cell diameter of 0.5 (Johnson and Seiburth 1979) to 0.9 μ (Waterbury et al. 1979) reported for picoplankton. The GF/F filters used in the present study have a reported mini-

mum retention of 0.7 μ, and the smallest phytoplankton components may be incompletely removed. However, Li et al. (1983) found that GF/F filters retained 94% of the radioactivity retained by 0.2 μ Nuclepore filters.

Extraction Procedure

In the early 1960s, glass fiber filters, ground in acetone to extract chlorophyll, largely replaced Millepore filters, which were extracted in acetone for some period of time without grinding. Use of glass fiber filters and the grinding procedure offers the advantage of rapid sample analysis (one or two hours). In addition, extraction of chlorophyll may be more complete with ground glass fiber filters, especially when benthic or estuarine species are prevalent (Strickland and Parsons 1968). On the other hand, the grinding procedure is more time-consuming and requires more equipment on board ship. Preliminary work in the

GF/F FILTERS VS. GF/C FILTERS
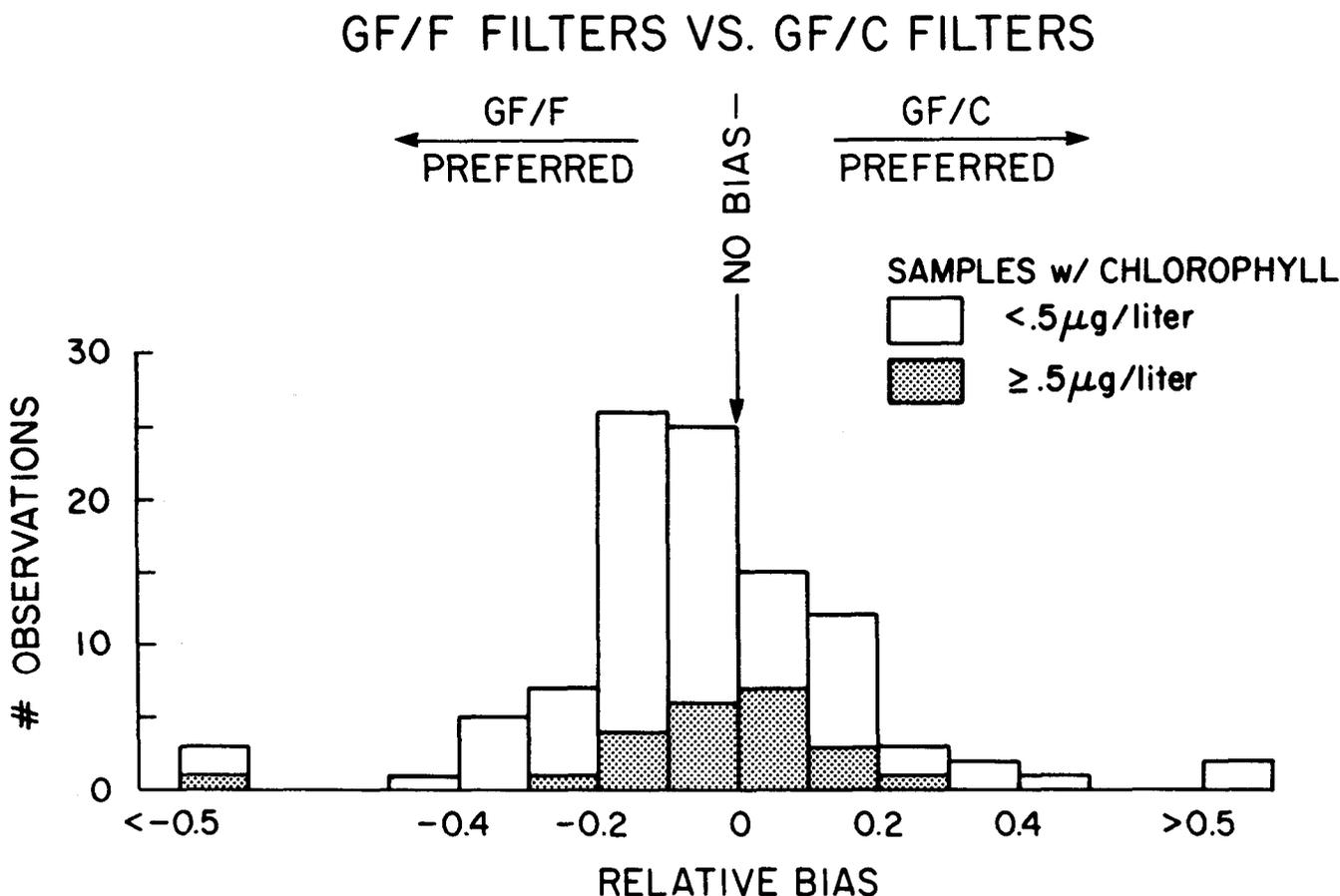
Figure 2. Data from Figure 1 (California Current only) expressed as a frequency distribution of relative biases. Relative Bias = (GF/F-GF/C)/(GF/F); GF/F = chlorophyll retained by a GF/F filter; GF/C = chlorophyll retained by a GF/C filter.

California Current suggested that in some situations grinding may recover even less chlorophyll (8%) than 24-hour extraction, apparently because some of the chlorophyll is degraded to phaeopigments during the grinding process (Table 1). Chlorophyll on past Cal-COFI surveys has been determined by the grinding procedure. Our decision to return to the 24-hour extraction procedure was based on the savings in time and effort, which appeared to justify the risk of a slight bias.

Two procedures were investigated from February to November 1983, using water collected from the end of the pier at Scripps Institution of Oceanography (SIO). Two replicate samples were collected with a Nansen bottle from just below the sea surface. From each bottle, four subsamples were drawn. Two were filtered through GF/C filters, ground in acetone, and the fluorescence determined within one hour; the other two subsamples were filtered through GF/C filters and allowed to extract, without grinding, for 20-24 hours. To determine bias, we compared the two means of the duplicate samples within the same Nansen bottle.

There were 72 such comparisons. Most of these, however, are paired (duplicate Nansen bottle samples on the same day) and, as discussed below, the results are not independent. Thus, the effective sample size is 38. In 80% of the observations, the recovery of chlorophyll was greater when the filter was ground ($p < .05$; Figure 3). The mean relative bias [(unground − ground/ground] was −7.6% (Figure 4). Examination of the fluorescence ratios, (before acidification:after acidification) did not indicate any differential degradation of chlorophyll, as was observed in the preliminary experiment. However, the chlorophyll concentrations during the pier experiment rarely dropped below 0.3 μ g/1, so that experiment did not include material from a truly oligotrophic environment where benthic and estuarine forms are rare.

There was no evidence for a difference in precision between the two techniques. Indeed, there was a tendency (sign test, $p \sim .18$) for the 24-hour extraction procedure to yield more precise replicates.

The two experiments run on the same day (one experiment from each of two Nansen bottles) tended to
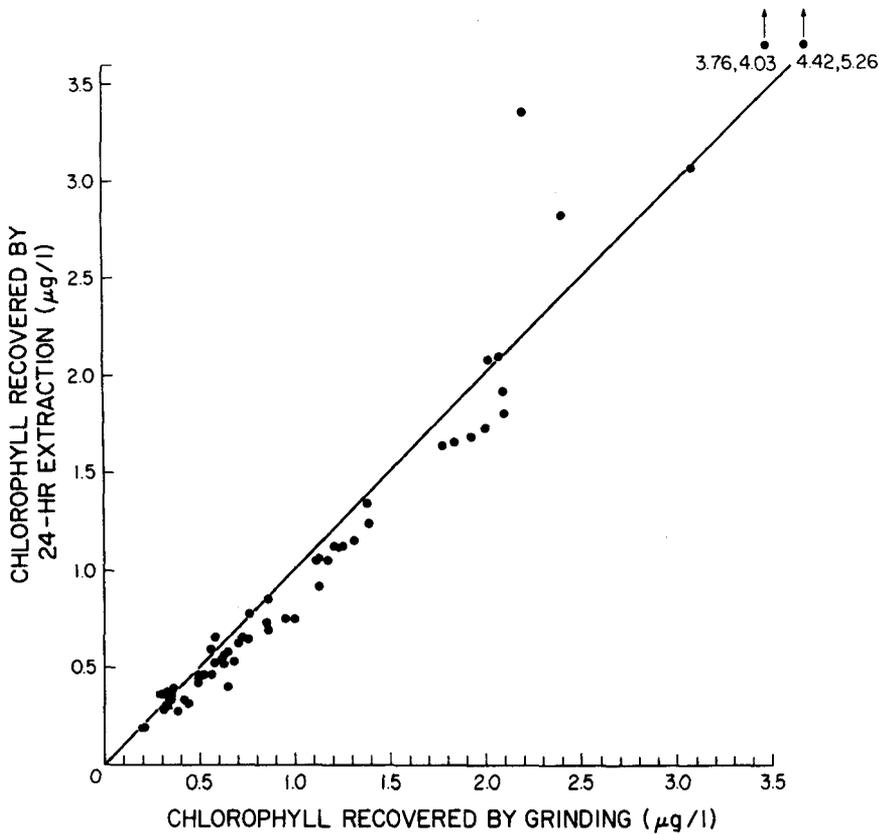
Figure 3. Comparison of the amount of chlorophyll recovered after 24-hour extraction to that recovered after grinding the filter. Solid line represents equal recovery.

TABLE 1

Preliminary Experiment on the Effects of Filter Size and Extraction Procedure on the Determination of Chlorophyll (Chl.) and Phaeopigments (Ph.) in the California Current*

Depth (m)	GF/C filters Extracted Chl.	GF/C filters Extracted Ph.	GF/C filters Ground Chl.	GF/C filters Ground Ph.	GF-F filters Extracted Chl.	GF-F filters Extracted Ph.	GF-F filters Ground Chl.	GF-F filters Ground Ph.
0	0.22	0.04	0.23	0.04	0.24	0.04	0.24	0.05
10	0.27	0.02	0.24	0.06	0.26	0.04	0.24	0.06
20	0.30	0.05	0.25	0.08	0.32	0.08	0.30	0.09
30	0.28	0.07	0.25	0.10	0.28	0.10	—	—
40	0.56	0.18	—	—	0.59	0.17	0.54	0.19
50	0.51	0.22	0.46	0.24	0.47	0.25	—	—
60	0.28	0.20	0.27	0.23	0.26	0.25	—	—
70	0.22	0.20	0.20	0.20	0.23	0.23	—	—
80	0.16	0.15	—	—	0.14	0.19	—	—
90	0.12	0.15	—	—	0.11	0.20	—	—

Summary of Chlorophyll Recovery

Extraction procedure: filters ground (G) vs extracted only (Ex)

	G > Ex	G = Ex	G < Ex
GF/C filters	1	0	6
GF/F filters	0	1	3

Filter type: GF/C filters vs GF/F filters

	GF/F > GF/C	GF/F = GF/C	GF/F < GF/C
G	4	1	6
Ex	2	1	0

*CalCOFI station 90.28, August 1982.
Filters (GF/C or GF/F) were extracted in acetone for 24 hrs, and the fluorescence of half of the extract was determined (Extracted). The filter was then ground in the remaining extract and a second determination was made (Ground). Results are µg/l.

GRINDING VS. 24-HR. EXTRACTION
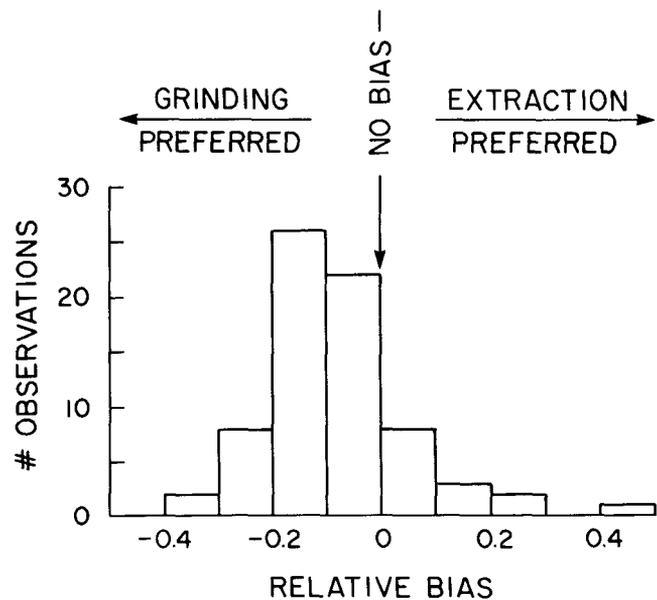
Figure 4. Data from Figure 3 expressed as a frequency distribution of relative biases. Relative Bias = (G - Ex)/G; G = chlorophyll recovered when filter is ground; Ex = chlorophyll recovered when filter is extracted for 24 hours.
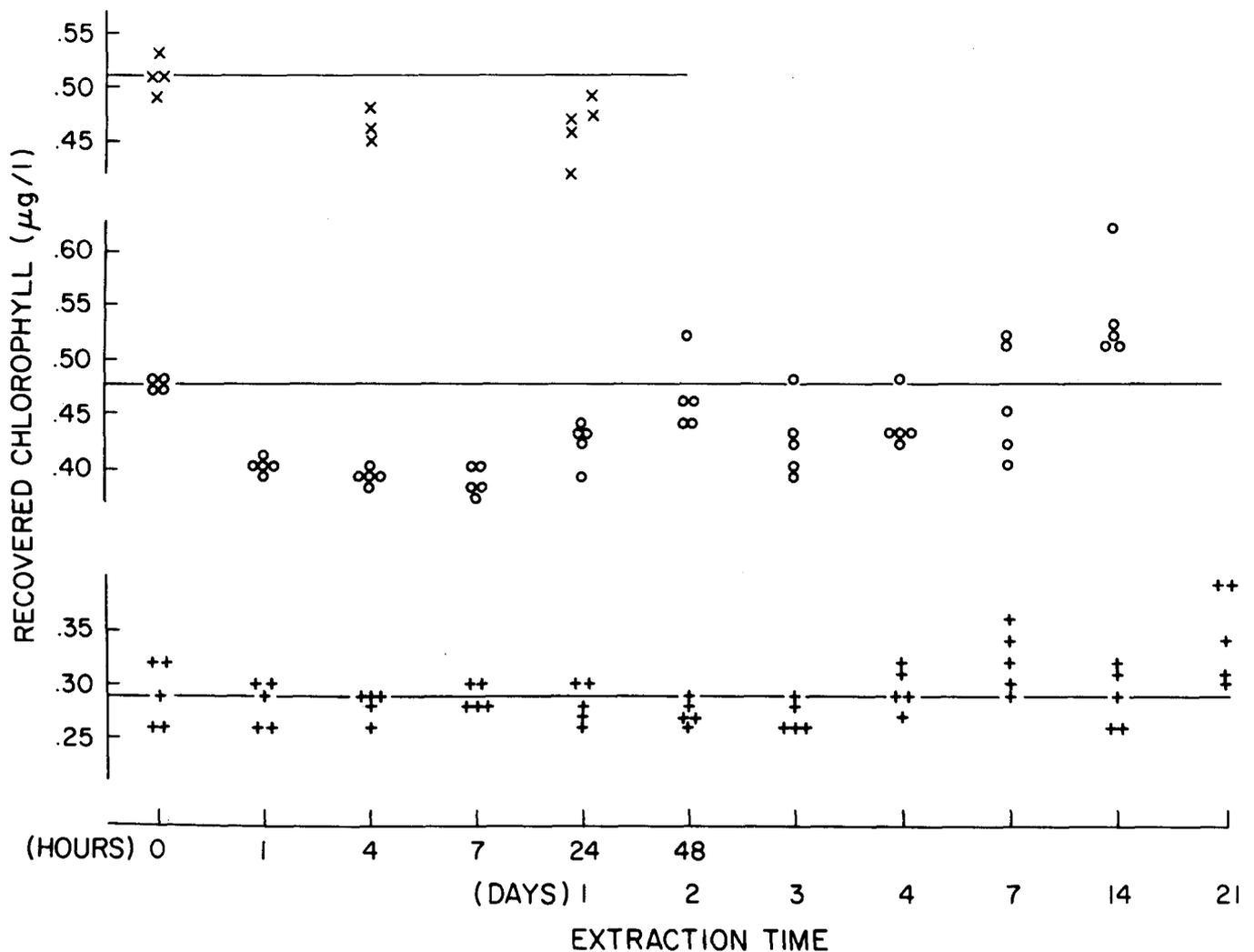
Figure 5. Recovery of chlorophyll after various extraction times. Time zero values were obtained by grinding the filters. Horizontal lines mark the mean values of the time zero controls.

give the same experimental result. On 31 of the 34 days, both experiments yielded either more chlorophyll from the ground filters or more chlorophyll from the 24-hour-extracted filters; on only 3 days were the results from the two experiments dissimilar. There were significantly more similar pairs than one would expect if the experimental results of the two replicate samples were independent (Chi-square = 16.8; $p <$ .01). This result does not appear to be an operator bias, but rather an interaction between the techniques and the composition of the flora being sampled.

Extraction Time

To examine the minimum and maximum acceptable extraction times, three experiments were run, using water from the end of the SIO pier. For each experiment a series of replicate subsamples was drawn from a 5-liter Niskin bottle. These were filtered onto GF/C

filters and randomly assigned to the various treatments. The controls were ground in acetone, and the fluorescence was determined immediately. Other samples were placed in acetone and stored in the dark, under refrigeration, for various periods of time, before we determined the fluorescence.

The results of the three experiments (Figure 5) were inconsistent. Experiment 2 showed a significant increase in recovered chlorophyll with time (Kendall τ, $p <$.05). Experiment 3 showed no trend whatever, and the recovery of chlorophyll after extraction for one hour was not significantly different from the control. On the other hand, all experiments showed a tendency to lose precision with increasing extraction times (Kendall τ: experiment 2, $p <$ .01; experiment 3, $p <$ .20). The choice of 24 hours as the target extraction time seems to offer acceptable accuracy without risking reduction of precision. However, under emer-

gency situations (such as the failure of a fluorometer), samples can be stored for at least 3 weeks without serious loss of chlorophyll. However, this conclusion is not supported by earlier observations of serious degradation of chlorophyll with time (Yentsch and Menzel 1963).

CONCLUSIONS

There are two sources of error in the CalCOFI 1984 chlorophyll data, arising from our choice of analytical procedures. The first is the loss of the smallest phytoplankton through the filter. The second is the failure to extract into acetone all of the chlorophyll retained on the filter. If these sources of bias are independent, their effects are additive. However, it is possible that the magnitudes of both biases are related to the composition of the flora being sampled, and that these two relationships are inverse. The loss of chlorophyll through the GF/C filter is proportionally greater in more oligotrophic systems. Conversely, the loss of chlorophyll in the absence of grinding is expected to be greater in nearshore systems where the tough-walled benthic and estuarine forms are more numerous. The information presently available does not allow us to determine whether these effects are independent or to directly evaluate the magnitude of the cumulative effects. We can only estimate that the average negative bias from the true chlorophyll concentration will be somewhere between 8%-15% (if the two effects operate in an inverse fashion) and 23% (if the two effects are additive). Expressing these biases in terms of the observed chlorophyll concentrations, we estimate the expected true value to be between 1.1 and 1.3 times larger than the observed value.

This discussion has primarily considered biases introduced by the adopted procedures. Such biases, if constant, will not distort the basic patterns of chlorophyll in the ocean, or the basic relationships between chlorophyll and other parameters. To the extent that these biases are a function of the phytoplankton composition, and thus not constant, some distortion may occur. However, the spatial variation of chlorophyll over the CalCOFI survey area is often at least a factor of 20 (Owen 1974; Hayward and Venrick 1982), so these biases are unlikely to obscure large-scale patterns. In any case, care must be taken in comparing chlorophyll values from the 1984 CalCOFI program with chlorophyll values derived with other analytical procedures. Since earlier CalCOFI cruises have used GF/C filters, the only bias in the 1984 data relative to past CalCOFI data will be due to the use of the 24-hour extraction procedure, and will be on the order of 8%. The available evidence does not indicate any loss of precision with the selected procedures, except perhaps in the case of prolonged extraction times. More exact determination of precision should be made during the 1984 CalCOFI program.

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COMPARATIVE QUALITY OF ROTIFERS AND COPEPODS AS FOODS FOR LARVAL FISHES

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ABSTRACT

The rotifer *Brachionus plicatilis* and the copepod *Tigriopus californicus* are easily cultured and commonly used as foods for larval fishes. Sizes of rotifers, nauplii, and copepodites, ranging in width from 74 to 221 μm, were related to their weight, volume, and caloric content. Between the smallest and largest size classes—a width increase of two times—rotifer dry weight increased from 0.10 to 0.47 μg/animal, and naupliar dry weight increased from 0.04 to 0.38 μg/animal. An individual rotifer contained more calories than a nauplius of the same width even though the organic tissue fraction of the rotifers had a lower caloric value (4.8 cal/mg) than that of the copepods (5.9 cal/mg). *Tigriopus* nauplii weighed less per unit width and contained more ash than rotifers. These width-specific differences in caloric content should be considered in any bioenergetic study in which rotifers and copepod nauplii are used as foods.

RESUMEN

El rotífero *Brachionus plicatilis* y el copépodo *Tigriopus californicus* son de fácil cultivo y son frecuentemente utilizados como alimento para larvas de peces. Las dimensiones transversales de los rotíferos, nauplios y copepoditos oscilan entre 74 y 225 μm. Estas tallas fueron relacionadas con el peso, volumen y valor calorico respectivo en cada grupo. Entre las tallas más pequeñas y las mayores, si la anchura se duplica, el peso seco de los rotíferos aumenta de 0.10 a 0.47 μg, y el de los nauplios de 0.04 a 0.38 μg por ejemplar. Un rotífero contiene más calorías que un nauplio del mismo ancho, aunque la fraccíon de tejido orgánico del rotífero tiene un valor calórico inferior (4.8 cal/mg) que en los copépodos (5.9 cal/mg). Los nauplios de *Tigriopus* pesaron menos por unidad de anchura y produjeron más cenizas que los rotíferos. Estas diferencias en valor calórico específicas en relación a la dimensión transversal de los organismos, debiera ser consideradas en las estimaciones bionergéticas, cuando rotíferos y nauplios son utilizados como alimento.

INTRODUCTION

In studies of larval fish energetics, it is necessary to know dry weights and caloric values of prey items. We have determined these values for the rotifer *Brachionus plicatilis* and for the nauplii and copepodites of *Tigriopus californicus*, a harpacticoid copepod, as part of a study on effect of diet on growth of larval northern anchovy, *Engraulis mordax*. Rotifers are widely used as food for larval fish in laboratories (Theilacker and McMaster 1971; Solangi and Ogle 1977; Fontaine and Revera 1980; Hunter 1981); harpacticoid copepods are an important food for many larval fish in the field (Mason 1974; Arthur 1976; Schmidt-Moser and Westphal 1980) and are also used as prey in laboratories (Kinne 1977; Kahan et al. 1982; Hunter MS[1]). We cultured *Brachionus* using the methods of Theilacker and McMaster (1971), and *Tigriopus* using the technique followed at the Southwest Fisheries Center, La Jolla, California.

Copepod biomass has been determined with several methods and expressed in different units (Table 1). Copepod total length and prosome length have been used as predictors for both dry and wet weight of Formalin-preserved adults (Pertsova 1967; Grusov and Alekseyeva 1970; Durbin and Durbin 1978; Feigenbaum 1979), Formalin-preserved copepodites (Mullin and Brooks 1967; Durbin and Durbin 1978), and Formalin-preserved nauplii (Durbin and Durbin 1978). Yet width is the dimension that limits fish larvae's selection of prey (Beyer 1980; Hunter 1981), and width is also a more accurate predictor of copepod wet weight than is length (Pearre 1980). Because copepods lose weight when preserved in Formalin (Ahlstrom and Thrailkill 1963; Omori 1970, 1978), and the dry weight lost varies among species (Omori 1970, 1978; Durbin and Durbin 1978), a width-weight relation for fresh samples is needed. Fresh dry weights available for copepods have been related to length (Comita et al. 1966) and to stage (Paffenhöfer 1971), or they have been given as a mean weight for a composite sample of field-collected nauplii and copepodites (Houde and Schekter 1981). The fresh dry weights reported for

[1]Hunter, J.R. Synopsis of culture methods for marine fish larvae. Presented at the Ahlstrom Memorial Symposium, La Jolla, California, August 1983. Manuscript.

TABLE 1
Copepod Weight and Caloric Data

Life stage[1]: 1-naup; 2-cop; 3-cop-V; 4-adults; 5-mixed	Fresh sample	Predictor of weight weight = 1-dry; 2-wet; 3-carbon weight		Caloric content	Ash content	Reference
		Length	Stage			
Individual species						
Acartia clausi	1;2;4	−	1	1	−	−	Durbin & Durbin 1978
Acartia tonsa	1;2;4	−	1	1	−	−	Heinle 1966
Calanus cristatus	3;4	−	1;2	1;2[2]	−	+	Omori 1970
Calanus finmarchicus	3;4	+	−	1	+	+	Comita & Schindler 1963
Calanus finmarchicus	3;4	+	1	1	+	−	Comita et al. 1966
Calanus helgolandicus	5	+	−	−	+	−[3]	Slobodkin & Richman 1961
Calanus helgolandicus	1;2;4	+	−	3	−	−	Mullin & Brooks 1970a; 1970b
Calanus helgolandicus	1;2;4	+	−	3	−	−	Paffenhöfer 1971
Calanus pacificus	1	+	−	3	−	−	Fernandez 1979
Centropages typicus	2	−	−	1;3	+	+	Razouls 1977
Rhincalanus nastus	2	−	1;3	−	−	−	Mullin & Brooks 1967
Rhincalanus nastus	2	+	−	3	−	−	Mullin & Brooks 1970a
Temora stylifera	2	−	−	1;3	+	+	Razouls 1977
Tigriopus californicus	5	+	−	−	+	−[3]	Slobodkin & Richman 1961
Individual genus						
Pseudocalanus	1;2;4	−	1	1;3	+	+	Corkett & McLaren 1978[4]
Many species treated individually						
	4	−	1	−	−	−	Conover 1959
	3;4	+	−	1	−	−	Conover 1960
	2;4	−	2	2	−	−	Pertsova 1967
	2;4	−	2	2	−	−	Krylov 1968
	3;4	−	2	2	−	−	Grusov & Alekseyeva 1970
	1;2;4	?	−	1	−	−	Hargrave & Geen 1970
	4	−	−	−	+	+	Laurence 1976
	3;4	+	1;3	−	−	+	Omori 1978
	1;2	+	1	−	−	−[3]	Breteler et al. 1982
Unidentified copepods or mixed samples						
	5[2]	+	−	−	−	−	Beers 1966
	5	−	1	−	−	−	Feigenbaum 1979
	5[5]	+	−	−	−	−	Houde & Schekter 1981
	5[6]	−	−	−	−	−	Hanson et al. 1982

[1]Cop = copepodite; cop-V = stage V copepodite
[2]Copepod carbon content is given as a percentage of dry weight
[3]Ash content is corrected for, but not given
[4]Review paper
[5]Copepod dry weight is related to mesh size used for sample (see text)
[6]Mean dry weight is given

rotifers (Theilacker and McMaster 1971; Doohan 1973; Eldridge et al. 1977) were given as averages for laboratory populations, and they do not reflect size-specific weight.

Not only is dry weight lower after Formalin pres-ervation, but significant amounts of carbon and nitrogen are also lost from copepod tissues (Durbin and Durbin 1978; Omori 1978). Thus, calorimetric measurements are most accurately performed on fresh samples. Calorimetric values are available for fresh

samples of adult calanoid copepods (Slobodkin and Richman 1961; Comita and Schindler 1963; Comita et al. 1966) and adult harpacticoids (Slobodkin and Richman 1961). No information was available on the width-specific dry weight and caloric content of fresh samples of rotifers, copepod nauplii, and copepodites that are commonly used as foods for larval fishes.

METHODS

Preparation of Rotifers

We harvested rotifers from cultures and placed them overnight in a one-liter cylinder containing seawater and algae. This procedure allowed debris to settle and insured that the rotifers were in a good nutritional state when sampled. Thus the nutritional characteristics of the rotifers when dried and weighed should be comparable to their state when used as food. We siphoned debris-free rotifers through a series of nitex screens (ranging in size from 44 μm to 194 μm), retaining samples in which the major component was animals of a single width class (Table 2). Pure samples ($n = 3$) were obtained for the 74-110 μm rotifer width class, but the other sieved samples ($n = 25$) were slightly contaminated by rotifers from adjacent size classes. For these samples, an aliquot was counted to estimate total numbers (the coefficient of variation for the aliquots was between .17 and .20) and numbers belonging to each width class. Next, we poured a volume containing 2,500-5,000 animals (usually about 30 ml) onto a preweighed Nucleopore filter (Durbin and Durbin 1978). To eliminate salt crystals, we rinsed the samples with 30 ml of isotonic ammonium formate (3.4%), which sublimates when heated, leaving no residue. Blanks of seawater and ammonium formate were run through filters and used to correct the final weights.

We estimated width-specific dry weight of the rotifers belonging to the three slightly contaminated width classes by using a multiple regression ($y = a_1x_1 + a_2x_2 + a_3x_3$) in which y was the total dry weight of the sample, x_1, x_2, and x_3 were the relative frequencies of the width classes, and a_1, a_2, and a_3 were the width-specific average dry weights (Draper and Smith 1966). We used the midpoint of the width range for the four width classes and corrected the total weight for the frequency of eggs, assuming egg weight was the same as the weight of the smallest rotifer, 0.10 μg, which agrees with an unpreserved egg weight of 0.092 μg determined for the same species by Doohan (1973).

Preparation of Copepods

Copepods were difficult to sieve because the appendages of the live animals caught on the mesh of the nets. Thus carapace width was not the limiting factor

TABLE 2
Prey Characteristics

Prey	Width class μm	Dry[1] weight μg (SE)	Volume ×10⁶μm³	Caloric value ×10⁻³ cal
Brachionus plicatilis (4.4 cal/mg)[2]				
Rotifers	74-110	0.10 (.01)	0.65	0.44
	110-147	0.22 (.04)	1.73	0.97
	147-184	0.41 (.06)	2.96	1.80
	184-195	0.47 (.08)	3.99	2.07
Tigriopus californicus (4.9 cal/mg)[2]				
Nauplii	74-110	0.04 (.01)	0.20	0.20
	110-147	0.13 (.01)	0.55	0.64
	147-184	0.25 (.01)	1.17	1.23
	184-195	0.38 (.00)[3]	1.77	1.86
Copepodites				
	147-184	0.63 (.15)	3.38	3.09
	184-221	1.20 (.26)	6.21	5.88

[1]Regression coefficients are used for average dry weights.
[2]Caloric value for total tissue dry weight; see text.
[3]<0.01.

in sieving. We found that anesthetizing the animals with dilute MS222 (0.06% MS222 in seawater) relaxed the appendages and permitted more effective sieving. The anesthetized animals were quickly revived in sea water. We rinsed sieved animals in ammonium formate solution and hand sorted them to width classes (Table 2) on a slide, forming nauplii and copepodites into piles of 200 to 400 animals. We sieved and sorted 10 copepod samples. Five of the sorted samples were composed of a single size (width) class, and the remaining samples were of two size groups. To estimate size-specific weights for copepods, we followed the same multiple regression procedure used for rotifers.

We placed slides of copepods and Nucleopore filters with rotifers in a 60°C oven and dried them overnight to constant weight (Lovegrove 1966). We then removed the piles of copepods from the slides by using a single-edged razor blade and weighed the copepod samples, as well as the rotifer samples with filters, on a Cahn electrobalance to ± 2 μg.

Calculation of Rotifer and Copepod Volumes

Rotifers and nauplii have similar length-width ratios, but they differ in body form and thus in volume. We approximated rotifer volumes as ellipsoids, naupliar volumes as oblate spheroids (dorsoventrally compressed spheres), and copepodite volumes as the sum of a dorsoventrally compressed and elongated ellipsoid (for the prosome or cephalothorax) plus a cylinder (for the urosome or abdomen). After measuring each dimension of individual animals ($n = 30$ for each width class) to find the relative ratios of the dimensions, we calculated

volumes using the midpoint of the width range (Table 2).

We used a Phillipson oxygen microbomb calorimeter to measure caloric content; samples weighed from 2 to 4 mg. Ash was estimated by incinerating dried specimens at 525°C overnight. We hand sorted about 10,000 nauplii and 1,000 copepodites for each calorimetric and ash determination.

RESULTS AND DISCUSSION

Rotifer Dry Weight and Caloric Value

Rotifer dry weight estimates range between 0.10 and 0.47 μg, depending on body width (Table 2). To compare these estimates with the fresh dry weights of B. plicatilis given as averages for laboratory populations (Theilacker and McMaster 1971; Doohan 1973; Eldridge et al. 1977), we calculated an average weight using the width-specific weights determined in this study and Theilacker and McMaster's (1971) width-frequency information. The calculated average weight, 0.20 μg, was similar to the average weight of 0.16 μg reported by Theilacker and McMaster (1971). Doohan (1973) also obtained a mean individual dry weight of 0.158 μg. The estimate given by Eldridge et al. (1977) was 0.905 μg, twice the weight of rotifers in our largest width class (Table 2). They observed a large number of egg-bearing females in their samples and did not adjust for egg weight, which may partially explain this weight difference.

We used ash content of 7.8 ± 2.0% dry weight in our expressions of ash-free caloric content (Table 3). Watanabe et al. (1983) give data for B. plicatilis from which we calculated a somewhat lower ash content (5.32 ± 1.83% dry weight, $n = 2$). Theilacker and McMaster's (1971) estimated caloric value for Brachionus was 5.3 ± 0.1 cal/mg ash-free dry weight, and we found a caloric value of 4.8 ± 0.3 cal/mg ash-free dry weight (Table 3). This variation in

ash-free caloric values may simply reflect differences in ash content. Apparently, weight and caloric content among Brachionus cultures maintained at the La Jolla laboratory have varied slightly over the years.

Copepod Dry Weight and Caloric Value

Naupliar dry weights ranged from 0.04 to 0.38 μg, and the weight increase was nearly proportional to the cube of the width. Copepodites weighed 2.5 to 3 times a nauplius of corresponding width (Table 2). Average dry weights given in Houde and Schekter (1981) for sieved samples of nauplii and copepodites were 0.15 μg per animal for the 53-110 μm fraction and 0.51 μg per animal for the 110-280 μm fraction. These width-weight estimates appear similar to ours (Table 2), but they are difficult to compare because the size component collected by sieving is not necessarily delimited by the sieve sizes used.

Assuming no between-culture differences, we averaged the caloric and ash values for each of the three copepod stages. The average caloric content of the organic fraction of Tigriopus adults and the young stages is similar, about 5.9 cal/mg (Table 4), and comparable to the 5.5 cal/mg reported for Tigriopus by Slobodkin and Richman (1961) and to the 5.6 cal/mg average for seven calanoid copepods given by Laurence (1976). (Laurence's values may be low because he used Formalin-preserved samples.) The value we

TABLE 3
Caloric and Ash Values

	n	% ash	(SD)	n	Calories/mg ash-free dry wt.	(SD)
Brachionus plicatilis						
Rotifers	7	7.8[1]	(2.0)	3	4.8	(0.3)
Tigriopus californicus						
Nauplii	2	16.2	(3.5)	3	5.8	(0.5)
Copepodites	2	17.0	(1.4)	2	6.0	(0.4)
Adults	2	7.3	(0.9)	2	5.9	(0.4)

[1]Theilacker and McMaster, 1971.

TABLE 4

Parameters (SE) for Nonlinear Equations ($y = a\ x^b$) for Estimating Rotifer or Copepod Dry Weight $(y)^1$ from Width, and Linear Equations ($y = a + bx$) for Estimating Dry Weight from Volume

Prey	n	Width[2] a	b	r^2	Volume[3] a	b	r^2
Brachionus plicatilis							
Rotifers	4	$1.4 \times 10^{-5}(2.1 \times 10^{-5})$	2.00 (0.29)	.970	0.029 (.033)	0.116 (.013)	.977
Tigriopus californicus							
Nauplii	4	$9.2 \times 10^{-8}(6.6 \times 10^{-8})$	2.90 (0.14)	.997	—	—	—
Nauplii and copepodites	6	—	—	—	0.020 (0.13)	0.189 (0.004)	.998

^1y = dry weight (μg).
^2x = width (μm).
^3x = volume × 10^6 μm^3.

used to estimate caloric equivalents of individual prey (Table 2) is based on total tissue dry weight, i.e., organic plus ash weight, and is less for young stages because they have a relatively high inorganic (ash) content (Table 3). Young copepod stages have a higher ash content than the adults because the carapace imparts the greatest proportion of the ash weight, and the ratio of carapace weight to tissue weight is larger for small organisms. Our data also showed that females carrying egg sacs contained more ash than non-egg-bearing females and males (10.4% as compared to 7.3%), presumably because of the increased numbers of embryos in the sample. Razouls (1977) found the ash-free caloric value was higher for copepodites than adults, but her values are for preserved specimens and may not be comparable.

Regressions of dry weight (y) and body width (x) gave a good fit for both rotifer and nauplii data (Figure 1); estimates of the parameters for the dry weight and body width equations are given in Table 4. Although the dry weight (y) is subject to sampling error because it was estimated from a multiple regression (see Methods), its use to produce the dry weight and body width equations should be of little concern because the errors were negligible (Table 2). The equations given in Table 4 can be used to predict rotifer and naupliar dry weight from measurements of body width. We did not include an equation for the copepodites because we had only two points, but it is clear that at any given width a copepodite has a greater dry weight and caloric content than a rotifer, and a rotifer has a higher dry weight and caloric content than a nauplius.
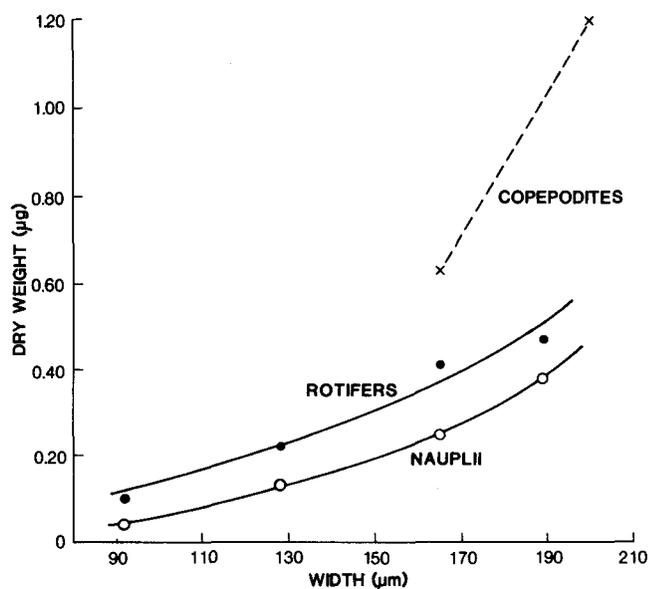
Rotifer and Copepod Volumes

Zooplankton biomass is often estimated using volume approximations (reviewed by Beers 1976), and the relations between copepod wet weight and volume are summarized by Pearre (1980). Because prey volumes are relatively easy to measure and have been used in feeding studies of marine fish (Sumida and Moser 1980), we related our dry weight measurements to estimated volumes and included equations for predicting dry weight for a given volume (Tables 2 and 4; Figure 2).

Copepod stages have a higher dry weight (and caloric content) than rotifers of the same volume (Figure 2). This may be due to unlike water content or to unlike densities, owing in part to dissimilarities in the weight or composition of their respective integuments. The average ash content of nauplii and copepodites was 16.2% and 17.0% as compared to rotifers, which had an assumed ash content of 7.8% (Table 3).

CONCLUSIONS

For any given width, rotifers have a higher caloric content than *Tigriopus* nauplii. First-feeding fish eating the smallest rotifers get twice as many calories per bite as they do eating *Tigriopus* nauplii of the same width (Table 2). Many first-feeding fish larvae select prey from the smallest size classes, yet older larvae eat prey belonging to all size classes. As a result, variation in estimated daily consumption by larval fish may be caused in part by the differences between the weight estimate for the average prey item and the actual weight of the item eaten. Clearly, an error in estimating food consumption can also result from

Figure 1. Relations between dry weight (µg) and body width (µm) for the rotifer *Brachionus plicatilis* and the copepod nauplii of *Tigriopus californicus*. Estimates of parameters for equations are in Table 2.
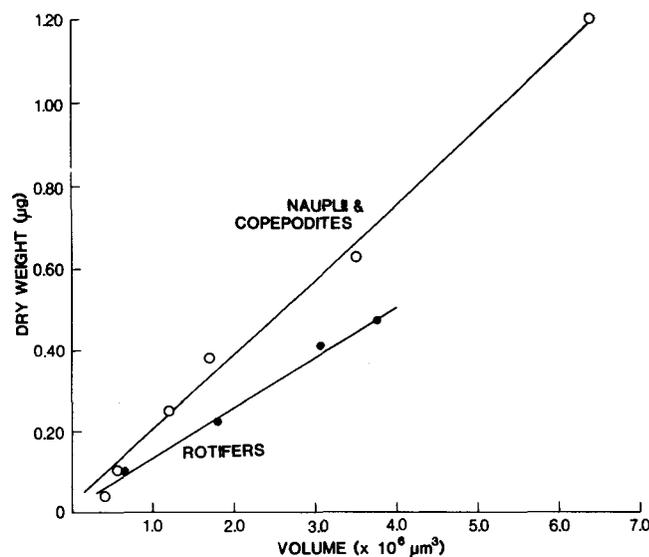
Figure 2. Relations between dry weight (µg) and volume of the rotifer *Brachionus plicatilis* and copepod *Tigriopus californicus*. Estimates of parameters for equations are in Table 2.

ignoring specific differences in caloric content among prey organisms.

Regressions of the width-weight measurements can be used to predict the dry weight of rotifers and nauplii of known width. The copepod width-weight model probably cannot be used for weights of calanoid life stages because calanoid nauplii are shaped more like an ellipsoid and thus would weigh more than dorsoventrally compressed harpacticoid nauplii of corresponding width. The copepod volume-weight model may be applicable to calanoid life stages.

ACKNOWLEDGMENTS

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VARIATION IN LARVAL MORPHOGENESIS WITHIN THE SOUTHERN CALIFORNIA BIGHT POPULATION OF *EUPHAUSIA PACIFICA* FROM WINTER THROUGH SUMMER, 1977-1978

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ABSTRACT

Two dominant pathways of pleopod development were observed among young furciliae of *Euphausia pacifica* during the winter-summer of 1977-78, within the population of the Southern California Bight. The larvae that progressed through the shorter, more direct pathway, with one instar per stage within furcilia stages I and II, were generally most abundant in spring and early summer, when environmental conditions appeared optimal for larval development. The larvae that progressed through the longer pathway, with two instars within stage II and often within stage I, were generally most abundant during winter and late summer, when environmental conditions appeared suboptimal. The degree of variation, apparently induced by environmental change during the nine-month survey period, suggests that patterns of pleopod development should not be used to characterize populations of *Euphausia* species without prior study of spatial and temporal variability in larval development across the range of a species. The apparent restriction of the capacity for marked variation in *Euphausia* pleopod development to one of three species groups, group III, supports the subgeneric classification based on adult morphology.

RESUMEN

Se observó dos vías principales en el desarollo de los pleópodos en furcilias juveniles de *Euphausia pacifica* durante el periodo invierno 1977-verano 1978, perteneciente a la población presente en la Bahía del Sur de California. Las larvas que siguieron la vía de desarollo más breve y directa, con una muda por estadío entre los estadíos furciliares I y II, fueron más abundantes en la primavera y comienzos de verano. En este período, las condiciones ambientales asociadas con el régimen estacional de surgencia parecían óptimas para el crecimiento y desarollo larvario. Las larvas que siguieron la vía de desarollo larga, con dos mudas durante el estadío II, y frecuentemente durante el estadío I, fueron más abundantes durante el invierno y a fines del verano cuando las condiciones ambien-

tales parecían subóptimas para el desarollo larvario. El grado de variación dentro de la población de *E. pacifica* en la Bahía del Sur de California, aparentemente inducido por cambios ambientales durante los nueve meses estudiados, sugiere que los patrones de desarollo de los pleópodos no deberían ser usados en la caracterización de poblaciones de *Euphausia* sin un estudio previo de la variabilidad espacial y temporal del desarollo larvario para cada especie. La aparente restricción de la capacidad para marcada variación en el desarollo de los pleópodos, dentro del género *Euphausia*, a uno de los tres grupos de especies, Grupo III, apoya su previa clasificación subgenérica basada en morfología adulta.

INTRODUCTION

The course of larval development within the crustacean family Euphausidae is generally well known (Gurney 1942; Mauchline and Fisher 1969; Mauchline 1980). There are three larval phases during ontogeny, and within phases one (nauplius) and two (calyptopis) the developmental sequence appears to be similar for all members of a species. In the third (furcilia) phase, however, there may be conspicuous variation in the addition and development of the five pairs of abdominal swimming appendages, or pleopods. The pleopods are added in sequence from anterior to posterior abdominal segments, with each pair appearing first as nonsetose rudiments which become setose and functional at the next molt (Fraser 1936; Mauchline and Fisher 1969). A larva may progress, for instance, during the course of three consecutive molts, from the final calyptopis stage, without pleopods, first to a form with 2 pairs of nonsetose pleopods, next to a form with 2 pairs of setose and 3 pairs of nonsetose pleopods, and finally to a form with the total complement of 5 pairs of setose pleopods.

The degree of pleopod development is a primary feature used to characterize the early furcilia stages of a species. Both number and relative abundance of forms within a stage may vary with respect to pleopod state, and the dominant forms in successive furcilia stages are presumed to indicate the most common pathway of development within a population (Fraser

1936). Both spatial and temporal variability in this aspect of euphausiid ontogeny have been discussed by, among others, Brinton and Townsend (in press), Makarov (1974), Makarov and Maslennikov (1981), and Mauchline (1980), who made the following observation: "A taxonomic group of species probably has a dominant pathway of development which is optimal for these species . . . and is used under optimal or near optimal environmental conditions for these species. When environmental conditions change, for example, later in the breeding season, and become less optimal for the species, the pathway of development changes in response to these conditions. This 'variant' pathway is probably not optimal for the species except possibly under the suboptimal environmental conditions."

Within the genus Euphausia, more than half of the described species—members of groups I and II of the three species groups established by Brinton (1975)—show little or no variation in this phase of larval development; members of group III may exhibit a variety of forms and dominant pathways. Endo and Komaki (1979) described the relative abundance of pleopod forms among furciliae in the Sea of Japan population of group III E. pacifica. The dominant forms and pathway of development differed from those previously described in the southern California population of the species (Boden 1950), and it appeared that the discrepancy might be evidence of intraspecific difference between the populations. The present study was prompted by the analysis of a sample of Southern California Bight E. pacifica larvae which showed a shift in dominant pathway of pleopod development from the one in Boden's sample. The appearance of two dominant pathways within one population of E. pacifica suggested that the apparent difference between the Japan Sea and southern California populations might be within the range of variation induced in this species by environmental change.

Euphausia pacifica inhabits the subarctic and transition zones of the North Pacific and ranges south in the California Current to 25°N (Brinton 1962a, 1967a, 1973). The biology of the population south of Point Conception, in the region of the Southern California Eddy, has been studied by Brinton (1976). He described the eddy as a reproductive refuge for this warm-temperate population, in which there is continuous larval recruitment of variable intensity. The maxima in spawning and recruitment coincide with events associated with seasonal upwelling in the area.

A study of the distribution of euphausiids in the California Current during the warm winter–spring of 1977-78 (Brinton 1981) found the southern California population of E. pacifica both diminished and re-

tracted northward in the winter, when ocean temperatures were 1°–2°C above average. The species became increasingly dense from May to July, apparently in a reproductive response to the development of coastal upwelling, and resumed its usual predominance among larger zooplankton in the area.

I selected the December 1977-August 1978 season for a study of variability of pleopod development during the furciliar phase within the Southern California Bight population of E. pacifica. It seemed likely that, if such variation were environmentally induced, a large number of forms within the genetic repertoire of the species might be expressed in response to the relatively wide range of environmental conditions during this period. The purpose of this paper is (1) to explore the type and extent of temporal variation in form of young furciliae, and (2) to compare the pattern of morphological variation with seasonal change in the larval environment and in abundance.

METHODS

For his investigation of the population biology of southern California E. pacifica, Brinton (1976) delimited a study area south of Point Conception. The area is subdivided into inshore and offshore halves: the inshore portion is strongly affected by the coastal upwelling regime; the offshore section tends to be influenced by the southerly flow of the mainstream of the California Current. I selected the inshore area for the present study (Figure 1) because of the almost continuous presence of young larvae in these waters. A distributional atlas of euphausiid growth stages off southern California from 1953-56 (Brinton and Wyllie 1976) showed young (3-4 mm) furciliae of E. pacifica to be present 80%-100% of the time at inshore stations.

Zooplankton was collected at 27-33 stations within the study area during each of seven CalCOFI surveys of December 1977-August 1978 (Figure 1). Samples were obtained with two 0.71-m diameter bongo nets, one with a mesh width of 333 μ and the second of 505 μ, towed obliquely from 200 m; the cod ends of both nets were of 333-μ mesh. The euphausiids in all of the 505-μ net night samples from these surveys were identified and enumerated by E. Brinton and A. Townsend in the course of their research, and they have permitted me to use their unpublished data to calculate the average number/1000 m^3 per station of E. pacifica larvae less than 4.5 mm in total body length for each survey. The sampling, subsampling, and counting procedures are discussed, and estimates of sampling and counting variability provided, by Brinton (1979, 1981) and Brinton and Townsend (1981). The numbers of young larvae were grouped,
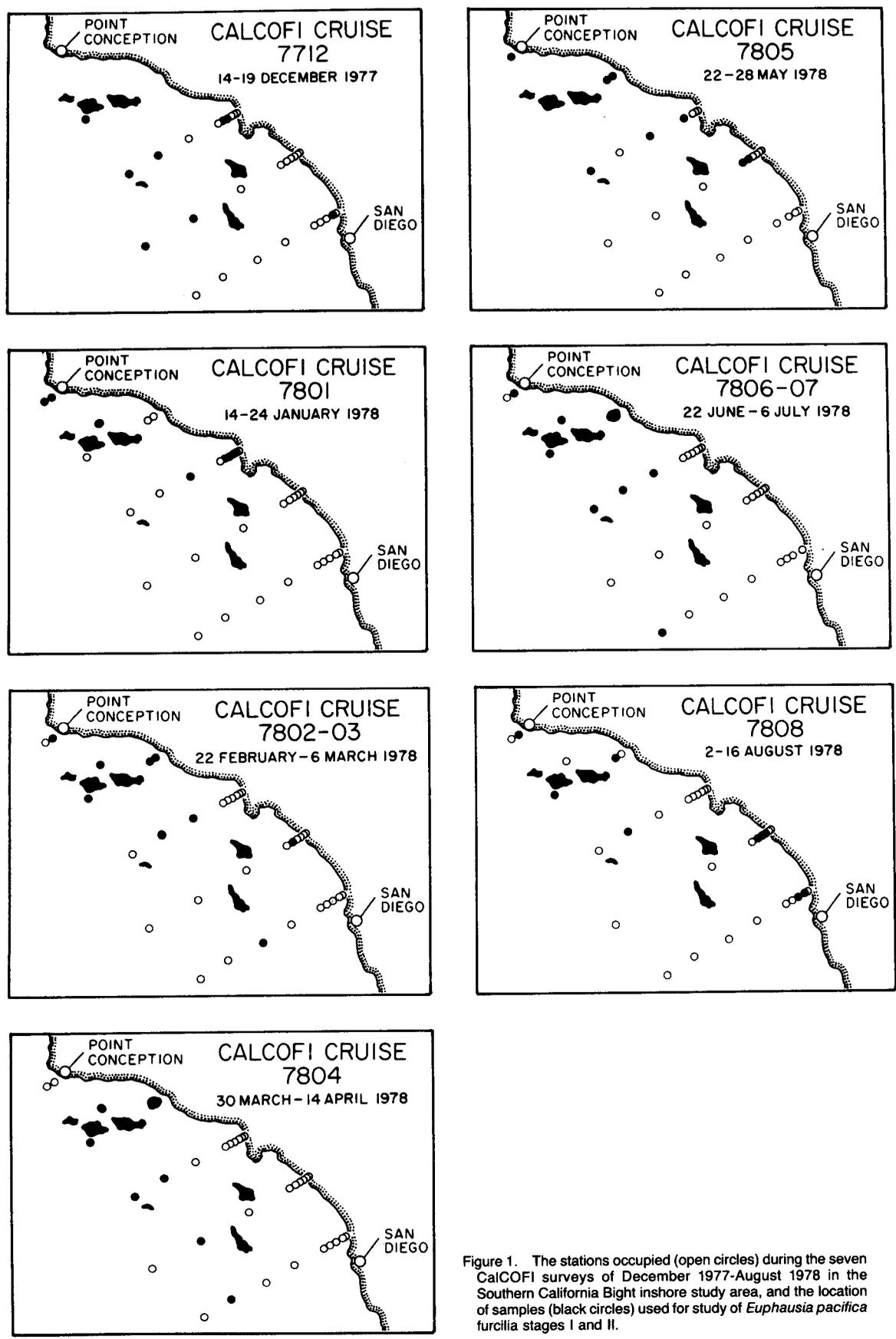
Figure 1. The stations occupied (open circles) during the seven CalCOFI surveys of December 1977-August 1978 in the Southern California Bight inshore study area, and the location of samples (black circles) used for study of *Euphausia pacifica* furcilia stages I and II.

when measured, by 1-mm increments of total body length, including the following stages: 1-2 mm, calyptopis stages I-III and a very few furcilia stage I; 3 mm, furcilia stages I-II; 4 mm, furcilia stage II and older larvae (A. Townsend, pers. comm., and author's data). Although absolute abundance of larvae smaller than 3 mm may be underestimated by a net with 505-μ mesh, the temporal change in relative abundance may be used as a measure of the recruitment of resident species to a population (Brinton and Townsend 1980).

For this study, the number of pairs and state (nonsetose or setose) of pleopods on *E. pacifica* furciliae with fewer than 5 setose pairs were counted in 8-9 samples from each of the seven surveys (Figure 1); 25%, 50%, or 100% of the sample was examined, depending on the density of larvae. If only one pleopod was present on an abdominal segment, it was counted as a pair; it was often difficult to determine whether the asymmetry was due to absence or breakage of the appendage. Both day and night samples were counted because the bulk of the larvae of *E. pacifica*, and most probably the young furciliae lacking a full complement of setose pleopods, remain above 150 m (Brinton 1967b; Youngbluth 1976).

I have followed Boden (1950) in assigning the various larval forms of *E. pacifica* to furcilia stages I (FI) and II (FII) and have added the pleopod state in parenthesis to describe the forms within each stage (Table 1). A pair of nonsetose (ns) pleopods is indicated by the symbol ', a pair of setose (s) pleopods by '': for instance, a form with 2 pairs of setose and 3 pairs of nonsetose pleopods in furcilia stage II would be described as FII(2''3').

In presenting the data, I subdivided stage FII (s + ns) into forms with 5 pairs of pleopods and those with fewer than 5 pairs, which would require at least one more instar within furcilia stage II to achieve stage III, a form with 5 pairs of setose pleopods. There may

be one or more instars in both stages FI and FII, and in predicting the pathway of pleopod development I assumed that a pair of nonsetose pleopods appears on an abdominal segment at one molt and becomes setose at the subsequent molt (Fraser 1936; Endo and Komaki 1979; Mauchline 1980). The various pathways of pleopod development may be inferred from Table 1. A calyptopis III larva, without pleopods, may molt to a form of furcilia I with 0-5 pairs of nonsetose pleopods; the form selected is presumed to place certain limits on the ensuing forms. For example, an FI larva with 3 pairs of nonsetose pleopods might develop by the following pathways requiring 3 and 2 molts, respectively, to achieve the stage III condition:

FI(3')—FII(3''1')—FII(4''1')—FII(5'')
FI(3')—FII(3''2')—FIII(5'').

The total body lengths of the dominant forms in furcilia stages I(ns) and II(s + ns) were measured in dorsal view along the midline from the anterior margin of rostral plate to the posterior margin of telson excluding terminal spines. The larvae were measured, to the nearest 0.04 mm, by ocular micrometer with the 25 × objective of a stereomicroscope. The average lengths of the dominant forms are based on the sum of measurements of individuals from surveys of January, February/March, May, and June/July 1978.

Seasonal change in the larval environment was represented by the temporal variation in temperature (°C) at 10 m, representative of the mixed layer and hence of the larval habitat (Brinton 1979), and in surface chlorophyll *a* (μg/l). Measurements of surface chlorophyll are believed to correlate significantly with integrated chlorophyll and primary production in the euphotic zone of the California Current (Peláez and Guan 1982).

The percent similarity index (PSI), which expresses the degree to which one sample resembles another with respect to proportions of species (McGowan and Miller 1980), was used to determine the degree of similarity between the percent frequency distributions of pleopod forms within stages FI and FII in the seven survey samples, and the samples of *Euphausia pacifica* described by Boden (1950) and Endo and Komaki (1979). PSI values range from 0 (no forms in common) to 100 (all forms in common with identical proportions), and in these comparisons PSI values > 60 were believed to indicate a strong similarity between samples.

Seasonal patterns of variation in dominant larval forms, numbers of larvae, temperature, and chlorophyll *a* in the inshore area were compared using ranked values for each category. The agreement between pairs and sets of ranks was assessed using Kendall's tau coefficient of correlation and coefficient of concordance W (Tate and Clelland 1957).

TABLE 1
Symmetrical States of Pleopod Development within Furcilia Stages I and II

Furcilia I		Furcilia II					
(0)	(ns)	(s + ns)					= 5 pairs
		<5 pairs					
<u>0</u>	1'	1''	<u>1''1'</u>	1''2'	1''3'		<u>1''4'</u>
	<u>2'</u>	2''	2''1'	2''2'			2''3'
	<u>3'</u>	3''	<u>3''1'</u>				<u>3''2'</u>
	<u>4'</u>	<u>4''</u>					<u>4''1'</u>
	5'						

The underlined forms were present in the Southern California Bight population of *Euphausia pacifica* within the inshore study area during December 1977-August 1978.
' = pair nonsetose (ns) pleopods, '' = pair setose (s) pleopods.

TABLE 2
Percent Similarity Indices for the Frequency of Pleopod Forms within Furcilia Stages I and II
in the 1977-78 Southern California Bight Population of *Euphausia pacifica*

FI	January	February/March	April	May	June/July	August
December	90.05	42.10	52.30	61.20	27.95	80.85
January	—	41.05	51.25	62.15	25.40	81.80
February/March		—	89.80	49.70	79.35	57.95
April			—	47.10	74.15	63.15
May				—	34.65	66.85
June/July					—	38.90

				Mean	Median	Range
Within group A (February/March, April, June/July)				81.10	79.35	74.15-89.90
Within group B (December, January, May, August)				73.95	73.85	61.20-90.95
Between groups A and B				44.29	44.60	25.40-57.95

FII	January	February/March	April	May	June/July	August
December	88.85	37.40	48.50	71.85	24.00	79.15
January	—	29.55	45.25	69.70	17.15	74.90
February/March		—	67.40	36.25	83.70	45.85
April			—	45.45	54.90	55.05
May				—	21.65	85.30
June/July					—	31.25

				Mean	Median	Range
Within group A (February/March, April, June/July)				68.67	67.40	54.90-83.70
Within group B (December, January, May, August)				78.29	77.03	69.70-88.85
Between groups A and B				36.45	36.85	17.15-55.05

RESULTS

Temporal Variation in Form within Furcilia Stages I and II

There was temporal variation both in dominant pathways of pleopod development and in the number of forms in furcilia stage II within the inshore population of *E. pacifica*. The percent frequencies of pleopod forms within stages FI and FII in samples from the seven CalCOFI surveys from December 1977–August 1978 are shown in Figure 2. I calculated percent similarity indices (PSI) for these frequency distributions (Table 2), and distinguished two groups—A (February/March, April, June/July) and B (December, January, May, August)—in which the indices were more similar between members of a group than between members of different groups. The mean PSI was considerably higher within than between survey groups in stages FI and FII. Within group A, the PSI between April and June/July surveys in stage FII was relatively low because of the abundance of form FII(1''4'), and within group B the May survey was least similar to the other surveys in stage FI because of the abundance of forms FI(3') and (4').

The mean percent frequency of pleopod forms for survey groups A and B is presented in Table 3. Features characterizing furcilia stages I and II within the two groups are summarized in Table 4.

The relative abundance of forms in group A indicated that most larvae required only two instars to advance through furcilia stages I and II to the stage III form having 5 pairs of setose pleopods, and that FI(2')–FII(2''3') and FI(1')–FII(1''4') were the dominant and subdominant pathways of pleopod development. The abundance of forms within group B, on the other hand, indicated that most larvae required at least two instars within stage II to achieve stage III, and that FI(1')–FII(1''3')–FII(4''1') was the most common pathway. Two instars were often required within stage FI also, in the B surveys, with FI(0) preceding FI(ns) to progress, probably, to FI(3') or FI(4'). The mean percent frequency for the seven surveys (Figure 2) illustrates the degree of variability, with respect to the number of forms expressed within each stage, and the two dominant developmental modes within the population, FI(2')–FII(2''3') and FI(1')–FII(1''3')–FII(4''1').

The total body lengths of *Euphausia pacifica* furciliae in the two dominant pathways of pleopod development are presented in Table 5. The growth factors (expressed as mean size in stage divided by the size in preceding stage) at the molt from FI–FII in pathways A and B, and from instar 1–2 with FII in the B pathway, are compared in Table 6. Average total length and average growth factor are larger among larvae in the more direct A pathway. There is a significant difference ($p = < 0.01$) between mean body lengths of forms FI(1') and FI(2') and between FII (1''3') and FII(2''3') presumed to be comparable instars.
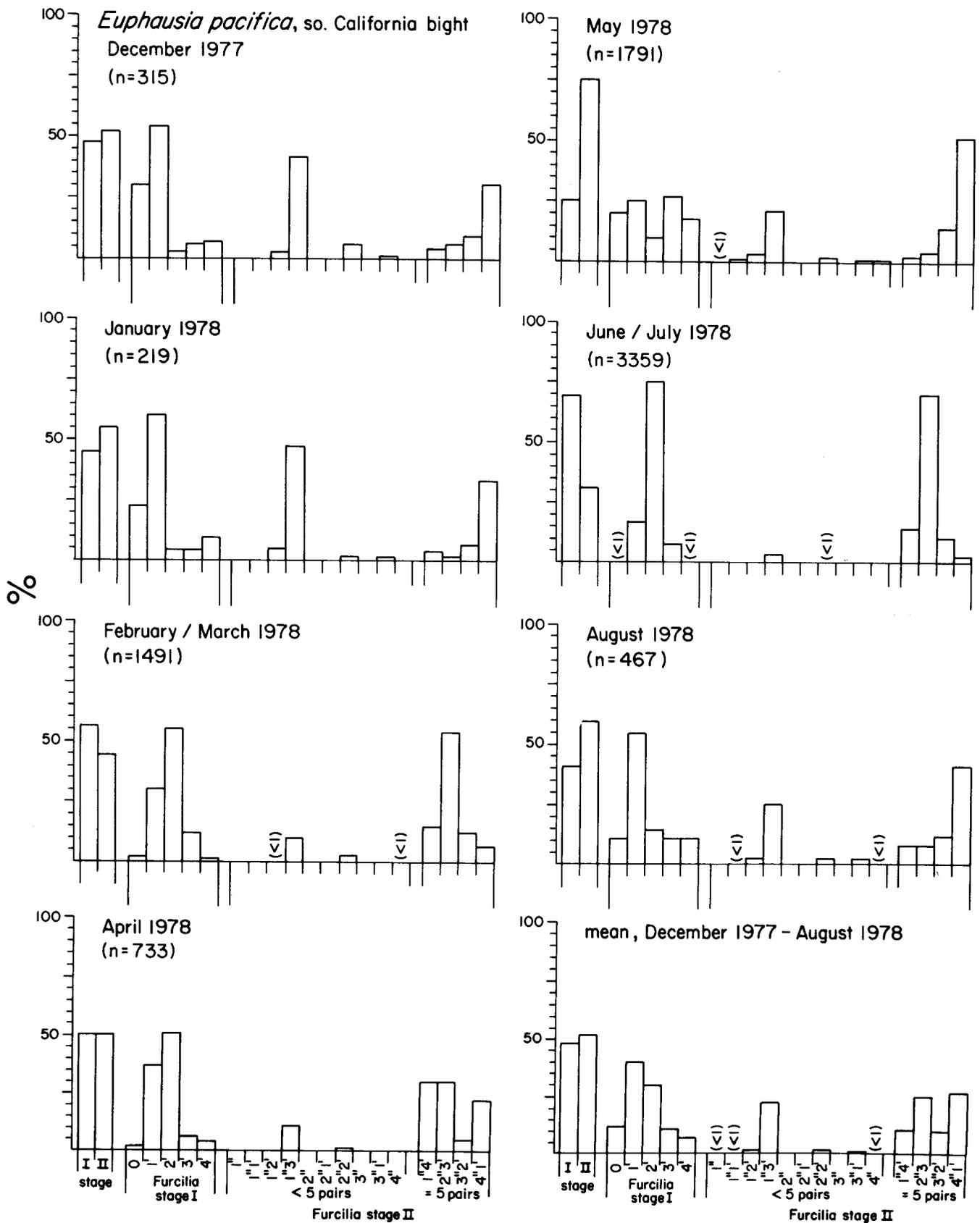
Figure 2.   The relative abundance of furcilia stages I and II and percent frequency of pleopod forms within each stage in the Southern California Bight population of *Euphausia pacifica* sampled by seven CalCOFI surveys.

TABLE 3
Percent Frequency of Pleopod Forms within Furcilia Stages I and II of *Euphausia pacifica* in Survey Groups A and B

Stage	Pleopod Form	Group A (Feb./Mar., Apr., June/July)		Group B (Dec., Jan., May, Aug.)	
		Mean	Range	Mean	Range
FI	0	1.3	0.2- 1.9	20.6	10.5-29.6
	1'	28.0	16.9-36.8	48.2	25.0-60.2
	2'	60.3	51.0-75.2	7.8	3.3-14.1
	3'	8.6	6.0-12.3	12.0	4.1-27.1
	4'	1.7	0.1- 4.4	11.3	7.2-18.3
FII					
<5 pairs					
	1''	0	0	<0.1	0 - 0.1
	1''1'	0	0	0.3	0 - 0.8
	1''2'	<0.1	0 - 0.1	3.3	2.5- 5.0
	1''3'	8.0	2.9-11.2	33.6	20.9-47.1
	2''2'	1.4	0.4- 2.6	2.6	1.6- 5.5
	3''1'	0	0	1.5	1.0- 2.2
	4''	<0.1	0 - 0.1	0.3	0 - 0.7
=5 pairs					
	1''4'	19.8	14.2-30.3	4.6	2.4- 8.0
	2''3'	51.4	30.3-70.1	4.6	1.6- 7.6
	3''2'	9.1	4.9-12.2	10.2	5.8-13.7
	4''1'	10.4	2.3-22.4	39.1	30.7-52.0
No. larvae		5583		2792	

Temporal Variation in Dominant Forms within Furcilia Stages I and II in Relation to the Environment and Larval Abundance

Temporal fluctuation in dominant pathways of pleopod development, depicted by the change in percent frequency of form FI(2') within stage FI representing the A pathway, was compared with coincident changes in (1) mean and range of temperature and chlorophyll *a* values in the larval environment, and (2) mean number/1000 m³ of larvae 1-2, 3, and 4 mm in body length in the inshore study area (Figure 3).

The mean temperature was 1°-2°C above the seasonal average from December to May, and average during the June/July and August surveys (Brinton 1981). The maximum chlorophyll *a* values increased with the onset of coastal upwelling, and both maximum and mean values peaked, along with the temperature minimum, in June/July (Figure 3a). There was a significant negative correlation between ranked mini-

TABLE 4
Features Characterizing Furcilia Stages I and II in Survey Groups

Stage	Survey group	
	A	B
FI(0)	0.2-2% of FI	11-30% of FI
FI(ns), Dominant form	FI(2')	FI(1')
FII(s+ns), No. of forms	6-8	8-11
No. with <5 pairs of pleopods	3-13% of FII	28-55% of FII
Dominant form	FII(2''3')	FII(1''3') and FII(4''1')

TABLE 5
Total Body Lengths of *Euphausia pacifica* Furciliae in the Dominant Pathways of Pleopod Development

Stage	Path-way	Pleopod form	Body length, mm			
			Mean	Range	SD	n
FI	B	1'	2.74	2.46-2.95	0.10	95
	A	2'	2.87	2.63-3.11	0.10	76
FII	B	1''3'	3.16	2.87-3.43	0.13	67
	A	2''3'	3.42	3.15-3.60	0.08	59
	B	4''1'	3.52	3.19-4.04	0.17	59

Larvae were measured in a sample pooled from surveys of January, February/March, May, and August 1978.

mum temperature and maximum chlorophyll *a* values for the seven surveys (Kendall's tau = −0.90, *p* = 0.01).

The mean numbers of young *E. pacifica* showed continuous production of 1-2-mm larvae with two peaks in abundance, the first in February/March and the second, and by far the larger, in June/July (Figure 3d), when the environment, with respect to tempera-

TABLE 6
Growth Factors* of *Euphausia pacifica* Furciliae in the Dominant Pathways of Pleopod Development

Molt	Path-way	Pleopod form	Growth factor
FI-FII	A	2'-2''3'	1.19
	B	1'-1''3'	1.15
FII, instar 1-2	B	1''3'-4''1'	1.11

*Expressed as mean size in stage divided by the mean size in preceding stage.
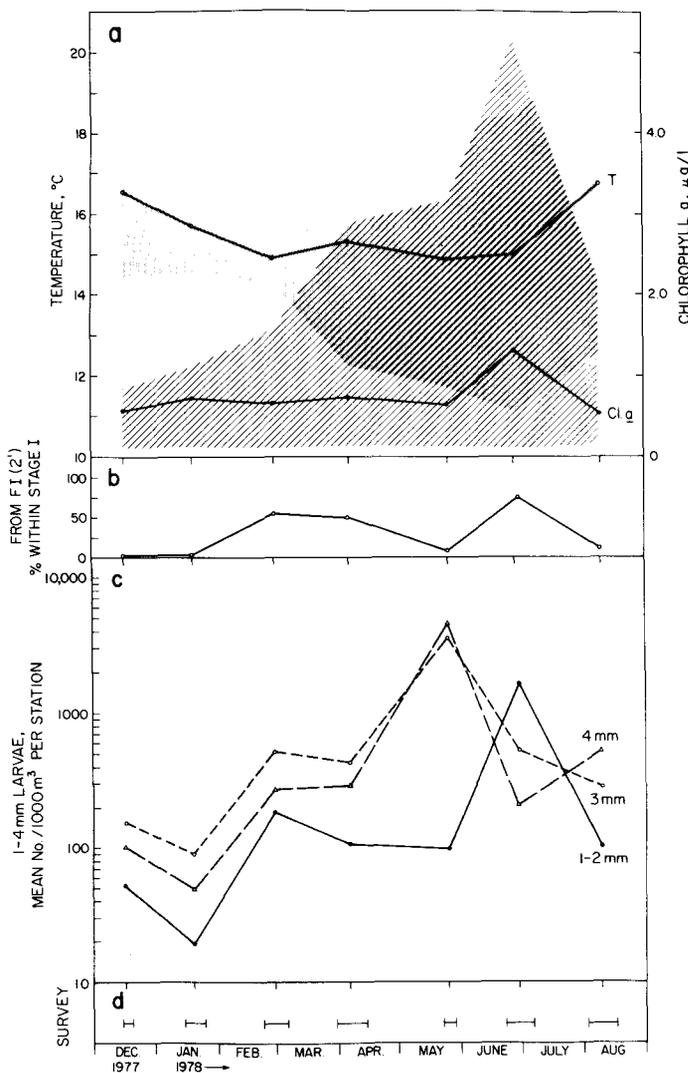
Figure 3. Temporal variation in the larval environment, the dominant pathways of pleopod development, and larval abundance of the Southern California Bight population of *Euphausia pacifica* sampled by seven CalCOFI surveys, depicted by:
a. mean and range of 10-m temperature (°C) (n = 27-33) and surface chlorophyll a (μg/l) (n = 4-16);
b. percentage of form FI(2') within stage FI representing the group A pathway;
c. mean number/1000 m³ of 1-4-mm larvae by 1-mm increments (n = 11-22;
d. duration of survey.

ture and chlorophyll a abundance, appeared optimal for larval survival. The pattern is consistent with this population's reproductive cycle; Brinton (1976) observed pulses in recruitment at a 2- to 3-month frequency with maxima in periods of temperature minima during seasonal upwelling. The fluctuation in abundance of 3- and 4-mm larvae was similar to that of younger stages through April but differed from May to August. A relatively high density of predominantly older larvae developed in May: 75% of the total number of FI and FII larvae were in stage FII (Figure 2), and within FII, 52% were in the second instar form FII(4"1'). In June/July, on the other hand, during

peak production of 1-2-mm larvae, 70% of total FI-FII larvae were in stage FI.

The direct A pathway of pleopod development, with relatively larger larvae in FI and instar 1 of FII, was dominant during surveys of February/March, April, and June/July, with the maximum percent frequency in June/July (Figure 3b). The longer B pathway, with smaller larvae, on average, in comparable instars predominated in December, January, May, and August.

The pattern of dominance by the A pathway of development in FI-FII generally coincided with the abundance pattern of recently hatched 1-2-mm larvae in the seven samples of inshore *E. pacifica*; there was a significant correlation between the ranked percent frequency of form FI(2'), depicting the A pathway, and mean numbers of young larvae (Kendall's tau = +90, p = 0.01). The first pulse in dominance of the A path and in recruitment corresponded with the decrease in temperature and increase in range of chlorophyll a values of February/March, whereas peaks in dominance of FI(2') and in number of 1-2-mm larvae coincided with the highest mean and maximum chlorophyll a values of June/July and hence, presumably, with the greatest abundance of larval food; the agreement between ranks for these categories was significant (Kendall's coefficient of concordance W, p = < 0.01).

The alternate B pathway of pleopod development was predominant during periods with relatively high mean temperatures and/or low chlorophyll a values (December, January, and August) or with a relatively high density of older and larger larvae (May). Reversion to the B path in May, a period of moderate temperature and abundant chlorophyll a, presumably reflected a change in the quality of the larval habitat, perhaps a reduction in the supply of appropriate food by the increasing number of late furcilia larvae.

Ross (1981) found that among larvae of *E. pacifica* reared in the laboratory at 12°C, the median duration of calyptopis stages I, II, and III, and furcilia stages I and II was 3.5, 4.0, 5.5, 5.5, and 4.5 days. Larval euphausiids begin to feed in the first calytopis stage, and the body length and form in furcilia stage I may be influenced by the variation in increments at three molts during a period of about 13 days, perhaps particularly by the accumulation of reserves within calyptopis stage III during the 6 days before the molt to stage FI. At the higher mean temperatures of the inshore area, the duration of these stages might be slightly less; a decrease in intermolt duration with an increase in temperature has been observed in laboratory culture of euphausiid larvae by Ross (1981) and Le Roux (1974).

The duration of surveys ranged from 6-15 days with a mean duration of 12.1 days; the interval between surveys ranged from 25-39 days with an average interval of 28.1 days, about five times the median duration of the third calyptopis instar. It appeared reasonable, therefore, to relate the pattern of development in furcilia stages I and II to the environmental conditions within the study area during the periods when the furciliae were collected.

Inferences from Observations

In general, the following trends in furciliar development within the Southern California Bight population of *E. pacifica* from winter-summer 1977-78 may be inferred: (1) dominance of a short, direct pathway of pleopod development—i.e., FI(2')–FII(2''3')—was most pronounced, and variability with respect to the number of forms in furcilia stage II was reduced, when conditions in the larval environment appeared optimal for growth and development (June/July) and there was maximum production of young (1-2 mm) larvae; (2) dominance of a longer path—i.e., FI(1')–FII(1''3')–FII(4''1')—was most pronounced, and the number of forms in stage II increased, when conditions appeared suboptimal for larval growth (December, January, and August) and production of young larvae was minimal.

DISCUSSION

Food and temperature are considered the primary extrinsic factors influencing molt increment and intermolt period, the two components of crustacean growth (Hartnoll 1982). In general, a diet of insufficient quantity or suboptimal quality depresses growth by reducing the increment and lengthening the duration of the intermolt. Both effects may occur together, and one or the other may predominate. An increase in temperature may decrease the increment, but usually the predominant effect is a decrease in intermolt duration, which results in an accelerated rate of growth.

Le Roux (1974) explored the effects of varied diet and temperature on the larval growth and morphogenesis of the euphausiid *Meganyctiphanes norvegica*, a species which can vary the development of pleopods. He found that the duration of intermolt was influenced primarily by temperature, whereas both the increment and morphogenesis were affected most strongly by the quality and quantity of food: with a poor diet, the increment decreased with age, morphogenesis was retarded, and the number of pathways of pleopod development, as well as variability in number of forms, increased. In general, the temporal variation in morphogenesis among *E. pacifica* furciliae in the inshore Southern California Bight population from December 1977-August 1978 is consistent with these observations. The indirect B pathway of pleopod development dominated when a decrease in the food supply, as in December and January, might be expected to reduce the increment, decrease morphogenesis per molt, and increase the number of instars required to achieve a given stage of development. The more direct A pathway dominated when an increase in the abundance of food, as in June/July, might be expected to increase both increment and morphogenesis per molt, and reduce the number of instars required to reach a comparable stage of development. The apparent decrease in increment, with predominance of the B pathway in May, might reflect a decrease in the quality of larval food associated with the relatively high density of 3-4-mm larvae. In a study of regional relationships between development and growth of larval Antarctic krill, *E. superba* (Brinton and Townsend, in press), the widest variety of pleopod forms in furcilia stages I and II, and most indirect developmental pathways, were associated with a range of relatively low to moderate chlorophyll values and very high larval densities.

Geographical Variation in Morphology of Furcilia Stages I and II

Larval forms in furcilia stages I and II of *Euphausia pacifica* have been described in populations of the Sea of Japan (Endo and Komaki 1979) and the Strait of Georgia (Heath 1977), and in a spring-summer sample of the population off southern California (Boden 1950). The percent frequency distribution of forms enumerated by Boden, calculated from his data, is shown in Figure 4. The FI(2')–FII(2''3') pathway of pleopod development predominated, as in group A surveys, and the relative abundance of each form is within the range of variability observed in this study except for FI(3') and FII(3''2'); this pathway was subdominant in the 1950 spring-summer sample. The PSI between the frequency distribution of forms within FI and FII in Boden's sample and in the group A survey mean is relatively high (Table 7): above 70 in both stages and within the range of group A indices in FI and FII, which indicates a strong similarity between the two samples of the species in southern California waters.

Heath (1977) presented a frequency distribution of pleopod forms among *E. pacifica* furciliae in Saanich Inlet, British Columbia, during May-June 1975, in which the dominant forms were again FI(2') and FII(2''3'). The sample differed from the California population in the relatively small number of forms in FII(s + ns)—5 only—and in abundance of form FI(5'). This form was not encountered in the Southern
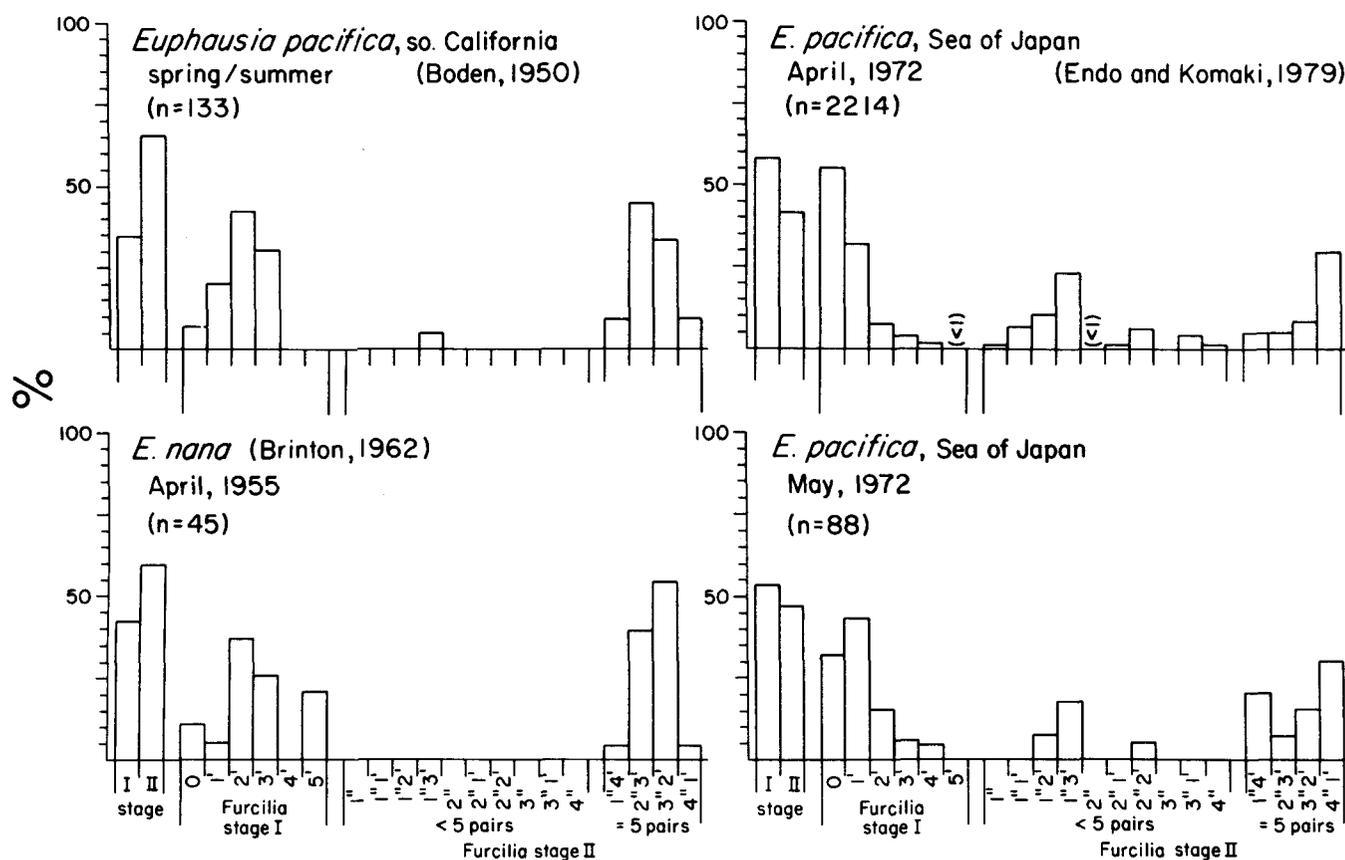
Figure 4.   The relative abundance of fucilia stages I and II and percent frequency of pleopod forms within each stage for (*upper left*) *Euphausia pacifica* from southern California; (*upper and lower right*) *E. pacifica* from the Sea of Japan; and (*lower left*) *E. nana*.

TABLE 7
Percent Similarity Indices for the Frequency of Pleopod Forms within Furcilia Stages I and II

	E. pacifica					*E. nana*[a]
	So. California			Sea of Japan[b]		
	Group A mean	Group B mean	Boden sample[c]	April	May	
FI						
E. pacifica						
So. California						
Group A mean	—	47.30	72.15	42.05	52.15	52.05
Group B mean		—	46.30	65.15	81.50	35.45
Boden sample			—	37.70	47.95	61.95
Sea of Japan						
April				—	76.55	26.70
May					—	36.85
FII						
E. pacifica						
So. California						
Group A mean	—	38.00	76.05	37.10	54.15	55.20
Group B mean		—	32.95	75.60	70.15	22.40
Boden sample			—	30.95	43.10	79.15
Sea of Japan						
April				—	75.45	20.40
May					—	28.05

[a]Brinton (1962)
[b]Endo and Komaki (1979)
[c]Boden (1950)

California Bight inshore area during the study period but was seen occasionally to the northwest, which suggests that there might be a latitudinal trend in its contribution to stage FI.

Endo and Komaki (1979) described the larval forms of *E. pacifica* in the Sea of Japan during April and May 1972, and found the dominant pathway of pleopod development to be FI(0)–FI(1')–FII (1''3')–FII(4''1'). The percent frequency of forms within furcilia stages I and II, as delimited in my study, was calculated from their data (Figure 4); the relative abundance of forms proved generally similar to that in group B surveys (Table 3). The frequency distribution of forms in the two samples from the Sea of Japan and the mean distribution of forms of California *E. pacifica* in survey groups A and B were compared by percent similarity index (Table 7). In both stages, the PSI between the group B mean and one of the two Japan Sea samples was slightly higher than the PSI between April and May surveys within the Sea of Japan, and all were within the range of group B indices in FI-II, indicating a strong similarity between the populations in the B pattern of pleopod development and variety of forms.

In these data, the Japan Sea population exceeds the California population in abundance of FI(0), presence of FI(5'), and in number and relative abundance of forms in FII. It differs from both North American populations in lacking dominance of the short FI(2')–FII(2''3') pathway of pleopod development, and this disparity might be evidence of divergence between the widely separated populations of the species. However, the degree of variation presumably induced by environmental change within the inshore southern California population during the nine-month survey period suggests that the pattern of pleopod development should not be used to characterize populations of *E. pacifica* without prior study of spatial and temporal variability in larval morphogenesis across the range of the species.

Variation in Early Furciliar Development within Euphausia Species Group III

Furciliar development has been described in 24 of the 31 species constituting the genus *Euphausia* (Mauchline 1980). The 31 species have been grouped by features of adult morphology into three assemblages (Brinton 1975). Variation in development of pleopods seems very rare in species groups I and II but is found in several species of group III, which includes IIIa, *E. mucronata, E. lamelligera, E. sibogae, E. distinguenda;* IIIb, *E. tenera;* and IIIc, *E. pacifica, E. nana, E. lucens, E. vallentini, E. frigida, E. superba, E. crystallorophias.* Brinton (1979) observed that spe-

cies of the group III lineage are adapted to environments that tend to vary in productivity, both temporally and spatially, compared with the central water masses of midlatitudes, i.e., eastern boundary currents, zones of equatorial divergence, or temperate to polar latitudes.

In addition to *E. pacifica*, three of these group III species—*E. superba* and *E. nana*, also of subgroup c, and *E. mucronata* of subgroup a—are known to vary considerably in pleopod development. These four species may also be related by their expression of form FI(2'), and related FII(s + ns) forms, which appear to be absent or very rare in other *Euphausia* species: FI(2') constituted 0.2% of 661 larvae in stage FI(ns) of group I species *E. sanzoi* (Knight 1976), but has not been recorded in other described species.

The pleopod development of Antarctic *E. superba* has been discussed at length by Fraser (1936), Makarov (1974), Makarov and Maslennikov (1981), and Brinton and Townsend (in press). The species resembles *E. pacifica* in range of variability in furcilia stages I and II but differs in dominance of pathways FI(4')–FII(4''1') and FI(5')–FII(5''); a form with 5 pairs of setose pleopods is not conventionally included in furcilia stage II of *E. pacifica* (Boden 1950).

Euphausia nana, with limited distribution south of Japan and in the East China Sea, is closely related to *E. pacifica* (Brinton 1962b); the frequency of forms in furcilia stages I and II sampled in April 1955, calculated from Brinton's data, is shown in Figure 4. Although it appears that *E. nana* may lack forms with fewer than 5 pairs of pleopods in FII(s + ns), the dominant pathways are similar to California *E. pacifica* sampled by Boden (1950) and the group A surveys of this study. Percent similarity indices between the frequency distributions of FI and FII forms in group A and B survey means, the Boden sample, and *E. nana* (Table 7) show only a moderate, < 60, similarity between *E. nana* and the group A mean, but a relatively strong, > 60, similarity between *E. nana* and Boden's sample. Both share subdominance of FI(3') and dominance or subdominance of FII (3''2'), a less important pathway in the southern California population of *E. pacifica* during December 1977-August 1978. In this sample, *E. nana* does not resemble the described neighboring population of *E. pacifica* in the Sea of Japan in either dominance or number of forms; the PSI between FI and FII forms of *E. nana* and the April sample of Sea of Japan *E. pacifica* were the lowest observed (Table 7).

Euphausia mucronata inhabits the Peru-Chile Current and may be considered the South American counterpart of California Current *E. pacifica*. Antezana (1978) studied the larval growth and development of

E. mucronata in both laboratory and field samples. The two dominant pathways he described for the field population, FI(2')–FII(2''3') and FI(1')–FII(1''3')–FII(4''1'), correspond to the dominant modes of southern California *E. pacifica*. *E. mucronata* may be somewhat less variable: FI(0) was not present and there were fewer forms of FII(s + ns). The growth factors from FI-FII in the A and B pathways of California *E. pacifica*, and from instar 1-2 within FII in the B pathway, were very similar to the growth factors in the same stages and pathways of *E. mucronata*. Antezana found that a greater number of molts, and minimal morphological change between molts, were associated with less growth per molt in the laboratory. He hypothesized that, in the field, dominance of the short FI(2')–FII(2''3') path would indicate optimal conditions for larval growth, while dominance of the longer FI(1')–FII(1''3')–FII(4''1') path would reflect a suboptimal environment. The results of this study support his hypothesis.

The close correspondence between the boundary current populations of *E. pacifica* and *E. mucronata* in variability of both habitat and larval development is consistent with the observed correlation within the family Euphausidae between the relative stability of a species's environment and pattern of furciliar development (Mauchline and Fisher 1969). Antezana (1978) inferred that a species such as *E. mucronata*, with a high degree of plasticity in larval development, was well suited to a habitat like the Peru-Chile Current, which is characterized by a diversity of water masses and strong upwelling; the inference applies equally to southern California *E. pacifica*.

The apparent restriction of the capacity for marked variation in larval pleopod development to species of group III supports the subgeneric classification of adults (Brinton 1975). When the complete description of larval development within the genus permits comparison, the further association of species by type of dominance and variation, and by use of form FI(2'), may convey information about specific relationships within the species groups.

ACKNOWLEDGMENTS

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SPOT PRAWN (*PANDALUS PLATYCEROS*) AND RIDGEBACK PRAWN (*SICYONIA INGENTIS*) FISHERIES IN THE SANTA BARBARA CHANNEL

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ABSTRACT

The Santa Barbara Channel prawn fishery, consisting of spot prawn (*Pandalus platyceros*) and ridgeback prawn (*Sicyonia ingentis*), has developed into a major fishery during the late 1970s. Increasing fishing pressure, along with oil drilling and seismic activities, warrants management of the resource.

The spot prawn fishery developed from a minor fishery in 1970, totaling 4,533 kg, to over 116,954 kg by 1981. Catch per unit of effort (CPUE) declined from 40 kg/hr in 1974 to 12.7 kg/hr by 1982.

The ridgeback prawn fishery rose dramatically from 1,813 kg in 1974 to 161,378 kg by 1979, but declined to 63,916 kg by 1982. CPUE declined from 59 kg/hr in 1979 to 19 kg/hr by 1982.

Age composition of spot prawn based on modal distribution revealed that two major age groups, 3 and 4, dominated the catch. Prawn were not recruited until the fall as age group 2.

Ridgeback prawn became recruitable at age group 1, but the adult population comprised age groups 2 and 3.

Management recommendations proposed a winter closure (November 1 through January 31) for spot prawns and a summer closure (June 1 through September 30) for ridgeback prawns.

RESUMEN

La pesca de los langostinos *Pandalus platyceros* y *Sicyonia ingentis* en el Canal de Santa Bárbara se ha convertido hacia finales de la década de 1970-1980 en una gran pesquería. El crecimiento de esta pesquería, junto con las perforaciones petrolíferas y las actividades sísmicas de la región, justifican que se establezcan regulaciones.

La pesca de *P. platyceros* evolucionó de una pesquería de poca importancia en 1970 con capturas de 4,533 Kg hasta alcanzar los 116,954 Kg en 1981. La captura por unidad de esfuerzo (CPUE) declinó de 40 Kg por hora en 1974 hasta 12.7 Kg por hora en 1982.

La pesca de *S. ingentis* incrementó dramáticamente de 1,813 Kg en 1974 hasta 161,378 Kg en 1979, mientras que en 1982 solamente se capturaron 63,916 Kg, pasando la CPUE de 59 Kg por hora en 1979 a 19 Kg por hora en 1982.

La composición de edades de *P. platyceros* basada en la distribución modal revela que en la captura dominan dos grupos de edad, individuos de 3 y 4 años. El reclutamiento se produce en el otoño, incluyendo la generación de dos años.

El reclutamiento de *S. ingentis* es al año de edad, pero la población adulta incluye grupos de 2 y 3 años de edad.

Para regular la pesquería se recomienda establecer una veda durante el invierno (del 1° de Noviembre al 31 de Enero) para *P. platyceros*, y una veda durante el verano (del 1° de Junio al 30 de Septiembre) para *S. ingentis*.

INTRODUCTION

Since 1974, the Santa Barbara Channel spot prawn and ridgeback prawn fisheries have developed into a substantial industry. In 1981 they yielded 200,721 kg (441,587 lb) and contributed nearly $750,000 to the local economy. Increasing fishing pressure, along with oil drilling and seismic activities, warrants management of the resource.

The spot prawn, actually a shrimp in the pandalid family, is larger and commands a higher price than does the smaller ridgeback prawn, a penaeid.

Spot prawns are commonly found from Unalaska, Alaska, to San Diego, California. They inhabit rocky and adjacent areas at depths ranging from 45 to 484 m, but generally are found between 198 and 234 m (Frey 1971). Juvenile spot prawns occur in shallow inshore areas (90 m or less), migrating to deeper offshore areas as they mature (Figure 1). These prawns are protandric hermaphrodites, with females spawning from September through November; they have an ovigerous stage lasting from October through April. They live an estimated 6 years; the maximum length recorded is 63 mm carapace length (CL).

Ridgeback prawns occur from Monterey, California, to Cedros Island, Baja California, at depths ranging from 45 to 162 m. The major concentration is in the Ventura-Santa Barbara Channel area. Their life span is probably 4 years, and sexes are separate in this species. Females reach a maximum length of 45 mm
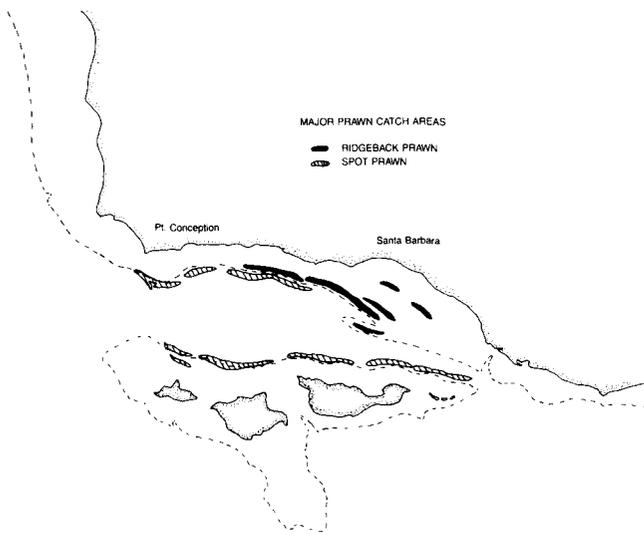
Figure 1. Trawling grounds for spot prawns and ridgeback prawns in the Santa Barbara Channel, California.

CL; males, 37 mm CL. Peak spawning occurs from June through September (Susan Anderson, pers. comm.).

METHODS

The catch per unit of effort for this trawl fishery is measured in kg/hr. When comparing single rig (use of one net) to double rig (use of two nets), I used the conversion factor of 1.6 to convert double-rig to single-rig effort. The 1.6 value was derived by comparing the catch rates of single-rig and double-rig trawlers fishing in the same area at the same time (Walter Dahlstrom, pers. comm.).

Since both species were fished by the same fleet, there was a problem deciding which species was the target. I decided to use the percent composition of the catch as determined by fish receipts, and used only log data from landings that contained 80% of one species to determine fishing effort for a given species. Logs were selected from boats known to submit accurate

information and that were representative in size and gear of boats involved in the fishery.

I determined ages of spot prawns and ridgeback prawns by differentiating size modes of the sampled catch using techniques described by Harding (1949) and Cassie (1954).

THE FISHERY

Fleet Description

The prawn trawl fleet comprises 12–16 vessels in Santa Barbara, 1–2 in Oxnard, and 7 in Ventura. These trawlers range from 10 to 22 m in length, the average being 14.5 m. Net tonnage is 7 to 55 tons, with an average of 18 tons. The fleet remained fairly constant (12 boats) during the past decade, with seasonal fluctuations. Standard gear is a single-rig shrimp trawl, either semiballoon or Gulf shrimp trawl. Beginning in late 1981, as many as 7 Pacific Northwest shrimp trawlers entered the fishery, all based in Ventura. These boats are larger, averaging 20.3 m and 58 tons. All these draggers are equipped with a double-rig shrimp trawl.

Spot Prawn

Landings. Spot prawns have been fished intermittently for years, but not until 1970 were landings significant. By 1974, nearly 82,955 kg (183,000 lb) were taken (Table 1). Catches in following years declined, reaching a low of 13,357 kg in 1977. Landings improved slightly in 1978 to 24,912 kg, but in 1979 many of the trawlers diverted their efforts towards fishing ridgeback prawn; thus catches diminished slightly to 21,668 kg. In 1980, the ridgeback prawn fishery began to wane, resulting in increased landings of spot prawns to 64,271 kg. The following year, a record catch of 117,093 kg was landed, much of it taken in the second half of 1981. The significant increase in landings was due to the entry into the fishery of up to seven Pacific Northwest trawlers. Because these boats

TABLE 1
Spot and Ridgeback Prawn Landings (Kilograms) in Santa Barbara Area 1970-82

Year	Spot prawn	Percent	Ridgeback prawn	Percent	Total
1970	4,795	100.0	0	0	4,795
1971	12	100.0	0	0	12
1972	0	0	0	0	0
1973	4,232	100.0	0	0	4,232
1974	82,834	97.8	1,820	2.2	84,654
1975	61,681	83.1	12,520	16.9	74,201
1976	23,459	94.3	1,419	5.7	24,879
1977	13,357	89.5	1,561	10.5	14,918
1978	24,912	57.2	18,663	42.8	43,575
1979	21,668	11.8	161,640	88.2	183,308
1980	64,271	33.9	125,216	66.1	189,487
1981	117,093	58.4	83,172	41.6	200,265
1982	105,632	62.2	64,158	37.8	169,790

TABLE 2
Monthly Landings and Catch Per Unit of Effort of Spot Prawn

	1981		1982	
Month	Catch (kg)	CPUE (kg/hr)	Catch (kg)	CPUE (kg/hr)
January	2,515	17.7	12,016	13.0
February	1,869	19.5	9,300	12.6
March	3,695	22.8	14,483	16.8
April	7,680	30.0	7,690	12.9
May	4,308	30.1	18,776	15.7
June	5,696	20.9	11,201	9.4
July	10,913	22.2	9,173	9.2
August	16,295	25.9	6,804	9.5
September	15,698	31.3	3,153	13.6
October	14,001	27.5	2,635	13.1
November	12,703	20.4	4,040	10.6
December	21,738	15.4	6,013	10.2

were equipped with double-rig nets, fishing effort was increased by a factor of 1.6. Landings declined in 1982 to 105,621 kg, although most catches occurred during the first half of the year (Table 2). The reduced landings in the latter half partly resulted from the departure of Northwest trawlers from the area. These boats returned late in 1982, contributing significantly to the landings.

Catch effort and total effort. Catch per unit of effort was collated both on an annual and monthly basis. CPUE for the sampled fleet was 39.8 kg/hr (86 lb/hr) in 1974 and 1975, but declined sharply to a low of 16.5 kg/hr in 1977 (Figure 2). During 1978 and 1979, significant effort was diverted to the ridgeback prawn fishery, although CPUE increased to 23.6 kg/hr during this period. The following year, CPUE remained near 25.5 kg/hr. CPUE in 1981 declined slightly to 23.6 kg/hr, but dropped sharply to 12.7 kg/hr by 1982.

Monthly CPUE and landings have fluctuated widely, with a high of 31.3 kg/hr in September 1981; but since then, CPUE displayed a gradual decline through 1982 (Table 2). Total effort (hours trawled) declined from 2,000 hours in 1974 to 818 hours in 1977, but began to double each year beginning in 1979, reaching over 8,000 hours by 1982 (Figure 2).

Declining catches and CPUE, coupled with increasing total effort portend a resource in distress.

Ridgeback Prawn

Landings. The ridgeback prawn resource off Santa Barbara has been known for years, but a lack of demand instilled little interest. Trawl fisherman finally did develop a small fishery in 1966, when 13,600 kg (30,000 lb) were landed. But the fishery quickly faded as a result of poor marketability. Annual landings were below 2,266 kg from 1974 to 1977, except in 1975 when landings reached 12,520 kg (Table 1). The
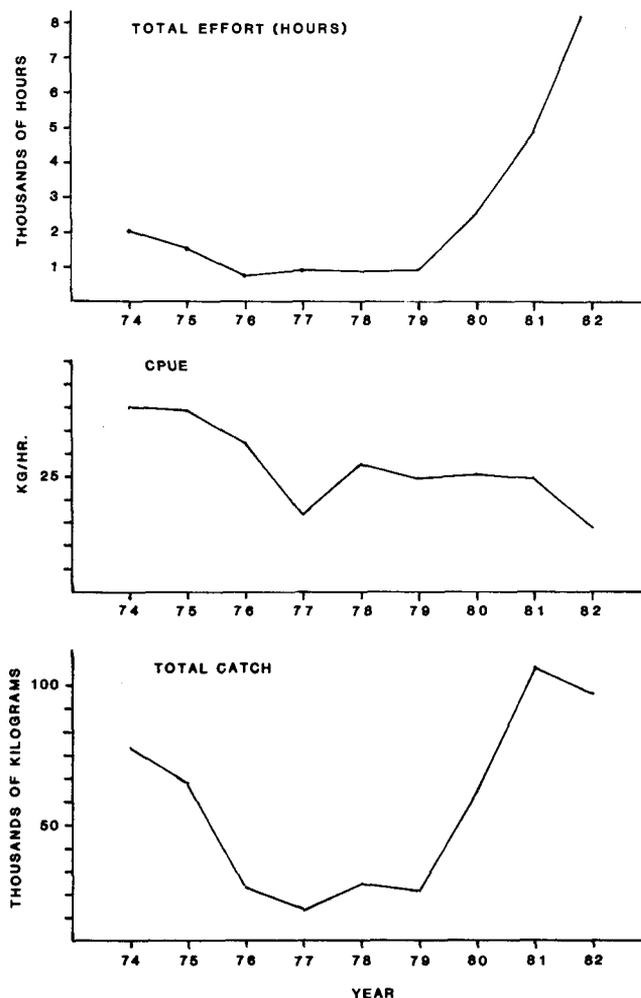
Figure 2. Annual total effort, catch per unit of effort, and annual total catch of spot prawns from 1974 to 1982.

fishery began to increase during 1978, when 18,663 kg were landed, and reached a record high of 161,640 kg in 1979. The dominant reason for such an increase was consumer acceptance coupled with reasonable retail prices. Landings declined to 125,216 kg the following year, and continued this trend in 1982 when 64,158 kg were landed (Table 1).

Most successful fishing occurred during fall, winter, and spring, with record monthly landings of 51,242 kg taken in May of 1979 (Table 3).

Catch effort and total effort. During the early years (1975 to 1977) CPUE was difficult to assess because of low landings and effort. Ridgeback prawn landings began to increase in 1978 and 1979, along with log information. Annual CPUE reached nearly 59 kg/hr (130 lb/hr) in 1979, but the CPUE declined to 49 kg/hr in 1980, reaching a low of 19 kg/hr in 1982 (Figure 3). Monthly CPUE analysis indicates highest CPUE during fall and winter. CPUE as high as 91.6 kg/hr was

TABLE 3
Monthly Landings and Catch Per Unit of Effort of Ridgeback Prawns

Month	1979 Catch (kg)	1979 CPUE (kg/hr)	1980 Catch (kg)	1980 CPUE (kg/hr)	1981 Catch (kg)	1981 CPUE (kg/hr)	1982 Catch (kg)	1982 CPUE (kg/hr)
January	524	—	11,500	91.1	9,585	43.4	5,291	31.9
February	4,466	81.1	11,480	68.1	16,029	31.4	7,840	20.4
March	11,353	56.8	21,907	77.5	13,022	27.2	7,057	18.6
April	44,744	71.0	10,648	46.0	9,129	17.0	3,860	9.4
May	51,242	91.6	4,173	27.6	6,615	24.7	671	18.1
June	12,330	38.0	6,570	27.6	3,057	—	1,023	4.5
July	16,052	38.1	7,791	39.9	7,188	23.5	828	—
August	8,024	30.3	7,660	27.4	3,450	12.9	684	—
September	969	22.6	4,511	20.4	3,398	25.6	364	8.0
October	5,469	44.4	20,105	41.1	1,320	19.9	352	7.0
November	3,457	—	11,413	33.7	6,428	28.5	10,377	24.5
December	3,040	73.7	7,478	24.5	3,964	13.2	25,820	26.7

noted in May of 1979, declining to 22.6 kg/hr by September (Table 3). Catch rates of near 90 kg/hr were recorded from January to April 1980, with a gradual decline during spring and summer. The declining trend in CPUE continued into 1982, when the catch rates reached a low of 4.5 kg/hr in June. The fishery recovered slightly in November of 1982, when CPUE rose to 24.5 kg/hr.

Estimated total effort (in hours) increased dramatically from 823 hours in 1978 to 2,738 hours in 1979, although total effort dropped slightly in 1980 to 2,532 hours (Figure 3). Since 1980, total effort has been increasing annually, reaching 3,357 hours by 1982. CPUE data and annual landings indicate a possible decline in total population of ridgeback prawns during 1980 and 1981. But by late 1982, the fishing success and landings indicated a possible recovery of the resource.

LENGTH AND AGE COMPOSITION

Spot Prawn

Age determination was accomplished by discerning modes in the length distribution (Harding 1949; Cassie 1954). Analysis of modes indicated that age groups 3 and 4 were dominant during 1981-82. These age groups, representing the 1978 year class (group 3) and 1977 year class (group 4), ranged near 40 mm CL and 50 mm CL, respectively (Figure 4). During the 1982-83 period, three modes were located near 36 mm CL, 45 mm CL, and 50 mm CL, which represented the 1979, 1978, and 1977 year classes, respectively (Figure 4). Spot prawn became fully recruited during the fall and winter as age group 2 when they appeared in increasing numbers.

Ridgeback Prawn

Age for ridgeback prawn was also determined by discriminating modes in the length distributions. Max-

imum age is estimated at 4 years, with females having a faster growth rate than males. Both male and female length distributions were analyzed separately. Length distributions of female ridgeback prawns during 1981
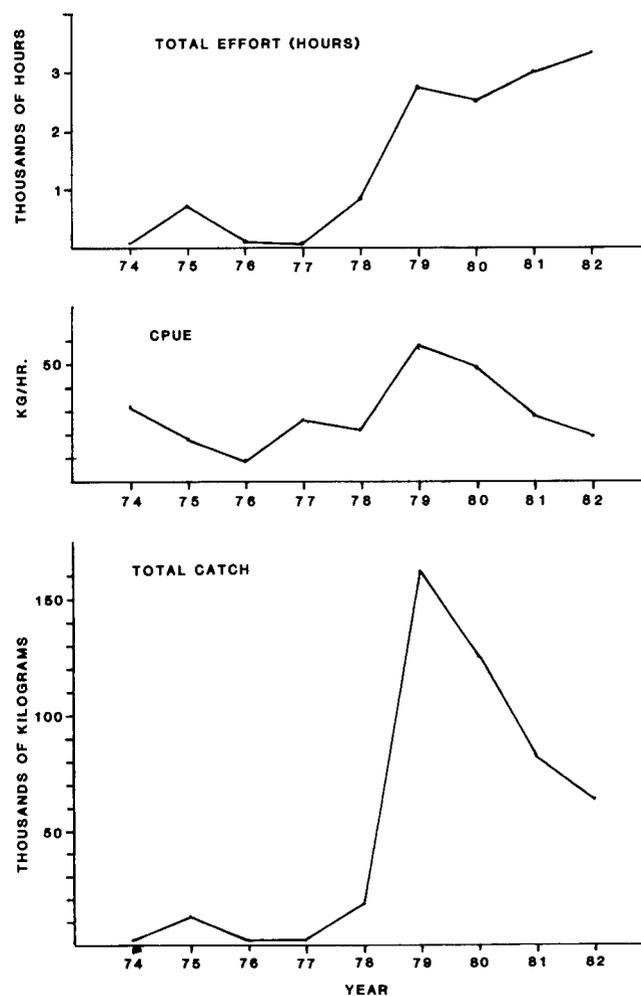
Figure 3. Annual total effort, catch per unit of effort, and annual total catch of ridgeback prawns from 1974 to 1982.
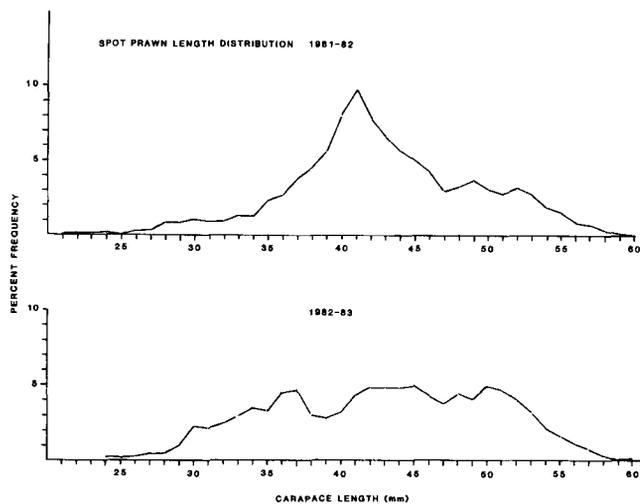
Figure 4. Spot prawn length distributions for 1981-82 and 1982-83.

Figure 5. Female ridgeback prawn length distributions for 1981 and 1982.

indicated the dominance of older age groups, as indicated with modes near 36 mm CL and 40 mm CL (Figure 5). Poor recruitment of the 1979 year class (age group 2) became evident during the fall of 1981, when very few animals of the cohort were present in the catch. By August 1982, the fishery showed a marked decline. Then in October 1982, large numbers of prawns from the 1981 year class (age group 1) appeared in the fishery; in fact, 50% of the 1982 catch consisted of this single year class (Figure 5).

MANAGEMENT RECOMMENDATIONS

Spot Prawn

Data from the age and reproduction studies revealed several trends. First, the population presently comprises older males and females (age groups 3 through 5). Spawning and ovigerous stage occur primarily from October through March. A winter closure from November through January was recommended to protect ovigerous females because the winter catches were the highest on record during 1981. This recommendation was adopted by the California Fish and Game Commission and implemented for the 1983-84 season. Incidental take of 22.7 kg of spot prawns is allowed during the closed season. Existing regulations include a 3-mile closure from the mainland and off-

shore islands to all trawling activities, and a restriction of 1½-in. mesh for single-walled bag or 3-in. mesh for double-walled bag.

Ridgeback Prawn

The ridgeback prawn resource, a relatively new fishery, has sustained heavy fishing pressure in only a few years. This rapid growth of landings and fishing effort coupled with recent declines in the catch rates indicates some distress of the population. Causes for this decline are numerous, but to provide protection for spawning females and the young-of-the-year prawns, a summer closure (June 1 through September 30) was adopted by the California Fish and Game Commission for the 1982 season. Incidental take of 22.7 kg of ridgeback prawn is allowed during the closed period. Other regulations include a 3-mile closure from the mainland and offshore islands to all trawling, and a restriction of 1½-in. mesh for single-walled bag or 3-in. mesh for double-walled bag.

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THE FEEDING HABITS OF JUVENILE-SMALL ADULT BARRED SAND BASS (*PARALABRAX NEBULIFER*) IN NEARSHORE WATERS OFF NORTHERN SAN DIEGO COUNTY

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ABSTRACT

The feeding habits of juvenile-small adult barred sand bass (*Paralabrax nebulifer*) are described, based on 165 specimens 123-523 mm standard length (SL) collected between San Onofre and Oceanside, California, at depths ranging from 8 to 30 m. Collections were made during an annual cycle from March 1981 to March 1982.

The diet of the barred sand bass indicates that it forages in close proximity to the substrate. Brachyuran crabs, mysids, pelecypods, and epibenthic fishes were the most important prey. These findings are contrary to previous studies, which found northern anchovy (*Engraulis mordax*) to be of major importance in the diet of similar-sized bass. Three functional foraging categories were identified based on body size. The diet of small (< 240 mm SL) barred sand bass was unique because it included crustaceans such as mysids and gammarid amphipods, whereas large (> 320 mm SL) barred sand bass consumed larger prey such as *Porichthys notatus* (80-160 mm SL) and *Octopus*. Bass of intermediate size (240-320 mm SL) contained the species found in both large and small fish.

The temporal and spatial aspects of *Paralabrax nebulifer*'s feeding niche are distinct from those of the other demersal fishes of shallow, soft-bottom habitats in the Southern California Bight. These differences are discussed.

RESUMEN

La descripción de la alimentación de la cabrilla de arena, *Paralabrax nebulifer*, jóvenes y adultos, se basa en 165 ejemplares de 123 a 523 mm de longitud estándar (LE), capturados entre 8 y 30 m de profundidad en la zona que se extiende desde San Onofre hasta Oceanside, California. Las capturas se efectuaron durante un ciclo anual, desde Marzo de 1981 hasta Marzo de 1982.

La dieta de la cabrilla de arena indica que se alimentan en las proximidades del fondo marino. Las presas más importantes son cangrejos, misidáceos, pelecípodos y peces epibentónicos. Estas observaciones no concuerdan con estudios previos, los cuales consideran a la anchoveta del norte, *Engraulis mordax*, como el elemento más importante en la dieta de *P. nebulifer* de tallas similares a las analizadas durante esta estudio. La dieta de *P. nebulifer* pequeños (< 240 mm de longitud estándar) es distinta debido a la presencia de crustáceos (misidáceos y antípodos gamáridos), mientras que los ejemplares grandes (> 320 mm LE) consumieron presas grandes como *Porichthys notatus* (80-160 mm LE) y *Octopus*. *P. nebulifer* de talla mediana (240-320 mm LE) contenían en su estómago presas similares a las consumidas por los ejemplares grandes y pequeños.

El nicho alimenticio ocupado por *P. nebulifer* en cuanto a sus aspectos temporal y espacial resulta distinto al de otros peces demeresales habitantes de zonas someras y fondos blandos de a la Bahía del Sur de California. Estas diferencias son discutidas.

INTRODUCTION

The barred sand bass (*Paralabrax nebulifer*) is among the most poorly known of the popular sport-fishes inhabiting the waters off southern California. Prior to 1957, *P. nebulifer* was insignificant in the partyboat catch, and it is believed that warm water conditions are responsible for its recent greater abundance (Frey 1971). Since the sixties, *P. nebulifer* has formed an important component of the sport catch (Feder et al. 1974). Unfortunately, catch statistics for barred sand bass have been combined with those for kelp bass (*Paralabrax clathratus*) within a general "rock bass" category (e.g., Frey 1971). The great abundance of barred sand bass on artificial reefs suggests that it may be the most valuable fish on such reefs (Turner et al. 1969). Most of the biological data gathered on *P. nebulifer* has been taken incidentally during studies of other species. Even management practices are based on life-history parameters determined for *P. clathratus* (Frey 1971).

Previous studies of the food habits of *Paralabrax nebulifer* have relied heavily on specimens collected on partyboats (Quast 1968b; Smith 1970). The authors of these studies have acknowledged that such collections attribute undue importance to northern anchovy (*Engraulis mordax*) as a prey item, since anchovies

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are used extensively as bait and chum on partyboats. In this report we characterize the feeding habits of *P. nebulifer*, from fish collected with a variety of methods in different habitats. Our findings should yield a more comprehensive understanding of the ecological interrelationships of the barred sand bass, its prey, and the fishes with which it co-occurs.

MATERIALS AND METHODS

Fish Collections

Paralabrax nebulifer were collected from 16 different locations ranging from 3-14 km northwest of Oceanside, California, from March 1981 to March 1982. Depths of capture were 8-30 m. (See Plummer et al. 1983 for a chart of the sampling region.) Fish were collected by spearfishing (40% of total specimens), otter trawls (36%), angling (23%), and lampara seines (1.2%). Angling was done during dawn and morning hours in the vicinity of giant kelp (*Macrocystis pyrifera*) beds and other rock and cobble reefs; spearfishing was done during midday (0900-1500 hrs). For angling, "scampi" lures were used in lieu of live bait. No collections were made in the vicinity of partyboats using live anchovies as chum. Cracked sea urchins were sometimes used as chum by spearfishers; however, urchin parts were easily identified in stomachs and were disregarded in the analysis. All trawling and seining were done over sandy substrates at various times of day and night.

Since, in most instances, fish were collected from particular locations with a consistent technique, at the same depth, and during the same diel period, these parameters were interrelated. Non-independence thus prevents us from comparing diets among microhabitats, longshore locations, diel periods, or depths. Different biases are inherent in each technique, and for each microhabitat and location. All data were therefore pooled to provide the best average characterization of feeding habits.

Analysis of Stomach Samples

Viscera were removed from *P. nebulifer* within one hour of capture and fixed in 10% Formalin. Eviscerated fish were returned to the laboratory to be sexed, weighed (0.1 g), and measured (standard length, SL in mm). After a minimum of four days fixation, viscera were soaked in tap water for 48-72 hrs and then stored in 70% ethanol.

Stomach contents were identified to the lowest taxonomic level permitted by condition of the material. In many cases, partially digested items could be identified only to the class level. Intestine contents were excluded from the analysis because these prey were

often unidentifiable. The number and wet weights (0.01 g) of prey items were recorded. Mysid weights were reconstructed wet weights based on standardized values determined for each species by Marine Ecological Consultants of Southern California (L. Gleye, pers. comm.). The extent of prey digestion and stomach fullness were estimated on a scale from zero (totally undigested or empty) to 10 (digested or completely full).

Statistical Analysis of Diet

Prey were grouped into major taxonomic categories, usually at the class level, for comparing diet among *Paralabrax nebulifer* of different body sizes (Table 1). All analyses were based on these categories unless otherwise stated. This grouping resulted in the loss of species-level information; however, the number of *P. nebulifer* collected was not sufficient to adequately describe its diet at the species level, based on an analysis of the cumulative numbers of prey species in bass of three different body sizes (Figure 1). Taxon accumulation curves based on prey categories showed that the number of stomachs examined was sufficient to characterize the diet of *P. nebulifer* at this level of resolution. Since all prey items could not be identified

TABLE 1
All Prey Categories for *Paralabrax nebulifer*, Ordered by Percent Index of Relative Importance Values for the Small Size Class

Prey category	Size class		
	Small[a]	Intermediate[b]	Large[c]
Brachyurans	39.34	27.39	23.32
Pelecypods	18.39	24.10	—
Mysids	18.00	6.56	—
Fish	4.39	6.98	12.26
Carideans	4.23	9.46	0.75
Crustacean parts	4.04	0.88	0.36
Amphipods	3.15	—	—
Pelecypod siphons	2.89	0.43	0.37
Unidentifiable	1.58	9.30	8.58
Porichthys notatus	1.46	7.70	39.58
Ophiuroids	0.53	2.66	—
Urechis caupo	0.47	—	0.62
Gastropods	0.41	0.92	1.46
Polychaetes	0.40	0.60	2.94
Isopods	0.25	—	—
Bryozoans	0.12	—	—
Copepods	0.09	—	—
Octopus	0.08	—	7.60
Hydroids	0.07	—	—
Decapods—unident.	0.05	—	—
Anomurans	0.02	0.76	—
Ascidians	0.01	—	1.66
Macrurans	0.01	—	—
Algae	0.01	0.05	0.51
Holothuroids	—	0.77	—
Stomatopods	—	1.45	—

[a]<240 mm
[b]240-320 mm
[c]>320 mm

SMALL < 240 MM S. L.

INTERMEDIATE 240 – 320 MM S. L.

LARGE > 320 MM S. L.
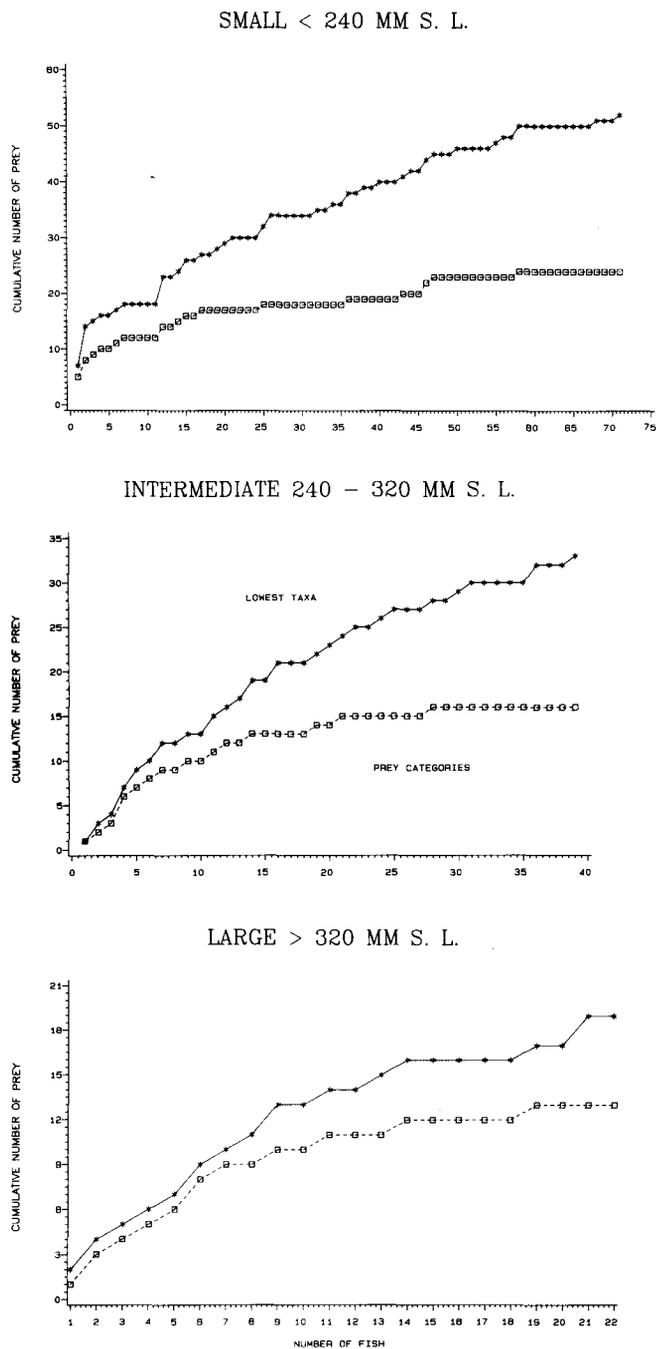
Figure 1. Cumulative frequency of prey categories and lowest prey taxa present in *Paralabrax nebulifer* of three different size classes. Analysis is based on prey present in individual fish selected randomly from the total fish in each size class.

to the species level, grouping prey into categories allowed comparisons to be made at a more uniform taxonomic level. When comparisons are made between prey categories at nonuniform taxonomic levels, the importance of more general categories such as "crustacean parts" obviously becomes exaggerated. Lowest-level identifications of all taxa with

percent IRI values (see below) greater than one are presented in Table 2.

The contribution of each prey category to the diet of *Paralabrax nebulifer* was evaluated based on three commonly used measures of importance: percent number (% N), percent weight (% W), and the frequency with which each prey category occurred among all of the *P. nebulifer* sampled (% FO). An index of relative importance, IRI = (% N + % W) % FO (Pinkas et al. 1971) was derived. The IRI is particularly useful in that it combines % N, % W, and % FO into a single measure that also allows its three components to be evaluated separately.

In order to determine how *P. nebulifer*'s size affected its food preference, feeding data were analyzed separately for barred sand bass of three length (size) classes: small < 240 mm; intermediate, 240-320 mm; and large, > 320 mm SL. These three "feeding stanzas" were determined based on the method of Tyler (1978), which uses an iterative contingency Chi-square process applied to the presence-absence of major prey in the diet. Prey categories chosen for this analysis were mysids and fish.

Percent IRI values for dietary arrays of the three size classes were compared pair-wise using the Percent Similarity Index (PSI) (Whittaker 1952):

$$PSI = 100 \sum_{i=1}^{S} \min{(a_i, b_i)},$$

where a_i and b_i were the percent IRI for the ith prey category in the diets of fish of sizes A and B, respectively, and S is the total number of categories in the diets of fish of both sizes. This index was chosen because it has been shown to be an appropriate measure for comparing the diets of predators that feed on unequal numbers and proportions of prey items (Cailliet and Barry 1978). The PSI has also been shown to be independent of sample size differences between the groups being compared (Kohn and Riggs 1982). The prey category "unidentifiable" was not included in the calculations because it would bias comparisons toward artificially greater similarities.

RESULTS

From March 1981 to March 1982, 170 *Paralabrax nebulifer* were collected. They ranged in size from 123 to 523 mm SL, including 81 "small," 50 "intermediate," and 34 "large" individuals. The stomachs of five of these specimens were ruptured or everted upon capture and were disregarded. Small *P. nebulifer* had a lower proportion ($x^2 = 8.1$, 2 d.f., $0.02 > P > 0.01$) of empty stomachs (12.3%) than either intermediate (22.0%) or large (35.3%) individuals

TABLE 2
Contribution of Prey Taxa[a] to Diet of *Paralabrax nebulifer*

Lowest taxonomic classification	Prey category	Pct. number	Pct. wt.	Pct. freq.	IRI	Pct. IRI
Small *P. nebulifer* (< 240 mm SL)						
Neomysis kadiakensis	Mysids	30.4	1.7	8.5	271.7	16.2
Misc. crustacean parts	Crustacean parts	4.4	1.2	29.6	166.5	9.9
Pelecypoda	Pelecypods	2.4	9.2	14.1	162.6	9.7
Caridea	Carideans	6.1	2.0	19.7	158.9	9.5
Solenidae-siphons	Pelecypod siphons	5.2	1.8	16.9	119.1	7.1
Majidae	Brachyurans	3.0	3.1	18.3	113.0	6.7
Solen sicarius	Pelecypods	1.2	13.6	5.6	83.5	5.0
Cancer—unident.	Brachyurans	2.2	2.6	14.1	67.6	4.0
Unident. material	Unidentifiable	2.4	0.9	19.7	65.2	3.9
Porichthys notatus	*Porichthys*	0.3	21.0	2.8	60.0	3.6
Caprellid amphipod	Amphipods	5.1	0.1	9.9	50.8	3.0
Brachyura	Brachyurans	1.9	1.6	14.1	48.9	2.9
Cancer—3 ident. spp[b]	Brachyurans	1.5	1.4	12.7	36.8	2.2
Engraulis mordax	Fish	1.2	10.4	2.8	32.6	1.9
Teleostei	Fish	1.5	1.2	11.3	30.7	1.8
Metamysidopsis elongata	Mysids	5.2	0.0	5.6	29.7	1.8
Ophiuroid	Ophiuroids	1.4	0.9	9.9	21.8	1.3
Pinnixa sp	Brachyurans	1.5	0.5	9.9	20.1	1.2
Urechis caupo	*Urechis*	0.2	13.6	1.4	19.4	1.2
Gammarid amphipod	Amphipods	1.7	0.1	9.9	17.3	1.0
Intermediate *P. nebulifer* (240-320 mm SL)						
Unident. material	Unidentifiable	6.4	1.7	33.3	271.4	18.1
Porichthys notatus	*Porichthys*	2.0	41.8	5.1	224.6	15.0
Pelecypoda	Pelecypods	4.5	5.4	15.4	151.8	10.1
Caridea	Carideans	5.9	0.9	17.9	123.6	8.2
Teleostei	Fish	2.0	8.3	10.3	105.6	7.0
Neomysis kadiakensis	Mysids	35.6	1.2	2.6	94.4	6.3
Ophiuroid	Ophiuroids	3.5	0.9	17.9	77.8	5.2
Brachyura	Brachyurans	2.5	2.0	12.8	56.9	3.8
Solen sicarius	Pelecypods	1.5	5.6	7.7	54.6	3.6
Alpheus sp	Carideans	2.0	3.1	10.3	52.1	3.5
Squilla sp	Stomatopod	1.0	7.3	5.1	42.3	2.8
Pyromaia tuberculata	Brachyurans	3.0	0.8	10.3	38.7	2.6
Cancer—unident.	Brachyurans	2.0	0.7	10.3	27.3	1.8
Misc. crustacean parts	Crustacean parts	2.0	0.5	10.3	25.6	1.7
Holothuroidea	Holothuroids	0.5	8.2	2.6	22.4	1.5
Anomura	Anomurans	1.0	3.3	5.1	22.2	1.5
Polychaeta	Polychaetes	1.5	0.8	7.7	17.4	1.2
Pectinidae	Pelecypods	5.9	0.2	2.6	15.8	1.1
Engraulis mordax	Fish	2.5	0.5	5.1	15.1	1.0
Large *P. nebulifer* (> 320 mm SL)						
Porichthys notatus	*Porichthys*	20.0	35.7	22.7	1266.5	49.0
Cancer antennarius	Brachyurans	12.5	12.2	13.6	337.4	13.1
Unident. material	Unidentifiable	10.0	5.1	18.2	274.5	10.6
Octopus sp	*Octopus*	5.0	21.7	9.1	243.1	9.4
Teleostei	Fish	7.5	0.6	13.6	110.6	4.3
Polychaeta	Polychaetes	7.5	2.8	9.1	94.0	3.6
Salpidae	Ascidians	2.5	9.2	4.5	53.0	2.1
Embiotocidae	Fish	2.5	8.0	4.5	47.7	1.8

[a]Only taxa with IRI values greater than or equal to 1.0% have been listed.
[b]Juv. rock crabs: includes *Cancer antennarius, C. anthonyi,* and *C. jordani.*

(Table 3). For bass whose stomachs contained food, there was no correlation between either fullness or the extent of prey digestion and the time of capture (fullness: Spearman's rho = −0.14, P = 0.12; digestion: rho = −0.12, P = 0.18; both n = 132). *P. nebulifer* fed almost exclusively on epibenthic prey. Sixty-nine total prey taxa were grouped into 26 categories based on taxonomic and, in a few cases, morphological criteria (e.g., pelecypod siphons) (Tables 1 and 2).

The extent to which many prey categories were exploited was a function of predator size (Figures 2 and 3). Small *P. nebulifer* consumed a large number of small prey like the mysid shrimp *Neomysis kadiakensis* and *Metamysidopsis elongata* (Table 2; Figure 3).

TABLE 3
General Characterization of the Feeding Habits
of *Paralabrax nebulifer*

	Size class (mm)			All sizes
	<240	240-320	>320	
No. stomachs	81	50	34	165
% empty stomachs	12.3	22.0	35.3	20.0
Total no. prey items	592	202	40	834
Total wt. prey items (g)	152.0	213.2	365.4	730.6
Mean no. prey items per stomach with food	8.3	5.2	1.8	6.3
Mean wt. prey items (g)	2.1	5.5	16.6	5.5
Mean no. prey categories per stomach	2.7	2.1	1.4	2.3
Mean no. lowest level prey taxa per stomach	3.2	2.3	1.4	2.6

The most important prey was brachyuran crabs, whose IRI value was over one-third of the total value (Table 1; Figure 3). Brachyurans were also important for *P. nebulifer* of intermediate size. Brachyurans ranked first in IRI and occurred in 41% of the stomachs that contained food (Table 1; Figure 3). Although mysids remained the most numerous prey, they were not as significant for intermediate-sized *P. nebulifer* as for small bass, owing to the increased importance of carideans and fish. Fish were even more important prey of large *P. nebulifer*. Like bass of intermediate size, large fish relied heavily on *Porichthys notatus*. This species of toadfish ranked first by IRI, whereas all other fish prey ranked third (Table 1; Figure 3). *Cancer antennarius* was the most important brachyuran found in large *P. nebulifer*.

Although many components of the diet of *P. nebulifer* change ontogenetically, certain prey were consistently found in bass of more than one size class.
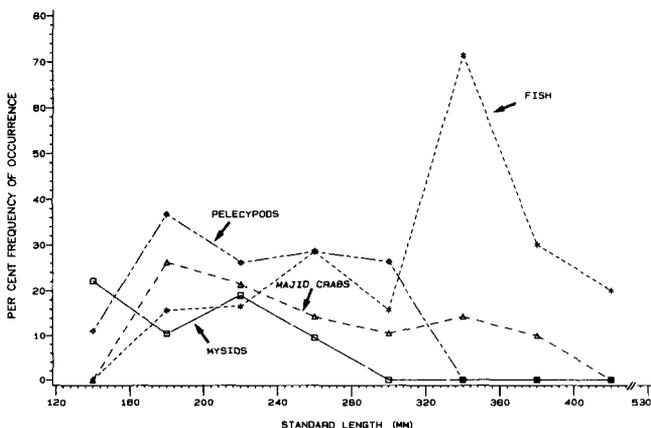
Figure 2. Four representative patterns of change in the frequency of prey occurrence for different sizes of *Paralabrax nebulifer*. Analysis is based on prey present in 40-mm size classes, with the exception of fish > 400 mm (N = 5 fish, with the largest 523 mm SL), for which the class interval was 130 mm. Data are plotted at midpoints of the class intervals.

Brachyurans (particularly majid crabs) occurred with approximately equal frequencies over nearly the entire size range of fish (Figures 2 and 3). Pelecypods were important to both small and intermediate *P. nebulifer*, although conspicuously absent from the diet of large fish (Figures 2 and 3).
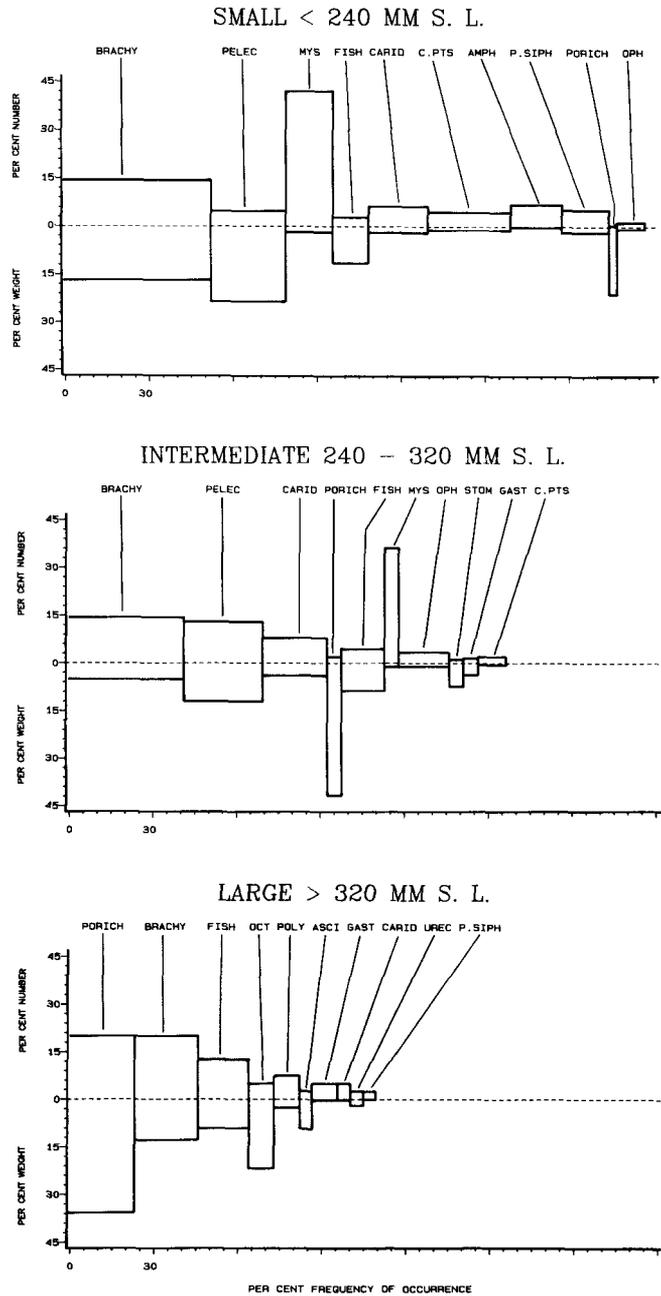
Figure 3. Relative importance of the top 10 (by IRI, ordered from left to right) categories of prey consumed by *Paralabrax nebulifer* of three different size classes, as expressed by % number, % weight, % frequency of occurrence and IRI.

Key to abbreviations: Amph = amphipods; Asci = ascidians; Brachy = brachyurans; C. pts = crustacean parts; Carid = carideans; Gast = gastropods; Mys = mysids; Oct = octopods; Oph = ophiuroids; P. siph = pelecypod siphons; Pelec = pelecypods; Poly = polychaetes; Porich = *Porichthys notatus*; Stom = stomatopods; Urec = *Urechis caupo*.

The greatest overall dietary similarity was between small and intermediate barred sand bass (PSI = 65.1); greatest dissimilarity was between the small and large size classes (PSI = 32.0). The diets of *P. nebulifer* of large and intermediate sizes overlapped to a moderate extent (PSI = 41.0).

DISCUSSION

The very generalized (Hobson 1974) serranid morphology of *Paralabrax nebulifer* allows it to occupy a uniquely cosmopolitan feeding niche in shallow sandy, rocky, and kelp bed habitats of the Southern California Bight. Diet, habitat preference, and feeding behavior also distinguish *P. nebulifer* from the species with which it co-occurs.

Habitat preference isolates *P. nebulifer* from two co-occurring congeners, the spotted sand bass (*Paralabrax maculatofasciatus*) and the kelp bass (*Paralabrax clathratus*). Although *P. nebulifer* can be found near kelp beds, rocky reefs, and within bays, it prefers shallow (generally < 30 m deep) sand-bottom habitats (Limbaugh 1955; Feder et al. 1974; Ebeling et al. 1980). Large numbers of these fish have been observed on sand plains in the vicinity of artificial reefs (Turner et al. 1969; Davis et al. 1982). *P. maculatofasciatus* prefers warmer water (Stephens and Zerba 1981) and is generally found near eelgrass beds and around harbors and rock jetties (Limbaugh 1955; Feder et al. 1974). *P. clathratus* prefers kelp beds and rocky reefs to sandy habitats (Limbaugh 1955; Quast 1968a; Feder et al. 1974); in kelp beds it frequently occurs throughout the water column (Ebeling et al. 1980). Although both *P. clathratus* and *P. nebulifer* could be classified as food generalists, the two species feed on fundamentally different prey because of microhabitat differences. *P. clathratus* feeds mainly on plankton and free-swimming nekton (Quast 1968a; Love and Ebeling 1978; Hobson et al. 1981), whereas *P. nebulifer* primarily consumes demersal prey (Limbaugh 1955; Quast 1968b; Turner et al. 1969; Smith 1970; Feder et al. 1974; Davis et al. 1982; this study, Tables 1 and 2; Figure 3).

There is some dietary overlap between *P. nebulifer* and other demersal fishes that occupy shallow, soft-bottom habitats off southern California. Major prey and foraging behavior, however, usually differ among the various species. The bothids *Citharichthys sordidus, C. stigmaeus, Hippoglossina stomata,* and small *Paralichthys californicus* feed on small epibenthic and meroplanktonic crustaceans such as copepods, amphipods, and mysids (Allen 1982; Plummer et al. 1983). Although small *P. nebulifer* feed on these prey (particularly mysids), demersal macroinvertebrates (brachyurans, pelecypods) are more important in the diet (Table 1; Figure 3).

The scorpaenid *Scorpaena guttata* and the bothid *Xystreurys liolepis* are the two demersal, soft-bottom species whose general food and habitat are most similar to that of *Paralabrax nebulifer.* Both *S. guttata* and *X. liolepis* also feed heavily on crabs (IRI values of 60% and 45%, respectively; Allen 1982). Each species forages at least partly by ambushing prey (Allen 1982; authors' obs.).

Paralabrax nebulifer, Scorpaena guttata, and *Xystreurys liolepis* are ecologically distinct, however, in their preferred depths, foraging microhabitats, and feeding behaviors. *Scorpaena guttata* appears to segregate bathymetrically from both *X. liolepis* and *P. nebulifer.* Shallow-water scuba surveys have characterized both *S. guttata* and *P. nebulifer* as species that prefer depths less than 26 m (Limbaugh 1955; Turner et al. 1969; Feder et al. 1974). Although this is likely true for *P. nebulifer,* trawl surveys reported in Allan (1982) showed that *S. guttata* was most common in deeper (50-m) water. *Xystreurys liolepis* occurred most frequently in trawls made at 10-m depth (Allen 1982).

Flatfishes like *Xystreurys liolepis* are adapted to forage in ways unlike those of roundfishes (Allen 1982). *Paralabrax nebulifer,* like *S. guttata,* feeds on prey that are active upon the substrate surface; but the frequent occurrence of entire pelecypods (in addition to clam siphons) in its diet suggests that the sand bass also is able to disinter prey buried close to the sediment surface. Burrowing forms such as callianassids and hoplocarid (mantis) shrimp and the echiuroid *Urechis caupo* probably are seized when they appear at the entrances to their burrows. Pinnotherid crabs, known to inhabit such burrows, and clam siphons (Prince 1975) were also found in some stomachs.

Paralabrax nebulifer and *Scorpaena guttata* are known to differ in diel foraging patterns. *S. guttata* is nocturnal (Turner et al. 1969; Fager 1971; Allen 1982). *P. nebulifer* is most active during the day (Fager 1971); the presence of certain nocturnal prey (*Porichthys notatus:* Arora 1948; Ibara 1970; *Octopus* and brachyurans: Ebeling and Bray 1976; Hines 1982) also support Fager's (1971) observations of some crepuscular activity.

Like the rockfishes (genus *Sebastes*) of California waters, *Paralabrax* spp possess a swim bladder. *Scorpaena guttata* does not. Most abundant shallow-water rockfishes of the bight are either limited to rough, rocky bottoms (e.g., *Sebastes chrysomelas, S. carnatus:* Larson 1980), are largely restricted to kelp forests (*S. atrovirens:* Coyer 1979), or have midwater habits (*S. mystinus, S. serranoides:* Love and Ebeling 1978).

The rockfishes that occupy soft-bottom habitats are most abundant in much deeper water (Allen 1982). *Paralabrax nebulifer* seems morphologically adapted to forage like a demersal rockfish, and has successfully adopted that feeding mode in sand-rock ecotone and sandy bottom habitats. A swim bladder affords enhanced mobility (Allen 1982) and has allowed *P. nebulifer* to forage in a manner unlike any other large-mouthed, demersal fish of local, shallow, soft bottoms.

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FOOD AND FEEDING OF BOCACCIO (*SEBASTES PAUCISPINIS*) AND COMPARISON WITH PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) LARVAE IN THE CALIFORNIA CURRENT

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ABSTRACT

The composition of the diet of larval bocaccio (*Sebastes paucispinis*) and Pacific hake (*Merluccius productus*) overlapped in copepod types and developmental stages, but important differences were evident from gut content analyses of specimens collected in 1975 CalCOFI cruises. Both bocaccio and Pacific hake larvae have large mouths, but first-feeding bocaccio preyed on smaller organisms than first-feeding hake (30-170 μm wide vs 40-350 μm in hake). Compared with small hake larvae, early stages of bocaccio ingested a greater diversity of food types including larval euphausiids, diatoms, dinoflagellates, tintinnids, and cladocerans. Although copepod nauplii constituted the dominant prey in bocaccio larvae less than 7.0 mm long, there was a total lack of adult copepods and very low incidence of copepodites in the diet. In contrast, adult copepods, primarily calanoids, made up a significant portion of the diet in all sizes of hake larvae examined, contributing about 74% of overall prey volume compared to about 33% in 7-13-mm bocaccio larvae.

Observations of feeding incidence in relation to time of capture suggested a faster rate of gut evacuation in bocaccio larvae.

RESUMEN

La composición del alimento ingerido por las larvas de *Sebastes paucispinis* y *Merluccius productus* abarca similares especies de copépodos adultos y sus fases de desarrollo, pero importantes diferencias fueron observadas en el análisis del contenido estomacal de los ejemplares recolectados durante los cruceros CalCOFI de 1975. Las larvas de *S. paucispinis* y de *M. productus* tienen boca grande. Las larvas de *S. paucispinis* al iniciar su alimentación, capturan organismos más pequeños que las larvas de *M. productus* (30-170 μm de ancho y 40-350 μm de ancho respectivamente). Las larvas más jovenes de *S. paucispinis* ingieren una mayor diversidad de organismos que las larvas de merluza, incluyendo las fases larvales de eufáusidos, diatomeas, dinoflagelados, tintínidos y cladóceros. Aun cuando en larvas de *S. paucispinis*

menores de 7 mm de longitud, los nauplios de copépodos constituyeron la presa dominante, hubo una total ausencia de copépodos adultos y escasos copeloditos. En contraste, en las larvas de merluza examinadas los copépodos adultos, principalmente Calánidos constituyeron el 74% del volumen total, comparado con un 33% en las larvas de *S. paucispinis* de 7-13 mm. de longitud.

La incidencia de alimentación en relación con la hora de captura sugiere que las larvas de *S. paucispinis* efectuan una evacuación del tramo digestivo más rapida.

INTRODUCTION

Rockfish (*Sebastes* spp, family Scorpaenidae) larvae are among the most commonly occurring larvae in the California Current; they rank third or fourth in relative abundance in California Cooperative Oceanic Fisheries Investigations plankton surveys, with peak abundance during January and February (Ahlstrom 1961, 1965). Identification of the more than 60 species that occur off California and Baja California is a difficult task, but complete larval series of some important commercial species have been described, including that of bocaccio, *S. paucispinis* (Moser 1967a; Moser et al. 1977). Bocaccio is the most abundant rockfish species in commercial catches from central and northern California (Frey 1971). In southern California this species is important in recreational fisheries: bocaccio constitute 37% of all rockfishes taken on partyboats (Hartman 1980) and rank first or second among rockfish species taken on private boats (Wine 1982; Racine 1982; Ono 1982).

Considerable biological information is available on bocaccio, including age and growth (Phillips 1964), fecundity (Phillips 1964; MacGregor 1970), reproductive biology (Moser 1967a, b; MacGregor 1970), and development and distribution of early life-history stages (Moser 1967a; Moser et al. 1977; Ahlstrom et al. 1978). There are no data, however, on the feeding of bocaccio larvae. Feeding studies of larvae of other major species in the California Current region were reported by Arthur (1976) for northern anchovy (*Engraulis mordax*), sardine (*Sardinops sagax*), and jack mackerel (*Trachurus symmetricus*) and by Sumida

and Moser (1980) and Bailey (1982) for hake (*Merluccius productus*). Bocaccio and other rockfishes differ from many marine fishes in their mode of reproduction. They are highly fecund live-bearers and give birth to larvae that are 4-5 mm long, with functional jaws, eyes, and pectoral fins. In *Sebastes*, the yolk-sac stage occurs within the ovaries, and newborn larvae are equivalent to the first-feeding larvae of oviparous species. As part of a continuing study of the feeding habits of larvae of California Current fishes, this paper summarizes data on stomach contents, mouth size, and feeding incidence of bocaccio larvae.

MATERIALS AND METHODS

Specimens examined in this study consisted of 96 larvae, 4.2-12.8 mm in body length, from 34 formaldehyde-preserved samples collected during the CalCOFI cruises of 1975 (7412, 7501, 7503, and 7505) aboard R/V *David Starr Jordan* and R/V *Alexander Agassiz*. Stations occupied represent an area bounded by 37°16.8'N, 124°19.9'W and 32°40.8'N, 117°52.4'W, approximately off San Francisco Bay south to San Diego, California. Samples were collected with a 505-m-mesh, 1-m aperture plankton net towed obliquely from an approximate depth of 210 meters to the surface.

Procedures for measuring larval body length, mouth width, and for dissecting the gut and identifying stomach contents are discussed in Sumida and Moser (1980). Food volume index was calculated for each food particle by treating copepod eggs as spheres, and nauplii, copepodites, and adults as ellipsoids. Details of the mathematical computations are explained in Sumida and Moser (1980).

RESULTS AND COMPARISONS

Composition of Food

Copepod nauplii were the dominant food items (75%-81%) consumed by bocaccio less than 7 mm long, with calanoid nauplii far outnumbering those of other groups (Table 1). Copepod eggs and eggs of other invertebrates, copepodites, tintinnids, coccoliths, cladocerans, and phytoplankton constituted a minor portion of the diet. Adult copepods were entirely lacking in the guts of larvae less than 7 mm long. Copepodites and adult copepods were found in increasingly greater numbers in larvae longer than 7 mm; however, copepod adults did not become significant prey until the larvae reached 10 mm. Copepod nauplii remained the dominant prey category until the larvae reached 9 mm, and declined thereafter. Of the other diverse categories found in larvae shorter than 7 mm, only invertebrate eggs were found consistently in larger larvae.

Food in bocaccio larvae contrasts with that found in hake larvae, where calanoid adults and copepodites made up the major portion of the diet in all sizes of larvae examined (Sumida and Moser 1980).

Size of Food, Mouth Width

The bulk of food particles ingested by bocaccio larvae less than 8.5 mm long was concentrated in a size range of 50-200 μm, and prey of this size range continued to be a major part of the diet in larvae larger than 8.5 mm (Figure 1). Beginning at about 7 mm, prey sizes up to 400-500 μm appeared in the guts; however, prey items less than 300 μm dominated in the diet even in the largest larvae (Figure 1).

Mouth width was about 0.3 mm at birth, doubled before the larvae reached 6 mm, and doubled again just before the larvae reached 9 mm (Figure 2). Maximum size of prey items ingested by first-feeding bocaccio larvae was about 50% of maximum mouth width, and reached a maximum of 60% in 5-mm larvae (Figure 1). In comparison, maximum prey size was about 90% of maximum mouth width for first-feeding hake larvae, 80% for 4-mm larvae, and about 70% for 5-mm larvae (Sumida and Moser 1980). This reflects dietary differences in first-feeding larvae of the two species; copepod nauplii were the primary constituent in the bocaccio, whereas adult copepods and copepodites composed much of the diet in hake. This is clearly seen in comparisons of the two species' total volumes of major prey items (Table 2). The total volume (in percent) of nauplii consumed by bocaccio larvae in this study was five times that found in hake larvae, whereas the volume (in percent) of adult copepods eaten by bocaccio was less than half that found in hake. Although first-feeding bocaccio larvae have smaller mouths than hake, the rate of increase in mouth width is greater in bocaccio, and mouth size in bocaccio exceeds that of hake at about 7 mm length (Figure 2). Coincidentally, this is also when notochord flexion occurs.

Feeding Incidence

Arthur (1976) defines feeding incidence as the percentage of larvae containing at least one food item in the gut for a given sample. This term refers to presence of food in the gut and does not necessarily reflect recent feeding activity. The plot of feeding incidence of bocaccio larvae at time of sampling shows a diurnal pattern, reaching a maximum from about 0800 to 1600 PST and declining rapidly thereafter (Figure 3). Although the sample size and temporal coverage are limited, the data suggest that bocaccio have a rapid rate of digestion and evacuation after cessation of feeding, compared with hake. This is also evident in plots of the mean food volume index and mean num-

TABLE 1
Food Composition of Bocaccio Larvae

Food item	4.0-4.9 No.	4.0-4.9 %	5.0-5.9 No.	5.0-5.9 %	6.0-6.9 No.	6.0-6.9 %	7.0-7.9 No.	7.0-7.9 %	8.0-8.9 No.	8.0-8.9 %	9.0-9.9 No.	9.0-9.9 %	10.0-10.9 No.	10.0-10.9 %	11.0-11.9 No.	11.0-11.9 %	12.0-12.9 No.	12.0-12.9 %
Copepod adults																		
Clausoclanaus sp	—		—		—		—		—		2		—		4		7	
Paracalanus sp	—		—		—		—		2		—		—		3		—	
Oithona sp	—		—		—		2		3		2		31		26		73	
Calanoid	—		—		—		—		—		4		—		—		20	
Total adults	—		—		—		2	1.2	5	3.9	8	2.9	31	43.7	33	31.1	100	45.2
Copepodites																		
Oithona sp	2		11		—		10		2		2		11		5		18	
Calanoid	7		2		1		8		21		3		2		37		23	
Cyclopoid	2		2		—		2		—		—		—		—		—	
Disintegrated/ unidentifiable	4		6		3		—		12		—		4		—		12	
Total copepodites	15	2.4	21	3.9	4	14.8	20	12.0	35	27.1	5	1.8	17	23.9	42	39.6	53	24.0
Copepod nauplii																		
Calanoid	388		334		22		103		70		34		17		11		14	
Cyclopoid	82		78		—		22		6		13		1		3		1	
Harpacticoid	1		1		—		—		—		—		2		—		—	
Disintegrated/ unidentifiable	5		3		—		—		2		3		—		—		—	
Total copepod nauplii	476	75.3	416	77.6	22	81.5	125	75.3	78	60.5	50	18.0	20	28.2	14	13.2	15	6.8
Copepod eggs	21	3.3	6	1.1	—	—	—	—	—	—	212	76.5	1	1.4	—	—	47	21.3
Copepod egg clusters	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1.9	—	—
Euphausiid																		
Eggs	—	—	—	—	—	—	3	1.8	2	1.6	—	—	—	—	—	—	—	—
Nauplii	—	—	2	0.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Calyptopis	2	0.3	—	—	—	—	—	—	—	—	—	—	—	—	1	0.9	1	0.4
Metanauplii	—	—	1	0.2	—	—	—	—	—	—	—	—	—	—	—	—	3	1.4
Diatom	1	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dinoflagellate	1	0.2	3	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tintinnid	7	1.1	1	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Invertebrate eggs (.14-.26 most .14-.17mm)	79	12.5	66	12.3	1	3.7	14	8.4	8	6.2	2	0.7	2	2.8	14	13.2	—	—
Cladoceran	3	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Salp	—	—	—	—	—	—	1	0.6	—	—	—	—	—	—	—	—	—	—
Coccolith	5	0.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unid. crustacean	3	0.5	1	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unid. particle w/brown chloroplasts	12	1.9	12	2.2	—	—	1	0.6	—	—	—	—	—	—	—	—	2	0.9
Unid. particles	7	1.1	7	1.3	—	—	1	0.8	—	—	—	—	—	—	—	—	—	—
Total no. food particles	632		536		27		166		129		277		71		106		221	
No. larvae examined* (Σ=96)	55		19		6		6		3		2		1		1		3	
No. larvae with food (Σ=66)	33		17		2		4		3		2		1		1		3	

*None with yolk

TABLE 2
Cumulative Frequency Distribution of Numbers and Volume for Major Prey Types in Bocaccio and Hake Larvae

Prey type	Range max. width (μm) Bocaccio	Range max. width (μm) Hake	Mean vol. ($10^6\mu m^3$) Bocaccio	Mean vol. ($10^6\mu m^3$) Hake	Frequency of occurrence Bocaccio	Frequency of occurrence Hake	Freq. × vol. ($10^9\mu m^3$) Bocaccio	Freq. × vol. ($10^9\mu m^3$) Hake	% of total vol. Bocaccio	% of total vol. Hake
Copepod and other invertebrate eggs	40-430	50-100	4.270	0.364	475	674	2.028	0.245	14.9	0.7
Copepod nauplii	50-370	40-300	3.088	4.013	1210	441	3.736	1.770	27.5	5.3
Copepodites	80-250	80-450	8.752	14.698	212	393	1.855	5.776	13.6	17.4
Copepod adults	120-390	110-600	25.202	57.418	179	426	4.511	24.460	33.2	73.8
Other	20-470	40-550	16.424	49.401	89	18	1.462	0.889	10.8	2.7
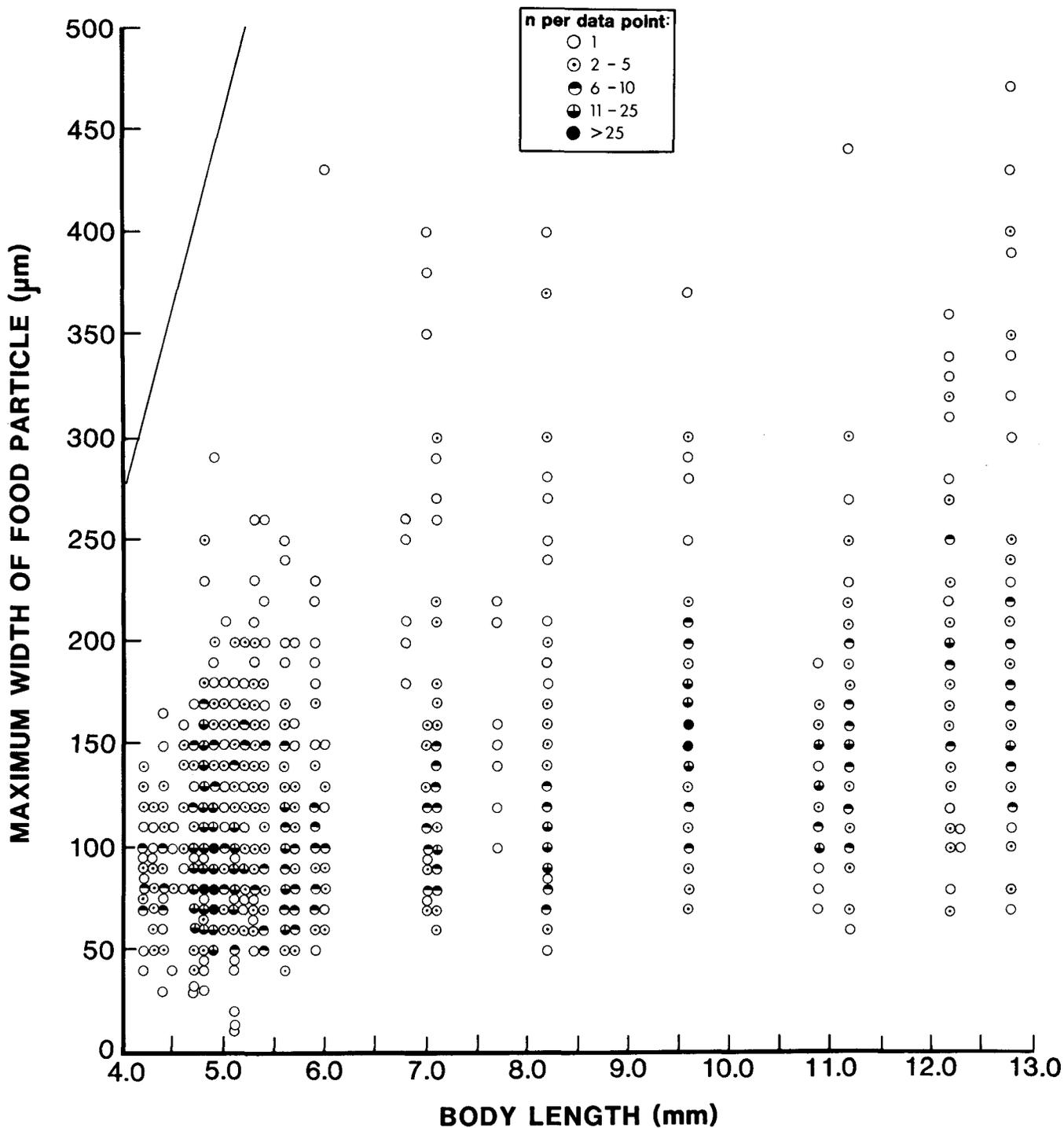
Figure 1. Size of food particles ingested by 66 bocaccio larvae. Oblique line represents maximum mouth width.

ber of food particles (Figure 4). The two plots agree closely except for the single large volume at time 0001-0300. This point represents a single 9.6-mm sample larva (others were empty), which consumed an unusually large number of adult copepods and copepodites.

DISCUSSION

Prey composition in the sample of bocaccio larvae studied is similar to that found in many marine teleosts—a diet dominated by copepod nauplii in the early larval stages, with copepodites and adult copepods becoming increasingly more important in later larval
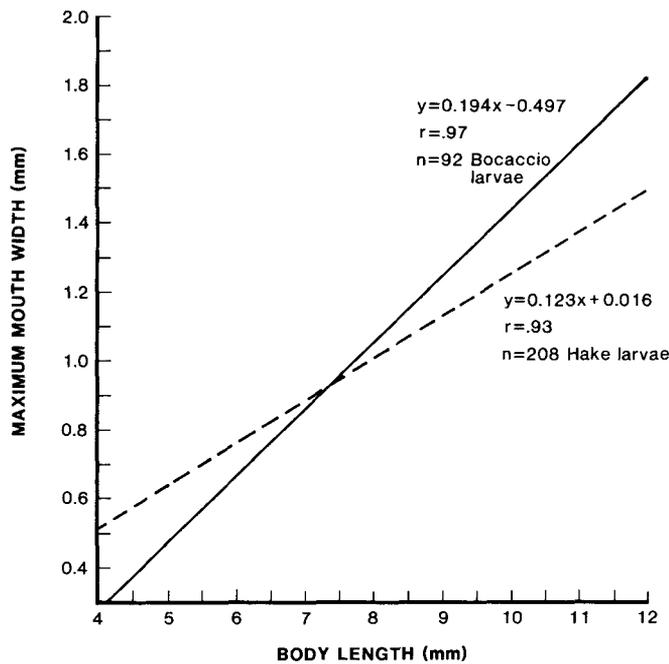
Figure 2. Mouth width of bocaccio (solid line) and Pacific hake (dashed line) larvae.

stages (Arthur 1976; Hunter 1981). The maximum size of prey increases with bocaccio larval growth, although small prey are consumed throughout the larval period, during which the minimum prey size changes little. This pattern contrasts with that seen in hake (*Merluccius productus*) larvae, where copepodites and adult copepods were eaten by the smallest larvae and were predominant prey in larvae larger than 4 mm.

Bainbridge and McKay (1968) observed similar contrasting patterns in two north Atlantic species: the redfish (*Sebastes* spp, a congener of bocaccio) and cod (*Gadus morhua*, a relative of *Merluccius*). Copepod eggs and nauplii dominated the diet of redfish, whereas postnaupliar stages predominated in cod. The contrast in feeding patterns may be partly explained by differences in mouth size: mouths are considerably wider in early hake larvae compared with bocaccio, although this relationship is reversed in larvae larger than 7.5 mm (see Figure 2). Another factor may be the depth distribution of larvae of the two species. Ahlstrom (1959) found *Sebastes* spp larvae in the upper mixed layer and thermocline, with an abundance maximum at about 40 m, whereas hake were within and
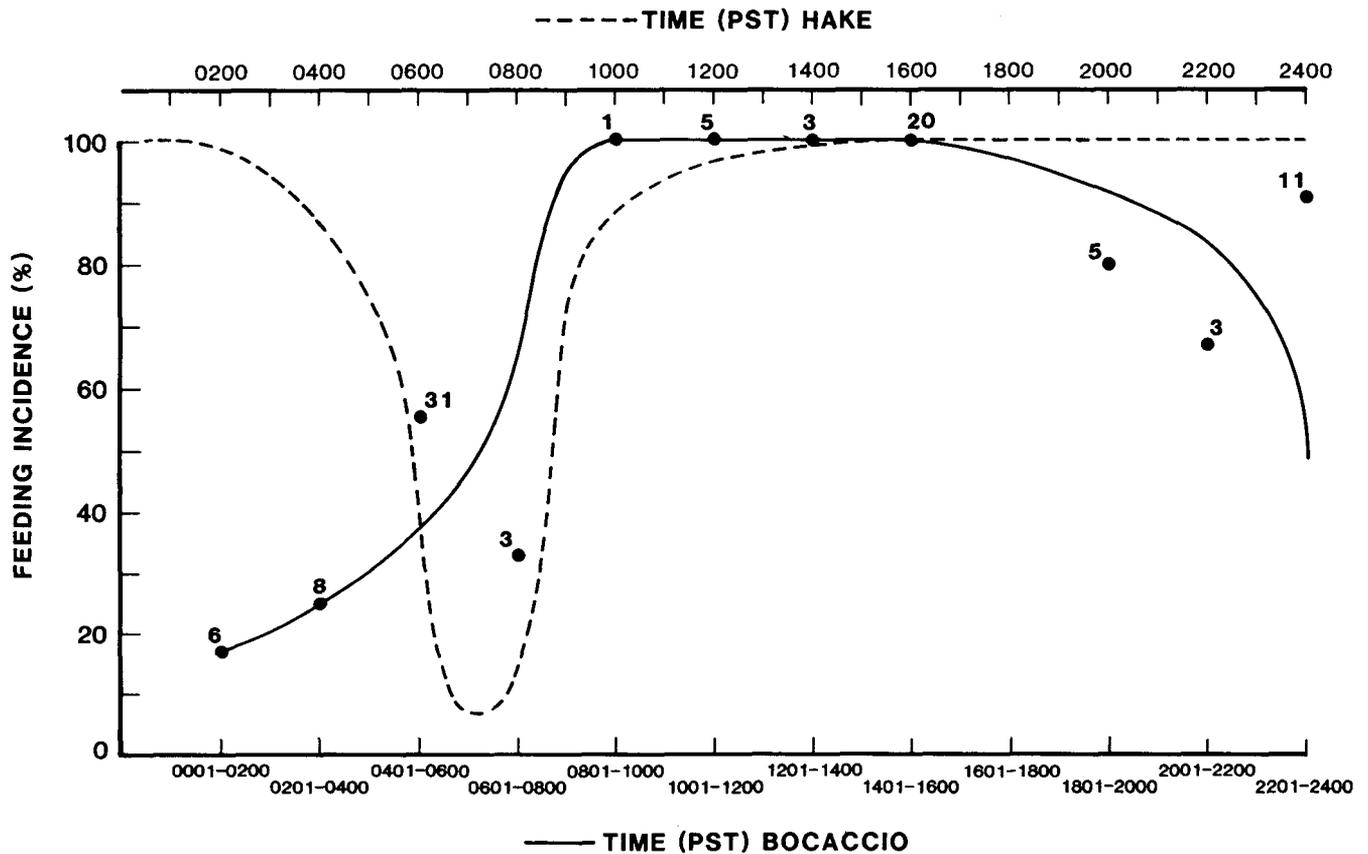
Figure 3. Feeding incidence of bocaccio and Pacific hake larvae at time of capture. Bocaccio data (solid line) grouped in 2-hour intervals, hake data (dashed line) in 1-hour intervals. Values of data points indicate sample size of bocaccio larvae. Curve for hake taken from Sumida and Moser, 1980.
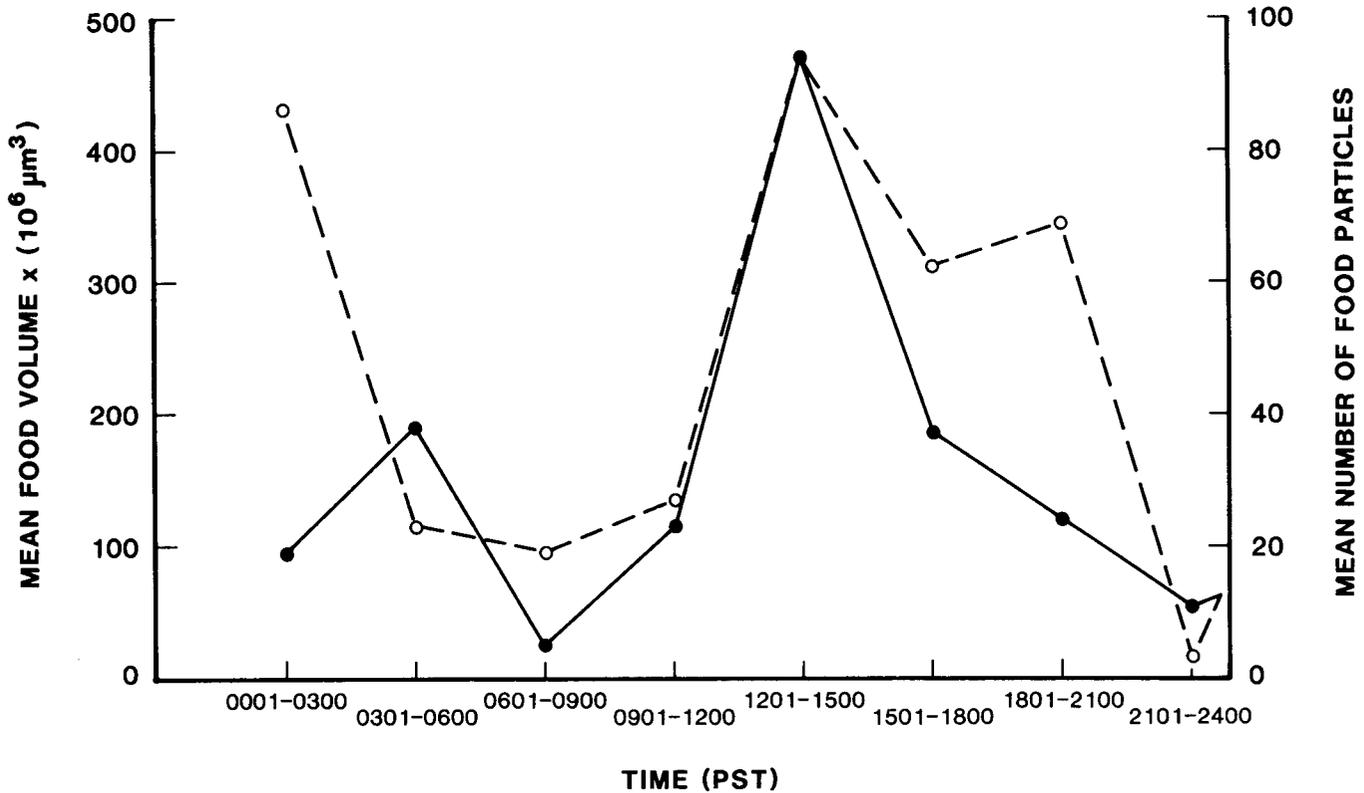
Figure 4. Mean food volume index (dashed line) and mean number of food particles (solid line) of bocaccio larvae. Samples grouped into 3-hour time intervals.

below the thermocline and had a peak abundance at about 70 m. Bailey (1982) examined Ahlstrom's samples of hake larvae for size-related vertical distribution, and found larvae < 8 mm at 50-100-m depth, but larger larvae at greater depths to 300 m. Beers and Stewart (1969) showed a sharp decline in total microzooplankton at about 50 m at several stations off southern California. Although this decline was most marked for tintinnids and other ciliates, it was also evident for naupliar and postnaupliar copepods in the 35-103-μm and > 103-μm size categories. The data suggest that bocaccio are consuming relatively abundant nauplii in their vertical range, while hake are either selecting the larger postnaupliar stages or are capturing them more effectively because their size makes them disproportionately more perceptible at low prey densities.

Arthur (1976) showed a diurnal maximum of feeding incidence in Pacific sardine and northern anchovy, as did Bainbridge and McKay (1968) for redfish and cod. Sumida and Moser (1980) showed that hake reach a peak incidence of 100% at sunset and maintain this until about 0100 hours. Then the incidence declines rapidly until sunrise, when it increases rapidly to 100%. In bocaccio, incidence peaks in midmorning, is maintained at 100% until sunset, then decreases

steadily to a minimum at about 0100 hours. Incidence then begins to increase steadily to the midmorning maximum. The contrasting patterns could be explained by an intrinsically faster rate of digestion and evacuation in bocaccio compared with hake. Another possibility is that prolonged high incidence in hake is related to their larger prey size and the lower temperature of their habitat.

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DIEL VARIATION IN CATCH PARAMETERS FOR FISHES SAMPLED BY A 7.6-M OTTER TRAWL IN SOUTHERN CALIFORNIA COASTAL WATERS

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ABSTRACT

The species composition, diversity, numerical and biomass abundances, and length-frequency distributions of the fishes caught with a 7.6-m otter trawl (1.25-cm stretch mesh cod-end liner) were compared for 13 pairs of day and night samples. Monthly cruises were made from May 1980-May 1981, at two (18-m, 30-m) depths in the region of San Onofre-Oceanside.

The basic diel pattern found was of greater total numbers, total biomass, and species richness at night. Larger catches were made at night for 12 (numbers) and 9 (biomass) of the 20 most abundant species (total trawls). Average weight per fish (all species) and the length-frequency distributions of five of seven species, however, did not differ meaningfully between day and night samples. Nighttime estimates of the grand mean number of species and total fishes (numbers) per tow varied much less (average CVs of 13% and 31%, respectively) than did daytime estimates (CVs of 34% and 83%).

Many nearshore fishes are less contagiously distributed at night, hence samples are more precise. We conclude that, for otter trawls of the specified design towed at 2.3 knots, catch efficiency is greater during the night, even at shallow (18-m, 30-m) depths in turbid coastal waters. Nighttime trawls also provide more data on a greater number of species per unit of effort than daytime trawls. We feel that these advantages of nighttime surveys warrant their extra cost and suggest that night sampling be adopted in future trawl monitoring of fishes in the Southern California Bight.

RESUMEN

Cruceros mensuales, desde Mayo de 1980 hasta Mayo de 1981, se efectuaron con red de arrastre de 7.6 m (copo con malla de 1.20 cm), explorando la zona que se extiende desde San Onofre hasta Oceanside, California, abarcando profundidades de 18 m y 30 m.

En total se realizaron 26 arrastres, 13 de noche y 13 de día. Los peces capturados sirvieron de base para estudios comparativos sobre su distribución, frecuencia de tallas, conjunto de especies, índice de diversidad, abundancia y biomasa.

El patrón diario observado indica capturas nocturnas de mayor magnitud en cuanto a número total, biomasa total y abundancia de especies. Las capturas fueron más abundantes durante la noche para 12 (abundancia numerica) y 9 (biomasa) especies respectivamente, de las 20 especies mas abundantes, considerando todos los arrastres. El peso promedio de los peces (incluyendo todas las especies) y la frecuencia de longitud en cinco de las siete especies consideradas, no presentaron diferencias notables entre las capturas diurnas y nocturnas. Estimaciones del número promedio de especies y número total de peces por arrastre presentan menor variación en las pescas nocturnas (C.V. 13% y 31% respectivamente) que en las diurnas (C.V. 34% y 83% respectivamente).

Muchos peces costeros muestran distribuciones menos congregadas durante la noche, siendo así estas muestras más precisas. Estos resultados señalan que las redes de arrastre del diseño indicado, remolcadas a 2.3 nudos presentan una mayor eficiencia de captura durante la noche, aun a poca profundidad (18 m y 30 m) en aguas costeras y turbias. Los arrastres nocturnos, ademas proporcionan más información sobre un mayor número de especies por unidad de esfuerzo. Se considera que las ventajas proporcionadas por las exploraciones nocturnas compensan el costo adicional. Un programa de arrastres nocturnos es sugerido para las futuras observaciones regulares sobre los peces de la Bahía del Sur de California.

INTRODUCTION

Demersal fishes of the Southern California Bight have been extensively censused with otter trawls over the past two decades (for reviews see SCCWRP 1973 and LACSD 1981). Most trawl data, however, have been restricted to fishes of the outer shelf and slope (SCCWRP 1973) and harbors and embayments (Stephens et al. 1974; Horn and Allen 1981). Undoubtedly this past emphasis has been due to the interest of government agencies in environmental effects caused by waste discharges at deepwater outfalls, and impacts resulting from harbor construction and other

shoreline development. Relatively little is known of the distribution and abundance of the benthic fishes of shallow (<30 m) coastal waters within the bight (Allen 1982).

Gear and sampling techniques have been generally inconsistent among the studies performed by various monitoring agencies. Despite these inconsistencies, several studies (SCCWRP 1973; Mearns 1974; Allen 1976; LACSD 1981) have noted the larger size and more species-rich nature of night catches versus day catches in southern California waters. Numerous studies in other regions have indicated diel differences in the composition, species richness, and numbers of fishes in trawl catches (Roessler 1965; Hoese et al. 1968; Livingston 1976). Other studies have identified many factors, both environmental and related to gear design and technique, contributing to the diel variation (Parrish et al. 1964; Woodhead 1964; Beamish 1966; Blaxter 1970; Sissenwine and Bowman 1978; Bowman and Bowman 1980). To date no one has examined in detail the type and magnitude of diel variation in trawl catches for shelf fishes of the Southern California Bight.

Seasonal phenomena, differences in species composition and abundance with depth, and the interactions of these factors with diel patterns are not elaborated on in this report. A multiple-year diel trawl study of the benthic fishes encountered at six depths between 5 and 100 m off Bolsa Chica (Orange County) should provide a more comprehensive evaluation of biological patterns (M. H. Horn, California State University, Fullerton, pers. comm.).

Our specific objectives in this report are to (1) evaluate the nature and extent of diel differences in the catches of fishes, based on a series of paired, day and night otter trawls made at shallow shelf depths; (2) wherever possible, relate observed differences to plausible factors influencing catchabilities; and (3) discuss the implications of these differences for future coastal monitoring programs in the bight.

MATERIALS AND METHODS

Sampling Design

Thirteen pairs of diel cruises were made over the 13-month interval from May 1980 through May 1981. The two cruises of each pair were 36 hours apart in 11 cases, 60 hours apart in one case, and 10.5 days apart in one case. "Day" samples were made between sunrise and sunset; "night" samples were made between sunset and sunrise. On each cruise four trawl tows were made at each of two (18-m, 30-m) bottom depths, at two longshore locations (Table 1). Longshore locations were 18 km distant, off San Onofre

(33°20'N, 117°30'W) and off Stuart Mesa (33°10'N, 117°20'W), upcoast of Oceanside, San Diego County. (See Plummer et al. 1983 for a chart of the sampling locations.)

We attempted to make all trawl tows a standard distance; length of tow was determined from a combination of permanently moored spar buoys and Motorola Mini-Ranger III signals from a temporarily moored auxiliary craft. Each tow in a series of four trawls thus provided relative abundance (catch per unit of effort, CPUE) data that we could consider as a statistical replicate. Two of the four tows in each series were directed upcoast along the isobath; the other tows were directed downcoast in order to sample any variation in catchability caused by relative directions of the tow and longshore water current. Direction (upcoast, downcoast) and relative speed (nil, mild, strong) of surface current were noted for each trawl. Replicate tows were shifted slightly inshore and offshore in order to avoid resampling trawl tracks. Average duration of tow (time net on the bottom) was 3.5 ± 0.06 (SE) min, and average trawling speed was 2.3 knots for the 104 series of four replicate tows (locations, depths, and diel periods pooled). Mean tow distance was 248 ± 4 (SE) m for the 104 series of tows. Distance of tow was evaluated during a January-April 1980 pilot study in which we determined the shortest distance practical (see Discussion), based on minimizing zero catches of major species.

Gear Design

All samples were taken using the type and size of otter trawl recommended by Mearns and Allen (1978) for biological monitoring in southern California coastal waters. We used a single-warp Marinovitch-type otter trawl, with a 25-ft (7.6-m) headrope and a 29-ft (8.9-m) chain-rigged footrope, manufactured by J. Willis. Body mesh was 1.5 inch (3.8 cm), and the cod-end was fitted with a 0.5-inch (1.25-cm) liner of no. 15 thread nylon. (All measurements are stretch-mesh.) Length of bridles was three times the headrope length. Scope ratio was 5:1 for tows at 18- and 30-m depths.

Types of Data and Analysis Design

Numbers of individual fishes were recorded, by species, for each trawl tow. Biomass (wet weight) also was determined aboard ship for the aggregate of each species in each tow. Weights were recorded to ± 10 g for catches < 1 kg and to ± 0.1 kg for catches > 1 kg.

In addition, various species were selected for determination of length-frequency composition (at one or both trawl depths). Species were one small round-

TABLE 1
Summary of Sampling Effort for the Thirteen Paired Cruises

Longshore location	Depth (m)	No. trawl tows				
		Day		Night		Day & night
		Per cruise	Total	Per cruise	Total	total
San	18	4	52	4	52	104
Onofre	30	4	52	4	52	104
Stuart	18	4	52	4	52	104
Mesa	30	4	52	4	52	104
Both locations	Both depths	16	208	16	208	416

fish—the white croaker, *Genyonemus lineatus* (18, 30 m)—and three species of "small" (10-15 cm standard length, SL) demersal flatfishes—speckled sanddab, *Citharichthys stigmaeus* (18 m); longfin sanddab, *C. xanthostigma* (18, 30 m); and Pacific sanddab, *C. sordidus* (30 m). Also measured were three species of "medium-sized" (15-30 cm SL) flatfishes: fantail sole, *Xystreurys liolepis* (18, 30 m); California halibut, *Paralichthys californicus* (18, 30 m); and hornyhead turbot, *Pleuronichthys verticalis* (18, 30 m). Species were selected because of their numerical dominance in trawls made during the 1980 pilot study.

Standard lengths were recorded to the nearest millimeter aboard ship for a random sample of a maximum of 50 individuals of each selected species present in the four replicate tows. The length-distribution of catches of > 50 individuals was standardized to the total catch. Length data were later sorted and analyzed by 5-mm classes.

The length-frequency distributions of day and night sample fish were compared by Kolmogorov-Smirnov (K-S) two-sample test (Siegel 1956). The mean numerical and biomass abundances of day and night catches were compared for the most common and abundant species using Hotelling's T^2 (Morrison 1976). Additional diel comparisons were made for the CPUE of each of the top 20 ranked species (in day and night samples pooled) and for the aggregate of all fishes trawled. For particular species, we used either Wilcoxon's matched-pairs signed-ranks test (Siegel 1956), or paried t-test (Sokal and Rohlf 1969). Mean species CPUE (8-tow basis if longshore locations could be pooled, 4-tow if they could not) were transformed to common logarithms to normalize distributions before calculating paired t-tests. If transformation did not normalize a distribution, we used Wilcoxon's rank test. We compared relative abundances among species within day and night assemblages by Kendall rank correlation (Siegel 1956). We used either parametric or nonparametric paired comparison tests, as appropriate, for diel contrasts of several representa-

tive types of species diversity and evenness indices. We chose indices to provide a basis for comparison with prior analyses of trawl catches in the bight. In addition to species richness (S), indices used included Gleason's d, Shannon's H', Pielou's J', Simpson's D (the complement of lambda; Peet 1974), and Hill's (1973) numbers and ratios. We further characterized day and night sample assemblages by cluster analysis based on "ecological distance" (Bray-Curtis Index of Dissimilarity; Clifford and Stephenson 1975) of species CPUE, following square root transformation of CPUE to reduce the bias of disproportionately abundant species. All analyses were done using the Statistical Analysis System (Helwig and Council 1979).

RESULTS

General Patterns

Average total catch (numbers and biomass) of all fishes and the numbers of different species per tow did not differ (all $P > 0.10$) between tows made against or with surface currents. Therefore we ignored trawl direction relative to current velocity in the analysis.

On average, a greater number of individual fishes (Tables 2 and 3) whose aggregate weighed more (Tables 2 and 4) were caught in nighttime trawls. Most species were relatively more numerous at night (18 m: Wilcoxon's test, $z = 3.0$, $P = 0.001$; 30 m: $z = 1.75$, $P = 0.04$; Table 3), when catches were heavier (18 m: $z = 2.8$, $P < 0.003$; 30 m: $z = 2.0$, $P = 0.02$; Table 4). Greater mean numbers of species per tow were present in nighttime samples (18 m: $t = -8.1$, $P < 0.001$; 30 m: $t = -5.2$, $P < 0.001$; Table 5). Species richness scaled for the effect of number of individuals in samples (Gleason's index) was greater at night only at 30-m depth off San Onofre (Table 5). Shannon's H', a diversity index that emphasizes the equitability of moderately abundant species (Peet 1974), varied insignificantly ($P > 0.05$) between diel periods at either depth (Table 5). Day samples, however, were significantly ($P < 0.05$) more diverse

TABLE 2
General Catch Statistics and Results of Paired T-Test (or Wilcoxon Matched-Pairs
Signed-Ranks Test) Comparisons of Diel Effects on Mean (Median) Numbers, Biomass, and
Average Body Weight of Fishes Present in Single Trawl Tows

Category	(Depth)	Longshore location(s)	Day		Night		Test statistic	P
			$\bar{x}$	SE	$\bar{x}$	SE		
Total	18	Pooled	27	8	95	10	Paired t = −5.50	<0.001*
numbers	30	Pooled	90	16	190	14	Paired t = −6.15	<0.001*
Total	18	Pooled	3.4	0.6	8.5	1.0	Paired t = −4.33	0.001*
biomass (kg)	30	San Onofre	3.5	1.0	9.1	1.1	Paired t = −4.69	<0.001*
	30	Stuart Mesa	6.8	1.1	13.6	1.5	Paired t = −4.10	0.001*
Average	18	Pooled	199	21	99	8	Paired t = 4.83	<0.001*
body	30	San Onofre	59	11	52	6	Wilcoxon T = 37	>0.1(NS)
weight (g)	30	Stuart Mesa	85	12	67	4	Paired t = 2.69	0.16 (NS)

Sample size for paired comparisons was 13 cruises in all cases. Grand means are based on cruise means comprising either four (or eight, if locations were pooled) tows per cruise. Data for the two longshore locations were pooled only if locations were indistinguishable ($P>0.05$) using the more appropriate paired comparison test. T-test comparisons were made based on raw data, as cumulative frequency distributions of the deltas of raw data were indistinguishable from a normal distribution (K-S tests, $P>0.17$), for all categories except average body weight (San Onofre, 30 m).
*Paired comparison significant at $P \leq 0.05$.

at 18-m (but not at 30-m) depth, based on a number of other indices examined (Table 5). These included Simpson's index and both Hill's (1973) N_1 and N_2. At 18-m depth, daytime collections had a significantly ($P < 0.05$) more even distribution of individuals among species, whether measured by Pielou's J' or Alatalo's (1981) modified ratio of Hill's N_2 to N_1 (Table 5).

Diel differences in species composition were mainly due to the marked dissimilarity in the day-versus-night catches of several fishes (basketweave cusk eel, *Ophidion scrippsae*; plainfin midshipman, *Porichthys notatus*; and California tonguefish, *Symphurus atricauda*) that were typically present or abundant only in night trawls (Tables 3 and 4).

Despite these diel differences in species composition, day and night assemblages (characterized by the top 20 species in total trawls, Tables 3 and 4) were statistically similar for numbers and frequency of occurrence (per cruise) at the two depths (Table 6). However, diel similarity in total biomass was marginal at both depths. The basic numerical similarities of the assemblages sampled at both depths are illustrated by cluster diagrams based on the ecological distance between species within day and night samples (Figure 1).

Abundances of Selected Species

Despite the similar rank abundances of fishes in day and night trawls (Table 6), the mean catches of most of the top 20 species were greater in nighttime tows at each depth and location (numbers: Hotelling's T^2, all $P < 0.005$; biomass: all $P < 0.03$). The average catches of 12 (numbers) or 9 (biomass) of the top 20 species were significantly greater in night samples

(Tables 7 and 8). Daytime catches were larger than nighttime samples for another three (numbers) and two (biomass) species, while catches varied little between diel periods for five and seven species. The species that contributed most to larger nighttime catches were *Genyonemus lineatus*; pink seaperch (*Zalembius rosaceus*); *Ophidion scrippsae*; *Citharichthys xanthostigma*; queenfish (*Seriphus politus*); *Symphurus atricauda*; shovelnose guitarfish (*Rhinobatos productus*); and California skate (*Raja inornata*). Overall, more of the top 20 species were caught in greater abundance during the night at one or the other depth or location than expected by chance alone (numbers: $p = q = 0.5$, P [4 or fewer out of 24 significant cases] $= 0.001$; biomass: P [4 or fewer out of 20] $= 0.006$; binomial test, Siegel 1956). A virtually identical pattern was shown for numbers and biomass (Tables 7 and 8), and, in fact, numerical and biomass rankings were strongly correlated within diel samples at each depth (Kendall's tau, all $P < 0.01$).

Size-Composition of Fishes

The average size of fishes present in day and night samples was similar for all except several of the most common and abundant species at the two depths (Wilcoxon test, both $P > 0.05$; Table 9). This was also generally true for average fish weight in total catches at 30 m (Table 2). At 18 m, the average weight of total fishes caught was greater during the day, primarily because of the somewhat larger body sizes (Table 9) and slightly more numerous daytime catches of *Paralichthys californicus*, a relatively large species (Table 3). The data on average fish weight (Table 9) suggest that the length-frequency distributions of most species

TABLE 3
Composition of Day and Night Trawl Catches Ranked by Numerical Abundances at the Two Sampling Depths

	Numbers			
	18 m		30 m	
	Day	Night	Day	Night
Genyonemus lineatus	1,237	4,028	1,770	5,958
Zalembius rosaceus	1	21	2,629	4,690
Ophidion scrippsae	1	2,871	—	1,754
Citharichthys xanthostigma	253	499	1,064	1,891
Citharichthys sordidus	3	19	1,799	1,766
Seriphus politus	305	1,138	225	1,063
Symphurus atricauda	13	152	182	908
Citharichthys stigmaeus	226	301	370	322
Zaniolepis latipinnis	—	—	424	349
Pleuronichthys verticalis	96	196	124	172
Paralichthys californicus	154	148	69	23
Cymatogaster aggregata	19	70	201	102
Xystreurys liolepis	82	51	122	66
Phanerodon furcatus	196	22	31	22
Porichthys notatus	—	6	17	221
Raja inornata	4	15	37	127
Hippologlossina stomata	—	1	85	91
Hyperprosopon argenteum	100	52	—	—
Icelinus quadriseriatus	3	—	63	86
Rhinobatos productus	16	54	6	20
Synodus lucioceps	27	21	39	9
Paralabrax nebulifer	28	37	17	11
Scorpaena guttata	—	8	10	35
Parophrys vetulus	15	7	16	6
Pleuronichthys ritteri	28	11	—	1
Microstomus pacificus	—	—	12	22
Merluccius productus	—	1	—	28
Hydrolagus colliei	1	4	6	16
Porichthys myriaster	2	5	7	13
Myliobatis californica	5	12	1	—
Menticirrhus undulatus	3	14	—	—
Urolophus halleri	4	9	—	—
Lepidogobius lepidus	—	—	5	3
Damalichthys vacca	2	—	3	2
Hypsopsetta guttulata	4	3	—	—
Chilara taylori	—	—	—	6
Eptatretus stouti	—	—	—	6
Leptocottus armatus	—	—	—	3
Sebastes auriculatus	—	—	—	3
Torpedo californica	—	1	2	—
Paralabrax clathratus	—	1	—	1
Pleuronichthys decurrens	1	1	—	—
Squalus acanthias	1	1	—	—
Sebastes paucispinis	—	—	1	—
Mustelus henlei	—	1	—	—
Pleuronichthys coenosus	—	1	—	—
Stereolepis gigas	—	1	—	—
Brachyistius frenatus	—	1	—	—
Caulolatilus princeps	—	1	—	—
Chitonotus pugetensis	—	—	—	1
Platyrhinoidis triseriata	—	1	—	—
Atractoscion nobilis	—	—	—	1
Total fishes	2,830	9,843	9,337	19,798
Mean total fishes trawl^{-1}	27	95	90	190
Total species	30	40	30	37

Data are the total numbers of individuals of each species caught in 104 trawls depth^{-1} diel period^{-1} pooled over the 13 pairs of monthly cruises. Species are ranked according to their total numerical abundances in all 416 (day, night) trawls pooled. Total number of different species caught is also noted.

TABLE 4
Composition of Day and Night Trawl Catches Ranked by Wet Weight

	Biomass (kg)			
	18 m		30 m	
	Day	Night	Day	Night
Genyonemus lineatus	96.0	318.7	178.7	545.2
Paralichthys californicus	100.00	89.8	52.4	25.8
Ophidion scrippsae	<0.1	173.4	—	88.2
Citharichthys xanthostigma	20.3	38.9	57.1	106.2
Zalembius rosaceus	<0.1	0.3	50.1	92.8
Rhinobatos productus	22.1	63.6	9.2	45.6
Seriphus politus	14.9	40.1	13.1	58.3
Pleuronichthys verticalis	17.6	39.1	20.8	25.3
Raja inornata	3.8	13.6	16.6	41.7
Citharichthys sordidus	<0.1	0.5	28.6	28.8
Xystreurys liolepis	13.2	8.7	17.3	10.5
Symphurus atricauda	0.6	5.5	4.6	28.7
Paralabrax nebulifer	9.0	10.1	11.2	8.4
Torpedo californica	—	13.6	17.4	—
Myliobatis californica	7.1	22.6	0.6	—
Zaniolepis latipinnis	—	—	14.1	10.7
Phanerodon furcatus	15.4	1.4	4.5	2.4
Hippoglossina stomata	—	0.2	9.4	9.2
Scorpaena guttata	—	2.9	4.0	11.4
Hydrolagus colliei	0.8	3.4	4.0	10.0
Synodus lucioceps	6.9	5.6	3.8	1.8
Citharichthys stigmaeus	3.5	4.3	3.7	3.8
Parophrys vetulus	4.8	1.8	6.1	1.5
Cymatogaster aggregata	0.6	1.6	5.0	3.1
Urolophus halleri	2.4	5.4	—	—
Hyperprosopon argenteum	4.5	3.1	—	—
Pleuronichthys ritteri	4.8	1.6	—	0.3
Atractoscion nobilis	—	—	—	5.9
Menticirrhus undulatus	0.6	5.1	—	—
Porichthys myriaster	0.7	2.2	0.4	1.4
Porichthys notatus	—	0.2	0.3	3.9
Squalus acanthias	0.9	3.2	—	—
Microstomus pacificus	—	—	1.3	2.2
Merluccius productus	—	<0.1	—	3.3
Damalichthys vacca	0.6	—	1.3	0.5
Sebastes auriculatus	—	—	—	1.7
Hypsopsetta guttulata	0.9	0.5	—	—
Icelinus quadriseriatus	<0.1	—	0.5	0.6
Eptatretus stouti	—	—	—	0.7
Paralabrax clathratus	—	0.2	—	0.2
Pleuronichthys decurrens	0.1	0.2	—	—
Mustelus henlei	—	0.2	—	—
Platyrhinoidis triseriata	—	0.2	—	—
Stereolepis gigas	—	0.2	—	—
Pleuronichthys coenosus	—	0.1	—	—
Lepidogobius lepidus	—	—	<0.1	<0.1
Chilara taylori	—	—	—	<0.1
Brachyistius frenatus	—	<0.1	—	—
Chitonotus pugetensis	—	—	—	<0.1
Leptocottus armatus	—	—	—	<0.1
Sebastes paucispinis	—	—	<0.1	—
Caulolatilus princeps	—	<0.1	—	—
Total biomass (kg)	352.3	882.4	536.2	1,180.2
Mean total biomass (kg) trawl^{-1}	3.4	8.5	5.2	11.3

Data are the total biomass of each species caught in 104 trawls depth^{-1} diel period^{-1} pooled over the 13 pairs of monthly cruises. Species are ranked according to their total biomass in all 416 (day, night) trawls pooled.

Figure 1. Cluster diagram based on a measure of ecological distance (Bray-Curtis dissimilarity, see text) for fishes present in (A) day and (B) night trawls. Numerical data for the two (18-m, 30-m) sampling depths are combined (Table 3) to illustrate species clusters representative of each depth. Analysis is based on species that occurred in a minimum of ten trawls during one or the other diel period. Note the absence of *Ophidion scrippsae* and *Porichthys notatus* in day trawls.
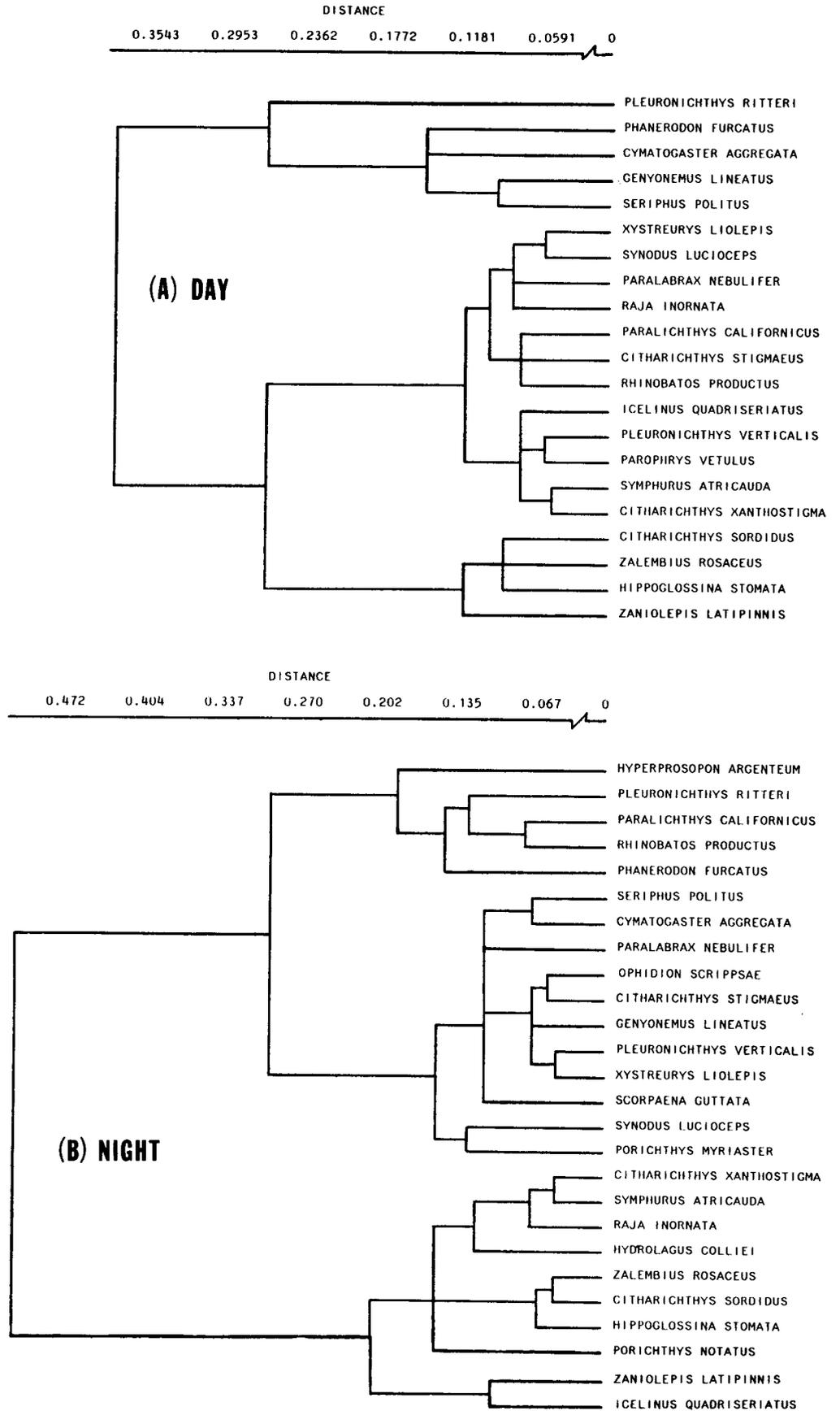
TABLE 5
Diversity of Fishes Present in Trawls as Represented by Nine Different Measures of Sample Species Diversity

Index	Depth	Location(s)	Day	Night
Species richness, S	18	San Onofre	5.0 ± .6	8.0 ± .5*
		Stuart Mesa	5.8 ± .5	9.5 ± .3*
	30	Pooled	9.1 ± .7	12.5 ± .3*
Gleason's d	18	San Onofre	2.0 ± .11	2.1 ± .13
		Stuart Mesa	2.5 ± .12	2.4 ± .15
	30	San Onofre	2.2 ± .15	2.6 ± .08*
		Stuart Mesa	2.6 ± .06	2.6 ± .07
Shannon's H'	18	San Onofre	1.6 ± .08	1.5 ± .08
		Stuart Mesa	1.8 ± .08	1.6 ± .09
	30	Pooled	1.9 ± .03	1.9 ± .04
Pielou's J'	18	Pooled	0.7 ± .04*	0.5 ± .02
	30	Pooled	0.6 ± .02	0.6 ± .02
D = (1-Simpson's λ)	18	Pooled	0.8 ± .03*	0.7 ± .02
	30	Pooled	0.8 ± .01	0.8 ± .01
Hill's N_1 = (exp H')	18	San Onofre	5.2 ± .38	4.7 ± .40
		Stuart Mesa	6.5 ± .48*	5.1 ± .52
	30	Pooled	6.6 ± .21	7.0 ± .29
Hill's N_2 = (1/λ)	18	Pooled	5.6 ± .63*	3.4 ± .21
	30	Pooled	4.8 ± .20	4.9 ± .29
Hill's ratio = (N_2/N_1)	18	Pooled	0.8 ± .04*	0.7 ± .01
	30	Pooled	0.7 ± .02	0.7 ± .02
Modified Hill's ratio = {($N_2 - 1$)/($N_1 - 1$)}	18	Pooled	0.7 ± .05*	0.6 ± .01
	30	Pooled	0.7 ± .02	0.6 ± .02

Indices tested were Gleason's index of species dominance; Shannon's index of diversity; Pielou's evenness; the complement of Simpson's index of concentration; Hill's N_1 and N_2; Hill's ratio (Peet 1974); and modified Hill's ratio (Alatalo 1981). Means ± one standard error (n = 13) are provided for each index. The data for each cruise are either the sum of 8 or 4 trawls, depending on whether data for the two longshore locations were indistinguishable ($P > 0.05$) with a diel period at a depth and thereafter pooled or not.
*P ≤ 0.05 that measure is not more diverse or even during the particular diel period.

measured did not differ between day and night samples; and this was, in fact, the case (Table 10). The size-composition of day and night sample fish did not vary meaningfully for any of the three species of "small" or for two of the three "medium-sized" flatfishes that we measured (Figures 2 and 3). Large sample sizes (great power), however, allowed detection of

TABLE 6
Results of Kendall's Rank Correlation between the Relative (Rank) Abundances and Frequency of Occurrence of Fishes in Day Versus Night Trawls

Measure of abundance	Depth (m)	Locations	Kendall's tau	N	P
Numbers	18	Pooled	0.40	20	0.01*
	30	Pooled	0.52	20	0.001*
Biomass	18	Pooled	0.29	20	0.07
	30	Pooled	0.26	20	0.10
Frequency of occurrence	18	Pooled	0.54	27	0.0002*
	30	Pooled	0.57	33	<0.0001*

Analysis (numbers and biomass) limited to the 20 most abundant species (longshore locations and diel periods pooled) at each sampling depth. Analysis (frequency occurrence depth^{-1} cruise^{-1}) limited to species that occurred in samples collected on ≥3 cruises during either or both diel periods. Longshore locations were pooled in all cases because rankings were invariably concordant ($P < 0.05$) between locations.
*Significant at P ≤ 0.05.

real, but trivial (3%) cumulative differences in length-frequency distributions for two species of sanddabs (Figure 2, Table 10). *Paralichthys californicus* caught at 18 m differed little in size between day and night samples (Figure 4, Table 10). At 30 m, however, *P. californicus* > 40 cm SL were more common (2 x 4 x^2 = 38.6, 3 df, $P < 0.001$) in night versus day samples than were halibut < 40 cm SL (Figure 4), even though meager data made evaluation based on small length intervals impractical using K-S tests. Diel size-frequency data for *Genyonemus lineatus* were trivially (1%) different at 18-m depth, but length-frequencies differed by a cumulative 10% at 30 m (Figure 5, Table 10). Greater nighttime catches of *G. lineatus* < 14 cm reversed (Table 9) the otherwise larger average body size of *G. lineatus* caught at 30 m during the night (Figure 5).

Precision of the Trawl Estimates

Table 11 lists the coefficients of variation (CV = standard deviation mean $^{-1}$; Sokal and Rohlf 1969) of the grand arithmetic means of numerical and biomass CPUE for total fishes present in day and night trawls. For total fishes, CVs averaged 63% and 40% smaller for numbers and biomass, respectively, during night
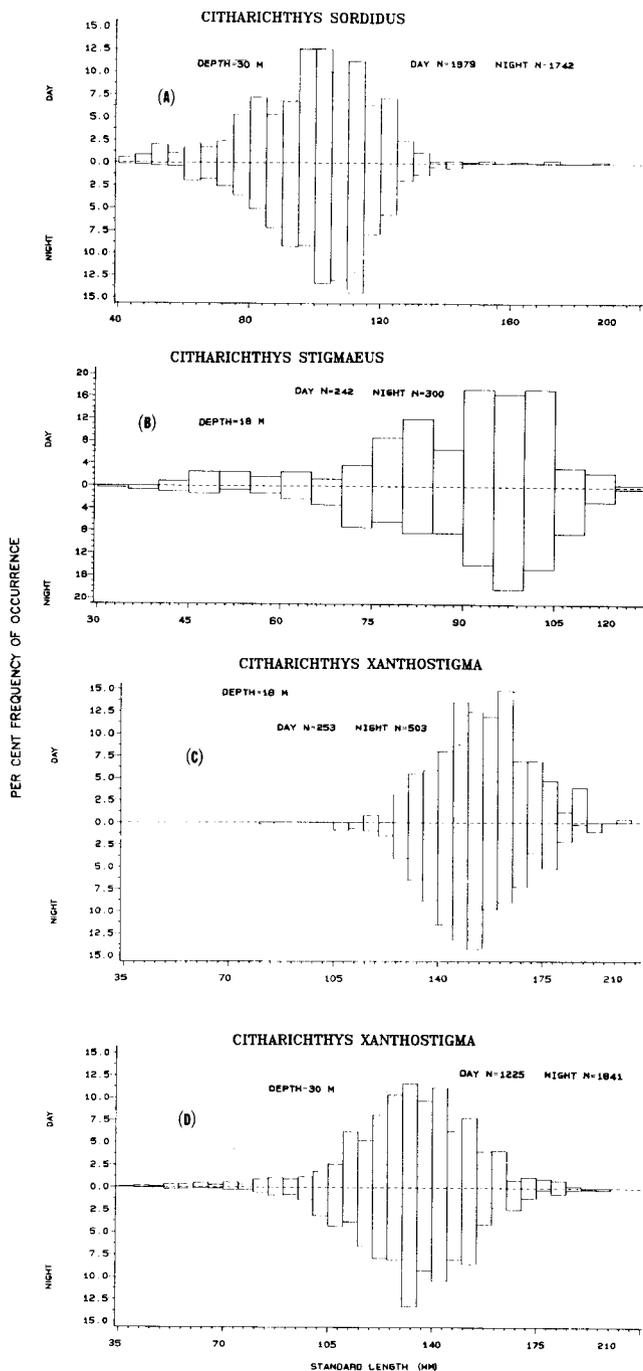
Figure 2. Length-frequency distributions of each of three species (*Citharichthys sordidus, C. stigmaeus, C. xanthostigma*) of "small" (10-15 cm SL) demersal flatfishes present in day and night trawls.

Figure 3. Length-frequency distributions of each of two species (*Pleuronichthys verticalis, Xystreurys liolepis*) of medium-sized (15-30 cm SL) demersal flatfishes present in day and night trawls.

versus day trawls. The CVs of mean weight per fish averaged 38% smaller for night trawls. The CVs of nighttime trawl CPUE were consistently smaller for 12 and 9 of the top 20 species, based on numbers and biomass, respectively. The number of instances in which nighttime catches had smaller CVs than day samples was greater than expected ($p = q = 0.5$, binomial test) based on chance alone for numbers (P [11 or fewer out of 38 nominally different cases] $<$ 0.01), but not for biomass (P [15 or fewer out of 34] $>$ 0.30). On average, the CVs of nighttime trawl samples for the top 20 species were 16% (numbers) and 11% (biomass) smaller than the CVs of corresponding daytime samples.

Estimates of diversity also were more precise when based on night trawl data. The CVs of numbers of species per tow (species richness) averaged 62% smaller for nighttime trawls (Table 11). The CVs of the remaining eight indices (Table 5) ranged from about 70% smaller to 40% larger for night compared to daytime trawl data.

TABLE 7
**Paired T-Test (or Wilcoxon Matched-Pairs Signed-Ranks Test) Comparisons of
Diel Effects on the Mean (Median) Numerical Catch per Trawl for 20 Species**

Species	Depth	Location(s)	Diel differences in catch (numbers)			
			Test statistic	N	P	Conclusion
Cymatogaster	18	Pooled	Paired t = −2.7	13	0.02*	N>D
aggregata	30	San Onofre	Wilcoxon T = 5.5	7	>0.10	N=D
		Stuart Mesa	Paired t = 1.3	13	0.21	N=D
Citharichthys sordidus	30	Pooled	Paired t = −1.2	13	0.26	N=D
Citharichthys	18	Pooled	Paired t = −2.4	13	0.03*	N>D
stigmaeus	30	San Onofre	Paired t = 1.1	13	0.30	N=D
		Stuart Mesa	Paired t = 1.3	13	0.21	N=D
Citharichthys	18	San Onofre	Paired t = 0.03	13	0.97	N=D
xanthostigma		Stuart Mesa	Paired t = −4.9	13	<0.001*	N>D
	30	San Onofre	Paired t = −3.0	13	0.01*	N>D
		Stuart Mesa	Paired t = −3.9	13	0.002*	N>D
Genyonemus	18	Pooled	Paired t = −4.3	13	0.001*	N>D
lineatus	30	San Onofre	Paired t = −6.4	13	<0.001*	N>D
		Stuart Mesa	Paired t = −2.9	13	0.01*	N>D
Hyperprosopon	18	San Onofre	Paired t = −0.1	13	0.95	N=D
argenteum		Stuart Mesa	—insufficient data—			
Hippoglossina stomata	30	Pooled	Paired t = −0.4	13	0.67	N=D
Icelinus	30	San Onofre	Wilcoxon T = 9	6	>0.10	N=D
quadriseriatus		Stuart Mesa	Paired t = 0.3	13	0.74	N=D
Ophidion	18	Pooled	Paired t = −28.5	13	<0.001*	N>D
scrippsae	30	Pooled	Paired t = −19.5	13	<0.001*	N>D
Paralichthys	18	Pooled	Paired t = 0.6	13	<0.56	N=D
californicus	30	Pooled	Paired t = 3.2	13	0.008*	D>N
Phanerodon	18	Pooled	Paired t = 3.8	13	0.003*	D>N
furcatus	30	Pooled	Paired t = 1.4	13	0.20	N=D
Porichthys notatus	30	Pooled	Paired t = −4.8	13	<0.001*	N>D
Pleuronichthys	18	San Onofre	Paired t = −5.2	13	<0.001*	N>D
verticalis		Stuart Mesa	Paired t = −0.6	13	0.57	N=D
	30	Pooled	Paired t = −1.8	13	0.10	N=D
Raja inornata	30	Pooled	Paired t = −7.8	13	<0.001*	N>D
Rhinobatos productus	18	Pooled	Paired t = −2.6	13	0.02*	N>D
Symphurus	18	Pooled	Paired t = −4.1	13	0.001*	N>D
atricauda	30	San Onofre	Paired t = −2.2	13	0.04*	N>D
		Stuart Mesa	Paired t = −6.4	13	<0.001*	N>D
Seriphus	18	Pooled	Paired t = −3.7	13	0.003*	N>D
politus	30	Pooled	Paired t = −4.9	13	<0.001*	N>D
Xystreurys	18	Pooled	Paired t = 2.1	13	~0.05*	D>N
liolepis	30	Pooled	Paired t = 4.6	13	<0.001*	D>N
Zaniolepis latipinnis	30	Pooled	Wilcoxon T = 31.5	12	>0.10	N=D
Zalembius	30	San Onofre	Paired t = −3.5	13	0.004*	N>D
rosaceus		Stuart Mesa	Paired t = −1.5	13	0.17	N=D

Species selected are the top 20 ranked in terms of numbers in the total of 416 trawls made at both depths and locations, during both diel periods.
*Significant at $P \leq 0.05$.

DISCUSSION

Diel Variations in Species Composition and Richness

The conspicuous absence of certain species in day-time trawls was one of the more notable diel differences that we observed. *Ophidion scrippsae* was virtually absent in our daytime trawl catches (Tables 3 and 4; Figure 1). Two species of midshipman, particularly the smaller and more numerous *Porichthys nota-*

TABLE 8
Paired T-Test (or Wilcoxon Matched-Pairs Signed-Ranks Test) Comparisons of
Diel Effects on the Mean (Median) Catch (Biomass) per Trawl for 18 Species

| Species | Depth | Location(s) | Diel differences in catch (biomass) | | | |
			Test statistic	N	P	Conclusion
Citharichthys sordidus	30	Pooled	Paired t = −1.2	13	0.26	N = D
Citharichthys xanthostigma	18	San Onofre	Wilcoxon T = 17	8	>0.10	N = D
		Stuart Mesa	Paired t = −5.4	13	<0.001*	N>D
	30	San Onofre	Paired t = −2.5	13	0.03*	N>D
		Stuart Mesa	Paired t = −3.1	13	0.009*	N>D
Genyonemus lineatus	18	Pooled	Paired t = −4.3	13	0.001*	N>D
	30	San Onofre	Paired t = −5.0	13	<0.001*	N>D
		Stuart Mesa	Paired t = −2.6	13	0.02*	N>D
Hippoglossina stomata	30	Pooled	Paired t = 0.5	13	0.64	N = D
Hydrolagus colliei	30	San Onofre	Wilcoxon T = 5	9	<0.05*	N>D
		Stuart Mesa	—insufficient data—			
Ophidion scrippsae	18	Pooled	Paired t = −34.3	13	<0.001*	N>D
	30	Pooled	Paired t = −38.7	13	<0.001*	N>D
Paralabrax nebulifer	ι18	San Onofre	Paired t = −0.2	13	0.85	N = D
	30	Stuart Mesa	Paired t = 1.2	13	0.26	N = D
		Pooled	Paired t = 0.5	13	0.60	N = D
Paralichthys californicus	18	Pooled	Paired t = 0.8	13	0.43	N = D
	30	Pooled	Paired t = 2.0	13	0.06	N = D
Phanerodon furcatus	18	Pooled	Paired t = 3.6	13	0.003*	D>N
	30	Pooled	Paired t = 2.2	13	0.04*	D>N
Pleuronichthys verticalis	18	Pooled	Paired t = −3.9	13	0.002*	N>D
	30	Pooled	Paired t = −1.2	13	0.26	N = D
Raja inornata	30	Pooled	Paired t = −2.4	13	0.03*	N>D
Rhinobatos productus	18	Pooled	Paired t = −1.7	13	0.11	N = D
Scorpaena guttata	30	Pooled	Paired t = −1.7	13	0.11	N = D
Seriphus politus	18	Pooled	Paired t = −2.0	13	0.07	N = D
	30	Pooled	Paired t = −4.1	13	0.002*	N>D
Symphurus atricauda	18	San Onofre	Wilcoxon T = 1	6	>0.05	N = D
		Stuart Mesa	Paired t = −6.4	13	0.001*	N>D
	30	San Onofre	Paired t = −6.4	13	<0.001*	N>D
		Stuart Mesa	Paired t = −5.7	13	<0.001*	N>D
Xystreurys liolepis	18	Pooled	Paired t = 2.1	13	~0.05*	D>N
	30	Pooled	Paired t = 3.6	13	0.004*	D>N
Zalembius rosaceus	30	San Onofre	Paired t = −3.2	13	0.007*	N>D
		Stuart Mesa	Paired t = −1.8	13	0.10	N = D
Zaniolepis latipinnis	30	San Onofre	Wilcoxon T = 26.5	13	>0.10	N = D
		Stuart Mesa	Paired t = 0.1	13	0.93	N = D

Species selected are 18 of the top 20 ranked in terms of biomass in the total of 416 trawls made at both depths and locations, during both diel periods. Data were statistically intractable for the remaining two species.

*Significant at $P \leq 0.05$.

tus, were also more abundant on nighttime cruises (Tables 3 and 4; Figure 1). Wenner (1983) has recently noted some striking parallels in the diel trawl catches of several ophidioids and one species of midshipman in the South Atlantic Bight. Our nighttime catches of California tonguefish (Symphurus atricauda) also were large relative to daytime trawls.

It is obvious that the striking differences in the day-versus-night catches of these species reflect behavior patterns that make them largely inaccessible to trawls during the day, yet very susceptible to capture at night. Ophidion scrippsae is a burrow-dwelling cusk eel that is active only at night and at other times when illumination near the seabed is low either because of

TABLE 9

Average Biomass (Wet Weight) Per Individual for Selected Species Present in Day Versus Night Trawls

	Average biomass (g)			
	18 m		30 m	
	Day	Night	Day	Night
Genyonemus lineatus	78	79	101	92
Zalembius rosaceus	—	—	19	20
Ophidion scrippsae	—	60	—	50
Citharichthys xanthostigma	80	78	54	56
Citharichthys sordidus	—	—	16	16
Seriphus politus	49	34	58	55
Symphurus atricauda	—	—	26	32
Citharichthys stigmaeus	16	14	10	12
Zaniolepis latipinnis	—	—	33	31
Pleuronichthys verticalis	183	200	168	147
Cymatogaster aggregata	30	24	25	30
Paralichthys californicus	649	607	759	1,123
Xystreurys liolepis	161	171	142	158
Phanerodon furcatus	79	62	144	107
Porichthys notatus	—	—	16	18
Raja inornata	—	—	448	328
Hyperprosopon argenteum	45	60	—	—
Icelinus quadriseriatus	—	—	8	7
Hippoglossina stomata	—	—	111	101
Paralabrax nebulifer	323	274	—	—
Rhinobatos productus	1,382	1,178	—	—
Synodus lucioceps	255	268	—	—

Only species represented by ≥ 15 individuals per diel period in trawls made at the respective sampling depth are included. Absence of *Ophidion scrippsae* from nearly all daytime trawls precluded comparison for this species.

Figure 4. Length-frequency distributions of a third species of medium-sized (15-30 cm SL) flatfish, *Paralichthys californicus*, present in day and night trawls at each of the two sampling depths.

very turbid water or greatly reduced light (Greenfield 1968). *Ophidion scrippsae* apparently leave their burrows at night to feed on epibenthic invertebrates (Allen 1982). Juvenile (Arora 1948) and adult *Porichthys notatus* cover themselves with sediment on the surface of the seabed during the day, and rise into the water column at night to feed on planktonic organisms (Ibara 1970, Allen 1982). Studies of the feeding habits

of *Symphurus atricauda* confirm its nocturnal activity pattern (Telders 1981; Manzanilla and Cross 1982). At least *O. scrippsae* and *S. atricauda* are primarily non-visual feeders (Allen 1982), so visual avoidance of trawls may be relatively low (hence catchability high) at night.

Species richness (number of species per tow), the simplest measure of diversity, was generally greater at

TABLE 10

Results of Kolmogorov-Smirnov Two-Sample Comparisons of the Length-Frequency Distributions of Selected Species Present in Trawls

Species	Depth (m)	Day	Night	D_{max}	D_{crit}	P
Genyonemus lineatus	18	1,267	4,025	.05	.04	.02>P>.01*
	30	2,144	5,958	.13	.03	<0.001*
Paralichthys californicus	18	165	141	.10	.16	>0.1(NS)
Citharichthys xanthostigma	18	253	503	.13	.10	0.01*
	30	1,225	1,841	.02	.05	>0.1(NS)
Citharichthys sordidus	30	1,979	1,742	.07	.04	<0.001*
Citharichthys stigmaeus	18	242	300	.05	.12	>0.1(NS)
Xystreurys liolepis	30	133	66	.13	.20	>0.1(NS)
Pleuronichthys verticalis	18	108	198	.09	.16	>0.1(NS)
	30	137	166	.13	.16	>0.1(NS)

No *Citharichthys stigmaeus* were measured from 30-m trawls. Too few *Citharichthys sordidus* and *Xystreurys liolepis* were caught at 18 m, and too few *Paralichthys californicus* at 30 m, to warrant two-sample K-S tests. D_{max} refers to the maximum observed deviation between day and night length-frequency distributions. D_{crit} is the critical value at $\alpha_2 = 0.05$.
*Significant at $P ≤ 0.05$.

GENYONEMUS LINEATUS
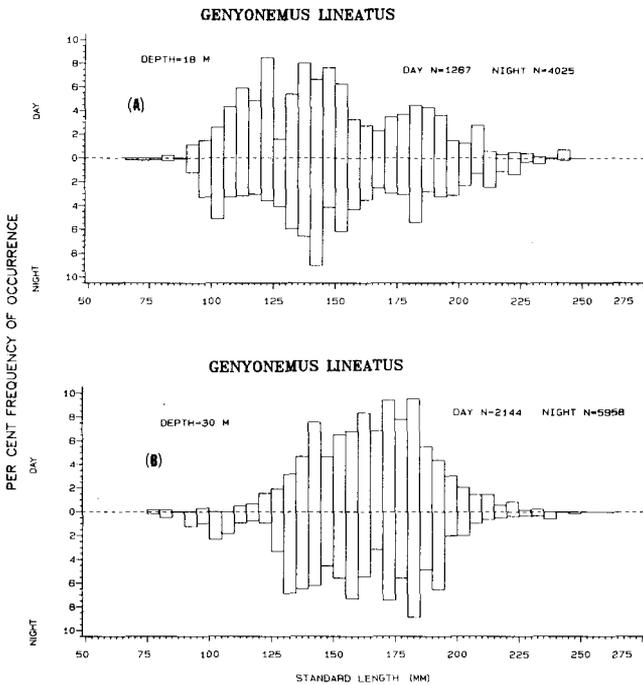
Figure 5. Length-frequency distributions of a small roundfish (*Genyonemus lineatus*) present in day and night trawls at each of the two sampling depths.

TABLE 11

Coefficients of Variation (CVs) of Grand Means of the Total Number, Biomass, Average Body Weight (All Species), and Species Richness per Single Trawl Tow

Category	Depth	Location(s)	CV (%)	
			Day	Night
Total numbers	18	Pooled	100	36
	30	Pooled	65	26
Total biomass (kg)	18	Pooled	63	43
	30	San Onofre	99	44
	30	Stuart Mesa	55	39
Average body weight (g)	18	Pooled	38	30
	30	San Onofre	67	41
	30	Stuart Mesa	50	21
Species richness, S	18	San Onofre	43	20
	18	Stuart Mesa	33	12
	30	Pooled	26	8

See Table 2 for rationale behind whether longshore locations were pooled or not.

night than during the day (Table 5), largely because of night-active species such as *Ophidion* and *Porichthys*.

There was an average 37%-64% increase in the number of species per tow at night (Table 5). Other researchers have also noted the generally greater species richness of nighttime trawl catches, both within the bight and elsewhere. Night sampling averaged over twice the number of species in a limited day-night comparison based on an unpaired series of 4 nighttime versus 15 daytime trawls made along the 61-m contour off Palos Verdes from 1970-72 (LACSD 1981). Allen (1976), in his study of the fishes of Newport Bay within the central bight, trawled an average of 58% more species per tow at night. Nighttime trawls also provided an average maximum of 2.5 times as many species per trawl in a study of the fishes of Biscayne Bay, Florida (Roessler 1965). A similar average maximum of 2.4 times as many species of fishes per trawl was noted by Hoese et al. (1968) at Aransas Pass Inlet, Texas. Livingston (1976) found a mean increase of 19% in the number of species per trawl at night in a study of the benthic fishes of Apalachicola Bay, Florida.

Increased species richness at night undoubtedly reflects the availability of night-active species (Hoese et al. 1968; Allen 1976). Greater richness probably is also due to general increases in catchability at night (Blaxter et al. 1964; Blaxter and Parrish 1965). If

fishes are generally more susceptible to capture at night (see reference below), it is more probable that greater numbers of relatively rare species will be encountered then. These influences of diel variations in trawl catches are likely to be general, since they appear to transcend habitat as well as geographic region (Wenner 1983).

Diel Variations in Weighted Diversity and Evenness

Gleason's d, a measure of species richness standardized for the influence of variable sample size (number of individuals caught) on richness (Peet 1974), was significantly greater at night for only one of four sample cases (Table 5). We feel that this is due to the inappropriate and simplistic assumption that the richness of samples is accurately standardized by the logarithm of the numbers of individuals caught. We concur with Green (1975) that the Gleason index is a poor measure of species diversity for benthic assemblages sampled by otter trawls in the Southern California Bight.

The general equivalence of weighted diversity and evenness values for day and night trawls (Table 5) was unexpected. In fact, the greater diversity and evenness (J') of daytime 18-m trawls were opposite our predictions, since there was prior reason (LACSD 1981) to have expected greater nighttime diversity. Lower values of Simpson's dominance (one minus lambda) for daytime 18-m trawls were supported by analogous results using Hill's (1973) N_2, a more accurate characterization of Simpson's index (Routledge 1979). Hill's N_1, thought to be a more accurate analogue of Shannon's diversity index (Routledge 1979), in fact was sensitive enough to detect a diel difference at 18 m, whereas Shannon's index was not (Table 5). The grea-

ter evenness of daytime 18-m samples is substantiated by Alatalo's modification of Hill's N_2/N_1 ratio, a less-biased measure of evenness than Pielou's J' (Alatalo 1981).

Hill's (1973) numbers and ratios have heretofore not been used to describe sample assemblages of benthic fishes in the bight. We encourage their use because recent developments in diversity theory have demonstrated their greater accuracy. However, we acknowledge that most patterns of interest are likely to be gross enough to trivialize the biases resolved by these new indices. We have provided these new measures for the sake of completeness and to facilitate future comparisons.

Greater diversity and evenness at 18 m during the day, although unexpected, is not enigmatic in retrospect. The relatively few moderately abundant species (like *Genyonemus lineatus* and *Seriphus politus*) present in daytime 18-m trawls produced an apparently "even" distribution of numbers among species compared to night samples at 18 m. At 30 m there were disproportionately more species that were numerically dominant during both diel periods (Table 3).

Diel Variations in Relative Abundances

Most of the abundant and frequently encountered species were caught in similar proportions during both diel periods (Table 6). The aforementioned differences in species composition of day-versus-night trawls, although striking for a few species, were insufficient to override general similarities in rank CPUE. This suggests that fish "communities" (*sensu* Allen 1982) based on assemblages sampled by otter trawls are equivalently (and oversimplistically) described by rank-order statistics such as Kendall's tau using either day or night trawl data. We feel that these types of characterizations may disregard important differences in functionally dominant species by overemphasizing the similarities of other abundant species. This is probably the reason that the similarity between diel periods was marginally insignificant for the biomass of assemblages sampled at 18-m and 30-m depths (Table 6). Specifically, the presence of many species of relatively rare, but large-bodied fishes in night trawls introduced more diel dissimilarity to the abundance rankings based on biomass versus numbers (Tables 3 and 4).

Diel Variations in Abundance of Major Species

Our total fish catches averaged 2.1-3.5 times larger at night for numbers, and 2.0-2.6 times larger for biomass (Table 2). Obviously, most species are more catchable at night. We can only speculate as to why catches of white seaperch (*Phanerodon furcatus*), fan-

tail sole (*Xystreurys liolepis*), and *Paralichthys californicus* were generally larger during the day. Perhaps the distribution of *P. furcatus* is centered at 18 m and shallower during daylight, since the species is commonly observed in shallow areas by day (Ebeling et al. 1980). There are only meager data to suggest how *P. californicus* and *X. liolepis* might be more catchable during the day, perhaps because of more effective herding by trawls. *P. californicus* is an "ambusher" that lies buried in wait for free-swimming prey. Its habits are primarily diurnal (Allen 1982), so it might be herded more effectively during the day. *X. liolepis* is a "stalker-ambusher" of motile, epibenthic decapods; however, its diel habits are uncertain, so its response to the trawl is unknown.

Numerically larger catches also have been reported at night for research trawls made elsewhere in the bight and in other regions. For example, an average sixfold increase in total numerical catch was reported for nighttime trawls in the aforementioned survey at 61-m depth off Palos Verdes (LACSD 1981). Nighttime trawls averaged 162% and 24% larger for numbers and biomass, respectively, in Allen's (1976) Newport Bay study. Night otter trawl catches exceeded day catches by 33% for numbers and 101% for biomass in a study of the fishes from the Cabrillo Beach section of Los Angeles Harbor (Allen et al. 1983). At night, Roessler (1965) caught an average of twice as many individual fishes per trawl. Nighttime trawls also averaged 1.3- to 9.2-fold larger for total numbers of fishes in the Aransas Pass study (Hoese et al. 1968). Total fish catches averaged 73% larger at night in Livingston's (1976) diel trawl study.

In summary, various diel research studies indicate generally greater catches by otter trawls at night. Numerous evaluations of fisheries trawl data (e.g., Parrish et al. 1964; Woodhead 1964; Beamish 1966) have reached the same conclusion.

Diel Variations in Size-Composition

Diel differences in the size-composition of fishes were evident only for one roundfish (*Genyonemus lineatus*) and one medium-sized flatfish (*Paralichthys californicus*, see below) out of the seven species for which length measurements were taken (Table 10 and Figures 2-5). The average weight of *G. lineatus* captured was equivalent in day and night trawls (Table 9). However, this average value is misleading because at least several size-modes of fish are involved; Figure 5 illustrates that proportionally greater numbers of small (< 14 cm) *G. lineatus* were captured in night trawls at 30 m. Adult white croaker migrate offshore from 5- to 10-m depths at dusk (Allen and DeMartini 1983). Perhaps, like *Seriphus politus* (DeMartini et al., in

press), the proportion of smaller *G. lineatus* present at a given bottom depth is greater at night than during the day.

For all species of small and two of the three species of medium-sized flatfishes measured, diel differences in length composition were trivial (Table 10; Figures 2 and 3). The average body weight per individual fish differed little between day and night for these and other flatfishes, as well as most other species abundant in our trawls (Table 9).

Little comparative data on average fish size exists for other research trawl studies; biomass data have usually not been provided in addition to numerical CPUE (Roessler 1965; Hoese et al. 1968; Livingston 1976). Commercial trawl data, however, generally indicate that nighttime trawls catch larger individual fish of a given species (Parrish et al. 1964; Woodhead 1964; Beamish 1966). This might reflect, as Jones (1956) implies, the fact that research trawls, with their typically fine-mesh (0.75 or 1.25 cm) cod-end liners generally vary less in their catch efficiencies between day and night than do their larger-mesh, commercial counterparts.

We feel that the average body sizes of the fishes caught in our day and night trawls were generally indistinguishable (Table 2) because most individuals in the populations sampled were juveniles (see Sherwood 1980) and other fishes too small to outswim a 7.6-m otter trawl towed at > 2 knots. One notable exception to this general rule illustrates this. The average body size of juvenile-small adult California halibut, *Paralichthys californicus*, increases with bottom depth over the range of 6-30 m (Plummer et al. 1983). Halibut of equivalent 25-40 cm SL were captured both day and night at 18 m (Figure 4A). At 30 m, however, where *P. californicus* > 30 cm SL are more abundant, relatively more fish > 40 cm long were caught at night (Figure 4B). It is likely that halibut > 40 cm SL are better able to avoid our trawls during the day. Most species of large, mobile fishes, though, probably avoid the trawl effectively any time.

Diel Contrasts of Precision

Precision based on CVs was consistently greater and, in many cases, increased > 50% when abundance (CPUE) and other variables were estimated using nighttime rather than daytime trawl data (Table 11). This undoubtedly reflects the fact that many nearshore fishes are more contagiously distributed during daylight (also see Allen and DeMartini 1983). No day-night comparisons of precision are available for otter trawl data elsewhere in the Southern California Bight, but several analogous studies made in widely separated geographic areas have had similar findings.

Roessler's (1965) trawl study produced CVs that averaged 23% and 7% smaller at night for estimates of species richness and total fishes (numbers), respectively. Roessler used a relatively small 10-ft (3.1-m) otter trawl, towed for 2 minutes, with two replicates per station-cruise. Median CVs of nighttime trawls were 44% and 86% as large as the CVs of day catches for number of species and total fishes caught per trawl in Livingston's (1976) diel study. Livingston also used a relatively small 16-ft (4.9-m) trawl and 2-min tows, but estimates were based on three replicates.

We are unaware of any direct, diel comparisons of sampling precision for commercial fisheries trawl data. We feel that we can state, based on our and other research trawl data, that nighttime trawl samples are generally less variable than daytime samples.

Moreover, research trawl data (Roessler 1965; Livingston 1976; this study) provide good empirical proof that Taylor (1953) was correct when he concluded, based on evaluation of fisheries trawls, that multiple, short tows are better than single (or even the same number of) long tows. These data specifically confirm the general case discussed by Green (1979): relatively small samples typically yield more precise estimates than larger samples when sampling contagiously distributed organisms. Shorter tows are probably more precise than the same number of longer tows because longer tows, particularly when made during the day, more closely approximate patch size of benthic fishes (hence inflate CPUE variance, Elliott 1971) on some relevant spatial scale (Barnes and Bagenal 1951; Taylor 1953).

The benefit of shorter tows is especially pertinent considering the design of trawl monitoring studies in the Southern California Bight. The present standard in deepwater pollution monitoring is a daytime survey using unreplicated 10-min tows. Drag speeds have averaged about 2.7 knots since 1973 (LACSD 1981). The particularly large diel differences reported for trawls at 61 m, together with the relatively small average daytime catches at outer shelf and slope depths (175 fishes of 11 species weighing 7.1 kg: Allen and Voglin 1976) suggest that, despite sufficient drag speeds, there are serious problems with both catchability (accuracy) and precision for these daytime trawl series. Precision would be increased if shorter tows were made and mean CPUE reduced (Taylor 1953). Many studies at shallow shelf (< 30 m) depths (e.g., Stephens et al. 1974; LACSD 1981) have used 10- or even 20-min tows. Our trawl data suggest that the precision of trawls made at shallow shelf depths in the bight can be increased appreciably by taking shorter tows at night, thereby reducing mean CPUE (even if no additional replicate tows are made).

CONCLUSIONS

Our results generally confirmed other less extensive evaluations of diel trawl data collected elsewhere in the Southern California Bight. The basic pattern was one of greater total numbers, total biomass, and species richness per tow for night samples. Larger catches were made at night for 12 (numbers) and 9 (biomass) of the 20 most abundant species (total trawls). In addition, night catches averaged from 3.0 to 3.7 more species per tow than day catches at 18 and 30 m, respectively. Diel differences in species composition in part reflected diel changes in behavior and availability for several abundant species, notably basketweave cusk eel (*Ophidion scrippsae*); plainfin midshipman (*Porichthys notatus*); and California tonguefish (*Symphurus atricauda*). However, diel differences in composition were generally insufficient to distinguish day and night catches of the top 20 species based on their rank abundances.

Average weight per fish (all species) and the length-frequency distributions of five out of seven species measured differed little between day and night samples. The length frequencies of each of three small and two out of three medium-sized species of flatfishes were equivalent in day and night samples. Disproportionately more large individuals were caught at night only for California halibut (*Paralichthys californicus*) at 30 m, and this most likely reflected diel differences in catchability. Relatively more small white croaker (*Genyonemus lineatus*) were caught during night at 30 m. For *G. lineatus*, a diel shift in onshore-offshore distribution probably was involved.

Growing concern (MacCall et al. 1976) over the status of fish stocks within the Southern California Bight makes it increasingly important that we understand the significance of factors such as diel variability when designing monitoring studies. Is the nature and magnitude of diel differences in trawl catches sufficient to warrant the extra costs (overtime wages, etc.) of nighttime cruises? We think so. Questions such as this become ever more relevant as shoreline development, coastal power generating plants, and the number of monitoring studies using otter trawls continue to increase in southern California.

ACKNOWLEDGMENTS

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ESTIMATED ANNUAL FOOD CONSUMPTION BY NORTHERN FUR SEALS IN THE CALIFORNIA CURRENT

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ABSTRACT

Most of the world's northern fur seals, *Callorhinus ursinus*, migrate southward into the eastern North Pacific Ocean during late fall and early winter, with adult females and juveniles of both sexes ranging as far south as southern California. Peak numbers occur in February off California (268,000), and in April off Oregon (45,500) and Washington (86,000). Northward migration begins by early spring, and fur seals are mostly absent from these regions from July through December, with the exception of a small breeding population of approximately 5,000 animals on San Miguel Island, California.

Estimates of total annual food consumption by the fur seal population off the coastal regions of California (51,000 MT) and Oregon-Washington (35,000 MT) were derived using data from the literature on diet, feeding rates, and migration. Fur seals consume an estimated 48,100 MT of pelagic schooling fish (74%) and squid (26%) during the first 6 months of the year, when they are present off the coast of California in greatest numbers, and approximately 33,600 MT of fish (76%) and squid (24%) from December to June off the Oregon-Washington coast. In California, the most important prey of the fur seal are northern anchovy, *Engraulis mordax* (20,900 MT); Pacific whiting, *Merluccius productus* (8,600 MT); market squid, *Loligo opalescens* (6,200 MT); and onychoteutid squids, *Onychoteuthis* spp (6,200 MT). Off Oregon and Washington, fur seals consume approximately 5,900 MT of herring, *Clupea harengus pallasi*; 5,500 MT of rockfish, *Sebastes* spp; 4,000 MT of northern anchovy; and 3,800 MT of market squid. The fur seals' combined annual consumption of northern anchovy in these areas is approximately 13% of the commercial fishery; for Pacific whiting, consumption is 10%; for Pacific herring, 15%; and for market squid, 50%.

RESUMEN

La mayor parte de las focas *Callorhinus ursinus* emigran al sur, avanzando hacia el este del Pacífico Norte a finales del otoño y principios de invierno, cuando hembras adultas y juveniles de ambos sexos llegan hasta el sur de California. La máxima abundancia en aguas de California ocurre en Febrero (268,000 individuos), y en Abril en Oregon y Washington (45,000 y 86,000 individuos respectivamente). La migración hacia el norte se inicia a principios de la primavera, ausentándose de las regiones mencionadas de Julio a Diciembre, exceptuando una pequeña población de cría, con unos 5,000 animales, que permanece en la Isla San Miguel, California.

Estimaciones sobre el alimento total que consumen anualmente estas poblaciones de focas en las zonas costeras de California asciende a 51,000 Tm, y a 35,000 Tm para Oregon y Washington. En estos cálculos se ha tomado como base los datos publicados sobre dieta, tasa de alimentación y migración. Se estima que estas focas consumen 48,000 Tm de cardúmenes pelágicos de peces y calamares (74% y 26% respectivamente) durante los primeros seis meses del año, cuando se encuentran presente en las zonas costeras de California, y aproximadamente 33,600 Tm de peces y calamares (76% y 24% respectivamente) de Diciembre a Junio en las zonas costeras de Oregon y Washington.

Las presas más importantes para *Callorhinus ursinus* en California son, la anchoveta *Engraulis mordax* (20,900 Tm), la merluza *Merluccius productus* (8,600 Tm) y los calamares *Loligo opalescens* y *Onychoteuthis* spp. (con 6,200 Tm para cada especie).

En aguas de Oregon y Washington, estas focas consumen aproximadamente 5,900 Tm de arenque *Clupea harengus pallasi*, 5,500 Tm de *Scorpaenidae*, 4,000 Tm de anchoveta del norte *Engraulis mordax* y 3,800 Tm de calamares.

En relación con el monto de la pesquería comercial, combinando las áreas geográficas consideradas el consumo anual por las focas corresponde aproximadamente al 13% para *E. mordax*, 10% para *M. productus*, 15% para *C. harengus pallasi* y al 50% para los calamares.

INTRODUCTION

Biological data on northern fur seals, *Callorhinus ursinus*, at sea have been recorded since the days of

pelagic sealers in the late nineteenth century. Early literature describing fur seals' food habits and migration off the west coast of North America includes Townsend (1899), Clemens and Wilby (1933), Clemens et al. (1936), Scheffer (1950), Kenyon and Wilke (1953), Wilke and Kenyon (1954), and Taylor et al. (1955). Since 1958, intensive pelagic research on the northern fur seal has been conducted under the auspices of the North Pacific Fur Seal Commission (NPFSC).

The four member countries of the NPFSC (the United States, Canada, Japan, and the Soviet Union) designed this research to facilitate management of the fur seal by collecting information on its reproductive status, growth rates, migratory patterns, and food habits. After 17 years of pelagic research in the eastern North Pacific Ocean and Bering Sea, the United States and Canada suspended their programs to synthesize the accumulated data. Published literature containing summaries of these analyses of fur seals' food habits and migration includes NPFSC (1962, 1969, 1971); Fiscus (1979, 1980, 1982); and Kajimura (1982).

Despite this accumulation of information, few attempts have been made to estimate the biomass of prey consumed by northern fur seals off the western coast of North America south of 49°N latitude (exceptions include Food and Agriculture Organization of the United Nations—FAO 1978; and Bailey and Ainley 1982).

The objectives of this study are (1) to estimate the number of fur seals migrating into the coastal waters (defined as the oceanic region over the continental shelf slope, and not exceeding a distance of 300 km from shore) of California, Oregon, and Washington, and (2) to estimate the total biomass of pelagic fish and squid consumed by fur seals in the California Current. These foraging estimates will also be compared to recent commercial fisheries' catch statistics.

BACKGROUND INFORMATION

Despite a 20% decline in the world's population of northern fur seals over the past 5 years, the total population has been estimated at 1.4 million (NPFSC 1983). During the summer months, most northern fur seals are found on or near the breeding islands. In the eastern portion of the fur seals' range, the population on the Pribilof Islands, Alaska, is approximately 975,000; fewer than 100 are on Bogoslof Island, Alaska, and about 5,000 are on San Miguel Island, California (Kozloff 1981, 1982, 1983; NPFSC 1983; T. R. Loughlin, National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, Wash., pers. comm. 1983; G. A. Antonelis, Jr., pers. obs.).

In the Pribilof herd, most adult males, some of the adult females, and juveniles of both sexes begin the pelagic stage of their life cycle in the fall. The remaining portion of the population goes to sea by early winter. Most adult males winter in waters at the northern portion of their range. Females and juveniles of both sexes migrate south into waters over the continental shelf and slope of the eastern North Pacific Ocean during winter and early spring, ranging as far south as 30°–32°N latitude (Lander and Kajimura 1982). Although some may migrate only over continental shelf waters, others may move directly across the North Pacific from the Bering Sea to southern wintering areas. Fur seals begin their return migration northward in midspring, and by early summer most have returned to their breeding islands.

Kenyon and Wilke (1953) were the first to suggest, from their review of the literature and pelagic sealing records, that most of the migrating fur seal herd were off the coasts of California, Oregon, and Washington during the month of February. Seal distribution data collected by the United States and Canada from 1958–74 support their opinion: the largest number of seals seen per research effort-hour during winter months occurred in these areas, with the highest concentration off California during February (Kajimura 1980; Bigg 1982).

Kajimura (1980) reported that fur seals are most frequently found from about 74 to 130 km from land and are usually in greatest numbers along the continental shelf and slope where pelagic schooling fishes and squid are generally most abundant. He also reports that fur seals are most frequently found in water which ranges from 8°C to 14°C.

While at sea, fur seals feed on a variety of species. The relative proportion of each prey species in the fur seals' diet varies monthly (Kajimura 1982; Perez and Bigg 1984). This is due to apparent changes in foraging locations, and to seasonal movements, abundance, and availability of the prey. An example of the way the fur seals' diet changes during their winter and spring sojourn off the coast of California is shown in Figure 1. This figure illustrates the average diet as it changes from January to June; fur seals forage primarily on seasonally abundant anchovy in winter and Pacific whiting in spring.

Unfortunately, relatively little is known about the size of prey consumed by northern fur seals. However, on the basis of currently available information (Spalding 1964; Fiscus et al. 1964; Perez and Bigg 1984), we estimate that fur seals usually eat prey that is approximately 10 to 30 cm in length, although they sometimes take larger prey that they must break up before swallowing.
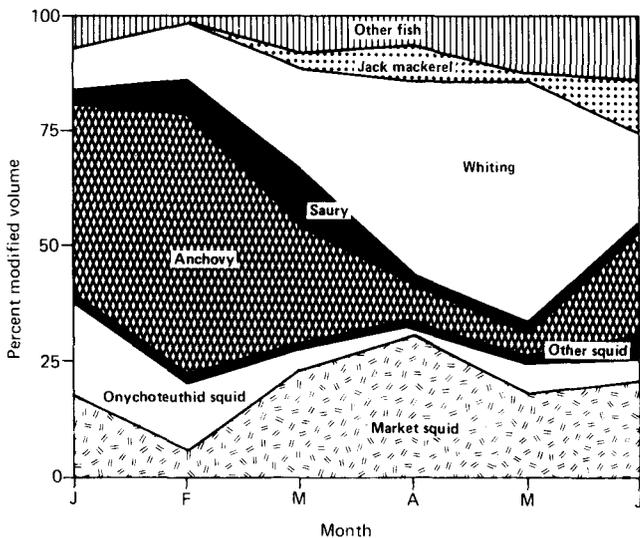
Figure 1. Monthly composition (percentage) of fur seals' diet by species off California from January to June, 1958-74 (modified from Perez and Bigg 1984).

METHODS

Estimates of fur seal abundance and food consumption in this paper were mainly calculated with data from the literature and unpublished manuscripts.

These estimates were based on pooled data for months and years during 17 years of pelagic research off the coasts of California, Oregon, and Washington (1958-74; no data for California after 1966). We assume there has been no change in the migratory behavior or feeding ecology of fur seals since these data were collected.

Population Estimates

Using data presented by Lander (1981) and NPFSC (1983), we calculate that there are about 340,000 adult female fur seals (age ≥ 5 yr) in the total Pribilof Islands stock (this estimate assumes that the current fur seal population decline is equal among all age groups, although there are no data to substantiate this). Using that estimate and data in Bigg (1982; his figures 5c-d) on the ratio of seals sighted at sea during 1958-74 by age, sex, and reproductive status, we calculated the total number of northern fur seals of the Pribilof Islands herd that migrate south of 49°N in the eastern North Pacific. We assume that at least 80% of all pregnant females from the Pribilof Islands population migrate to the west coast of North America between latitudes 32°N and 49°N (Kenyon and Wilke 1953; Kajimura 1980; Bigg 1982). We calculated the total number of seals off California, Oregon, and Washington by month from the 1958-74 pelagic data on seals sighted at sea per research-effort-hour on the basis of the total research area (km²) between months

and regions. (Kajimura 1980 and Bigg 1982 described the survey areas by month.) We also assumed most adult males (> 90%) and immature seals (> 70%) remain in the more northern latitudes, on the basis of sightings off British Columbia and in the Gulf of Alaska during February (Kenyon and Wilke 1953; Kajimura 1980; Bigg 1982).

Our monthly regional estimates were subdivided into three classes: pregnant females (age ≥ 5 yr), nonpregnant females (age ≥ 5 yr), and other seals (immatures, adult males, and pregnant females aged 4 yr). The estimated numbers of seals by class were also calculated using data from Bigg (1982; his figures 5c-d).

For this report, we assumed that most of the resident population from San Miguel Island remains in the waters off California through the summer and fall, although we have little evidence to support this assumption.

Food Consumption

Total food consumption (C) was calculated as:

$$C = N \times D \times R$$

for each region, month, and seal class, where N is the estimated number of seals in each of the three classes, D is the number of days in the month (assumed 30 for all months), and R is the daily food ration of the average individual seal. The daily food ration (R) equals $M \times F$, where M is the average body mass and F is the estimated feeding rate (expressed as a percentage of body mass). We calculated average monthly body mass values for the three classes of seals by weighting the data for each age given by Lander (1979) according to the relative proportion of the population at any age expected to be present in each region per month using data from Bigg (1982; his figures 5c-d). Since body mass data for the San Miguel Island resident population are not available for October–December, we used the September and January average values from the Pribilof Island herd (Lander 1979) as an approximation.

We assumed that all seals present in a region fed daily throughout the entire month, including those seals off California, Oregon, and Washington during the beginning (November–January) and ending (June–July) months of the migratory phase. However, some individual variability is to be expected, and within-month migratory patterns are virtually unknown. In addition, an insignificant number of seals from the Pribilof herd (which we ignored) may be found south of 49°N during August–October.

Perez and Mooney (1984) calculated a feeding rate relationship from data given by Bigg et al. (1978)

based upon captive adult female fur seal feeding studies:

$$Megajoules\ (MJ)\ =\ 1.571\ M^{0.75}$$

where MJ is the daily energy consumption and M is the seal's body mass in kilograms. The daily energy consumption values calculated by this relationship were converted to feeding rates (F). This was done by calculating the monthly average energy value of the seal's diet, by region, using estimates of the energy content (MJ) of fur seal prey summarized by Perez and Bigg (1984). For the months of July–December (for which fur seal food data are unavailable in the California region), we used the average values calculated for other months.

We calculated feeding rates for all seals (including immatures and an insignificant number of adult males) using the above relationship, although it was based upon data from primarily adult females.

Because most of the seals expected in the North Pacific off California, Oregon, and Washington during winter are adult females, any possible difference in food consumption by age or sex was assumed not to be significant. We also assumed there was no significant increase in ingestion because of pregnancy. However, for lactating females of the San Miguel Island population, we increased the estimated feeding rate by 1.6 to account for milk production, based on data for the Pribilof Island herd (Perez and Mooney 1984).

We used percentage values (modified volume) of fish and squid species in the fur seal diet given by Perez and Bigg (Beddington et al. in press) to estimate biomass of individual prey species consumed by fur seals in each region during winter and spring and also to determine the average energy value of the diet. For Oregon, except for the month of April, we used data taken from subregion 8 (northern Oregon and southern Washington in Perez and Bigg, 1981) as an approximation. We estimated the total biomass of each prey species consumed by multiplying total food consumption by these percentages for each prey. There are no available data on the consumption of prey by the relatively low number of seals utilizing these regions during summer and fall.

RESULTS

Population Estimates

Monthly estimates of population abundance, average body mass, daily energy consumption, average feeding rate, and individual food consumption for the three study groups—pregnant females ≥ 5 years of age; nonpregnant females ≥ 5 years of age; and others

(mostly juveniles of both sexes)—are shown in Table 1. Variations in individual food consumption for these three groups of fur seals are primarily due to differences in the estimated average body mass of individual seals in each group. The body mass estimates reflect the average value for all age classes in each group expected to be found in each region pooled by month (based on data in Bigg 1982 and Lander 1979), and do not necessarily indicate seasonal changes in body mass of any particular age class.

The estimated number of fur seals in the coastal waters of California and Oregon-Washington are shown in Figure 2. These estimates reflect the migratory patterns and relative proportions of fur seals seen by region and month as indicated by Bigg (1982). After the breeding season, about 1,000 fur seals are usually first seen off the coast of Oregon and Washington in November, while the resident population of about 5,000 from San Miguel Island presumably remains off California. By December about 5,600 fur seals are off California and 11,000 off the Oregon-Washington area. Fur seal abundance increases rapidly in California waters, from 68,000 in January to a peak of approximately 268,000 in February. However, some of these seals begin to return north during March, and their abundance off California declines to an estimated 85,000 in March and 24,000 in April. This northward movement is reflected in increased Oregon-Washington estimates, which also represent some southward-moving juveniles (Bigg 1982). After April there is a decreasing trend in the numbers of fur
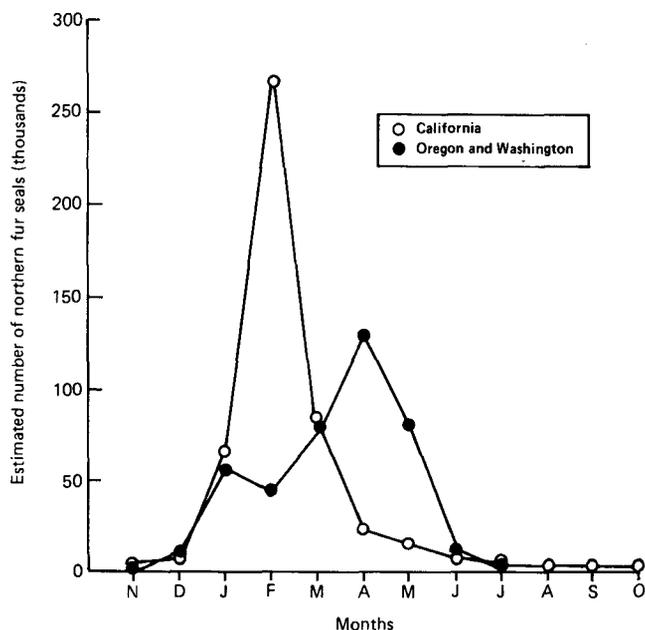
Figure 2. Monthly estimates of abundance of northern fur seals in the offshore waters of California, Oregon, and Washington.

TABLE 1
Average Energy Value of Diet, Population Abundance, Average Body Mass, Feeding Rate, and Daily Food Consumption of Northern Fur Seals

State and month (average energy value of diet)	Fur seal classification (age in years)	Population abundance	Average body mass (kg)[a]	Daily energy consumption per seal (MJ)	Feeding rate (% of body mass)[b]	Daily food consumption per seal (kg)
California						
January (5.9 MJ/kg)	Preg. females (≥5)	47,600	35.5	22.8	11.0	3.9
	Nonpreg. females (≥5)	11,500	33.7	22.0	11.0	3.7
	Other	9,000	22.7	16.3	12.3	2.8
February (6.6 MJ/kg)	Preg. females (≥5)	189,000	35.2	22.7	9.7	3.4
	Nonpreg. females (≥5)	45,000	31.7	21.0	10.1	3.2
	Other	34,000	19.3	14.5	11.4	2.2
March (6.1 MJ/kg)	Preg. females (≥5)	50,600	36.3	23.2	10.5	3.8
	Nonpreg. females (≥5)	16,500	30.7	20.5	11.1	3.4
	Other	18,000	18.5	14.0	12.4	2.3
April (5.2 MJ/kg)	Preg. females (≥5)	12,600	38.4	24.2	12.2	4.7
	Nonpreg. females (≥5)	4,500	31.3	20.8	12.8	4.0
	Other	7,000	17.5	13.4	14.9	2.6
May (5.3 MJ/kg)	Preg. females (≥5)	7,100	42.8	26.3	11.7	5.0
	Nonpreg. females (≥5)	3,000	33.9	22.1	12.4	4.2
	Other	7,000	17.5	13.4	14.9	2.6
June (5.9 MJ/kg)	Preg. females (≥5)	2,100	42.8	26.3	10.5	4.5
	Lact. females (≥5)	1,600	34.0	35.7	17.9[c]	6.1
	Nonpreg. females (≥5)	1,900	33.2	21.7	11.1	3.7
	Other	3,900	20.3	15.0	12.8	2.6
July (5.8 MJ/kg)	Lact. females (≥5)	1,600	35.6	36.6	17.7[c]	6.3
	Nonpreg. females (≥5)	500	33.9	22.1	11.2	3.8
	Other	1,400	17.6	13.5	13.2	2.3
August (5.8 MJ/kg)	Lact. females (≥5)	1,600	36.5	37.3	17.6[c]	6.4
	Nonpreg. females (≥5)	500	34.0	22.1	11.2	3.8
	Other	1,400	23.1	16.5	12.3	2.8
September (5.8 MJ/kg)	Lact. females (≥5)	1,600	36.8	37.3	17.5[c]	6.4
	Nonpreg. females (≥5)	500	32.1	21.2	11.3	3.6
	Other	1,400	23.1	16.5	12.3	2.8
October (5.8 MJ/kg)	Lact. females (≥5)	1,600	36.2	37.3	17.6[c]	6.4
	Nonpreg. females (≥5)	500	33.3	21.8	11.2	3.7
	Other	1,400	23.1	16.5	12.3	2.8
November (5.8 MJ/kg)	Preg. females (≥5)	1,600	36.9	23.5	11.1	4.1
	Nonpreg. females (≥5)	500	35.5	22.8	11.0	3.9
	Other	3,000	19.8	14.7	12.6	2.5
December (5.8 MJ/kg)	Preg. females (≥5)	1,950	36.7	23.4	10.9	4.0
	Nonpreg. females (≥5)	600	33.4	21.8	11.1	3.7
	Other	3,050	19.7	14.7	12.7	2.5
Oregon						
January (7.0 MJ/kg)	Preg. females (≥5)	1,000	34.8	22.5	9.3	3.2
	Nonpreg. females (≥5)	500	32.4	21.3	9.5	3.1
	Other	500	18.1	13.8	11.0	2.0
February (6.5 MJ/kg)	Preg. females (≥5)	1,000	34.5	22.4	10.0	3.4
	Nonpreg. females (≥5)	500	31.4	20.8	10.2	3.2
	Other	1,000	14.3	11.5	12.2	1.8
March (6.2 MJ/kg)	Preg. females (≥5)	4,000	35.9	23.0	10.3	3.7
	Nonpreg. females (≥5)	2,000	30.3	20.3	10.7	3.3
	Other	5,000	14.2	11.5	13.0	1.9
April (5.4 MJ/kg)	Preg. females (≥5)	22,500	37.4	23.8	11.7	4.4
	Nonpreg. females (≥5)	8,000	29.0	19.6	12.5	3.6
	Other	15,000	16.4	12.8	14.4	2.4
May (6.4 MJ/kg)	Preg. females (≥5)	700	39.8	24.9	9.7	3.9
	Nonpreg. females (≥5)	300	28.9	19.6	10.5	3.1
	Other	1,500	17.0	13.1	12.0	2.1
June (4.1 MJ/kg)	Preg. females (≥5)	100	43.1	26.4	14.9	6.4
	Nonpreg. females (≥5)	200	31.5	20.9	16.2	5.1
	Other	1,700	18.6	14.1	18.5	3.4
July-November	Preg. females (≥5)	—	—	—	—	—
	Nonpreg. females (≥5)	—	—	—	—	—
	Other	—	—	—	—	—
December (7.6 MJ/kg)	Preg. females (≥5)	500	38.2	24.1	8.3	3.2
	Nonpreg. females (≥5)	250	33.2	21.7	8.6	2.8
	Other	250	24.4	17.2	9.2	2.3

Table 1—*continued*

State and month (average energy value of diet)	Fur seal classification (age in years)	Population abundance	Average body mass (kg)[a]	Daily energy consumption per seal (MJ)	Feeding rate (% of body mass)[b]	Daily food consumption per seal (kg)
Washington						
January (7.6 MJ/kg)	Preg. females (≥5)	28,000	34.8	22.5	8.5	2.9
	Nonpreg. females (≥5)	11,000	32.4	21.3	8.6	2.8
	Other	15,000	18.1	13.8	10.0	1.8
February (6.6 MJ/kg)	Preg. females (≥5)	19,000	34.5	22.3	9.9	3.4
	Nonpreg. females (≥5)	7,000	31.4	21.0	10.1	3.2
	Other	18,000	14.3	11.9	12.3	1.8
March (6.4 MJ/kg)	Preg. females (≥5)	28,000	35.9	23.0	10.1	3.6
	Nonpreg. females (≥5)	12,000	30.3	20.3	10.5	3.2
	Other	34,000	14.2	11.5	12.7	1.8
April (6.8 MJ/kg)	Preg. females (≥5)	34,000	37.0	23.6	9.3	3.5
	Nonpreg. females (≥5)	14,000	29.7	20.0	9.9	2.9
	Other	38,000	15.5	12.3	11.6	1.8
May (6.8 MJ/kg)	Preg. females (≥5)	22,000	39.8	24.9	9.1	3.6
	Nonpreg. females (≥5)	10,000	28.9	19.6	9.9	2.9
	Other	49,000	17.0	13.1	11.3	1.9
June (7.9 MJ/kg)	Preg. females (≥5)	500	43.1	26.4	7.7	3.3
	Nonpreg. females (≥5)	1,000	31.5	20.9	8.4	2.6
	Other	8,500	18.6	14.1	9.5	1.7
July (7.0 MJ/kg)	Preg. females (≥5)	50	36.0	23.1	11.0	4.0
	Nonpreg. females (≥5)	100	34.7	22.5	11.1	3.9
	Other	850	19.2	14.4	12.9	2.5
August-October	Preg. females (≥5)	—	—	—	—	—
	Nonpreg. females (≥5)	—	—	—	—	—
	Other	—	—	—	—	—
November (7.0 MJ/kg)	Preg. females (≥5)	500	38.2	24.1	10.9	4.2
	Nonpreg. females (≥5)	200	33.2	21.7	11.2	3.7
	Other	300	24.4	17.2	12.1	3.0
December (7.6 MJ/kg)	Preg. females (≥5)	5,000	38.4	24.2	8.3	3.2
	Nonpreg. females (≥5)	2,500	33.0	21.6	8.6	2.8
	Other	2,500	24.3	17.2	9.3	2.3

[a]Average body mass for all ages combined expected to be present in the region by month. Body mass values at each age (Lander 1979) were weighted by the expected population abundance of each age group (based on data in Bigg 1982).

[b]Feeding rates were calculated after estimating daily energy consumption based upon the seal's average body mass, and accounting for the average energy content of the seal's diet in the region by month.

[c]The feeding rate for lactating females (pregant females during June-September) of the San Miguel Island population was estimated to be 1.6 times that of the feeding rate for postpartum females (same age and body mass) not producing milk, based upon data from the Pribilof Island population in Perez and Mooney (1984).

seals in both areas, and by July approximately 1,000 fur seals remain off the coast of Oregon and Washington, representing the last of the northward migrating seals. These estimates account for migration of 80% of the entire adult female (age ≥ 5 yr) fur seal population south of 49°N latitude, with peak numbers occurring in February. In addition, approximately 20% of all juvenile fur seals from the Pribilof herd were estimated to migrate into this region during winter, reaching their peak abundance in March.

Estimates of Food Consumption

Estimates of the total annual consumption of pelagic schooling fish and squid by northern fur seals in the coastal waters of California, Oregon, and Washington are given in Figures 3 and 4. Off the coast of California, fur seals consumed an estimated 51,000 MT, and off Oregon-Washington they consumed about 35,000 MT.

In the regions considered, the greatest biomass is consumed during winter and spring, when fur seals are most abundant in offshore waters. Estimates of the monthly biomass of the most common prey consumed
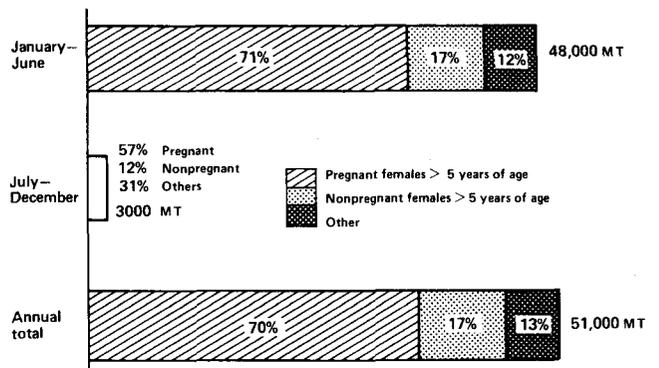
Figure 3. Biomass estimates of food consumed by northern fur seals in California coastal waters.
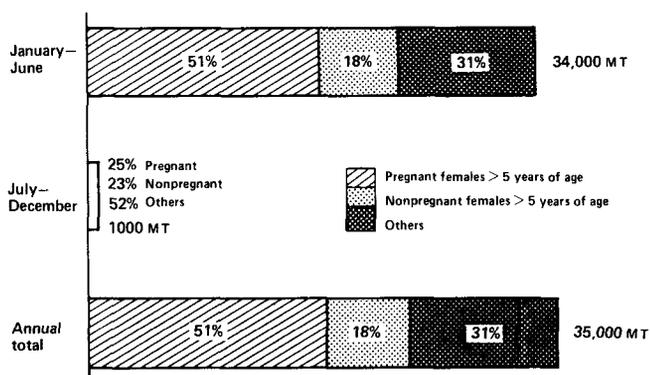
Figure 4. Biomass estimates of food consumed by northern fur seals in Oregon-Washington coastal waters.

TABLE 2

Estimated Consumption of Prey by Fur Seals off California

	Estimated biomass (metric tons) of food consumed					
Prey	January	February	March	April	May	June
Northern anchovy	3,120	15,060	2,042	243	130	248
Pacific saury	158	1,801	1,033	42	22	18
Pacific whiting	776	3,367	1,953	1,222	1,064	191
Jack mackerel	—	157	208	215	8	122
Rockfish	173	209	139	1	136	75
Sablefish	—	26	—	1	105	53
Other fishes	332	104	625	170	2	1
Subtotal (fish)	4,559	20,724	6,050	1,894	1,467	708
Market squid	1,319	1,436	1,997	862	349	209
Onychoteuthid squids	1,605	3,941	434	71	138	52
Other squids	53	1	200	3	20	39
Subtotal (squid)	2,977	5,378	2,631	936	507	300
TOTAL	7,536	26,102	8,681	2,830	1,974	1,008

during this time are shown in Tables 2 and 3. From January to June, fur seals consumed an estimated 48,100 MT of fish (74%) and squid (26%) in California waters, while approximately 33,600 MT of fish (76%) and squid (24%) were consumed in the Oregon-Washington region from December–June.

In Figures 5 and 6 the biomass of each prey is expressed as a percentage of the total biomass consumption estimates for the two regions. In California, northern anchovy (*Engraulis mordax*) is clearly the most important prey, and accounts for 20,900 MT (43.4%) of the population's estimated consumption in that region (Figure 5). This was followed by Pacific whiting (*Merluccius productus*) at 17.8% (8,600 MT) of the estimated consumption, and both market squid and onychoteuthid squids (mainly *Onychoteuthis borealijaponicus*) at 12.8% (6,200 MT). Each of the four remaining species (Pacific saury, *Cololabis saira*; jack mackerel, *Trachurus symmetricus*; rockfish,

Sebastes spp; and sablefish, *Anoplopoma fimbria*) appear to be relatively unimportant in California waters, contributing less than 10% of the total estimate.

A somewhat different and more diverse group of prey species was observed off the Oregon-Washington coasts (Figure 6). In this region, Pacific herring (*Clupea harengus pallasi*) and rockfish were the two most important prey, accounting for 5,900 MT (17.7%) and 5,500 MT (16.3%) of the estimated biomass, respectively. The next three most important species—northern anchovy, salmonids, and market squid—all had similar estimates ranging from 3,800 to 4,000 MT, which represented 11% to 12% of the estimated biomass. The remaining prey species that contributed less significantly (< 10%) to the biomass consumed off the Oregon-Washington area were onychoteuthid squids, Pacific whiting, capelin (*Mal-*

TABLE 3

Estimated Consumption of Prey Species by Fur Seals off Oregon and Washington

	Estimated biomass (metric tons) of food consumed						
Prey	December	January	February	March	April	May	June
Pacific herring	290	1,593	363	618	1,114	1,554	400
Northern anchovy	6	204	777	1,727	983	341	—
Salmonids	69	935	531	630	858	848	26
Capelin	91	109	401	341	177	88	—
Eulachon	93	117	168	58	170	1	—
Pacific whiting	66	46	1	1	828	420	49
Rockfish	—	270	853	2,078	2,139	136	—
Sablefish	152	231	1	6	347	158	—
Other fishes	34	109	143	449	1,089	233	1
Subtotal (fish)	801	3,614	3,238	5,908	7,705	3,779	476
Market squid	57	744	351	860	1,702	1	103
Onychoteuthid squids	1	1	18	133	1,056	1,586	223
Other squids	1	17	155	35	152	859	4
Subtotal (squid)	59	762	524	1,028	2,910	2,446	330
TOTAL	860	4,376	3,762	6,936	10,615	6,225	806

Percent of total biomass

Northern anchovy	20,9000 MT
Pacific whiting	8600 MT
Market squid	6200 MT
Onychoteuthid squid	6200 MT
Pacific saury	3100 MT
Jack mackerel	700 MT
Rockfish	700 MT
Sablefish	200 MT
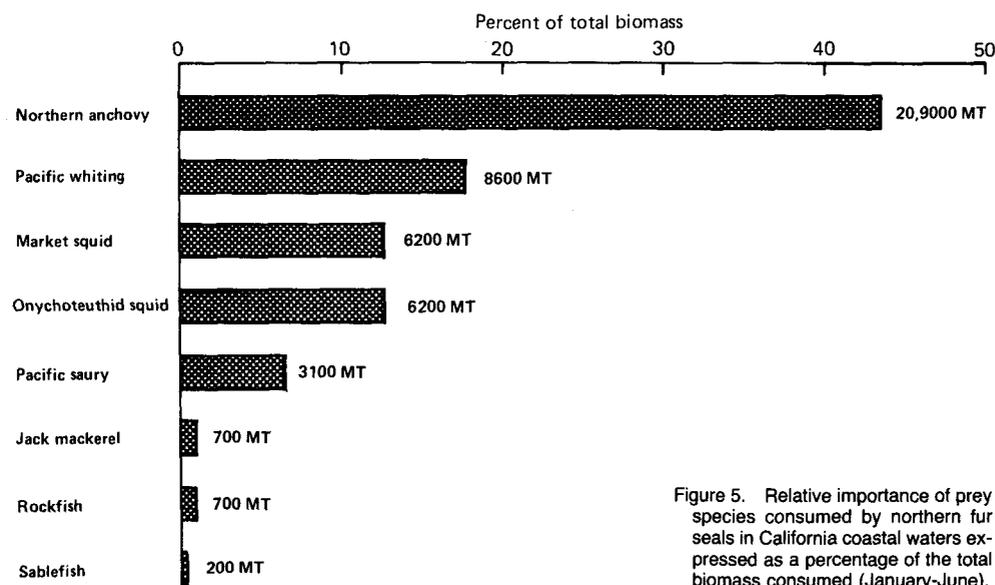
Figure 5. Relative importance of prey species consumed by northern fur seals in California coastal waters expressed as a percentage of the total biomass consumed (January-June).

lotus villosus), sablefish, and eulachon (*Thaleichthys pacificus*).

DISCUSSION

Comparisons with Other Estimates

Our estimates of population size by month (Table 1) should reflect patterns in fur seals' migrating behavior

Percent of total biomass

Pacific herring	5900 MT
Rockfish	5500 MT
Northern anchovy	4000 MT
Salmonids	3900 MT
Market squid	3800 MT
Onychoteuthid squid	3000 MT
Pacific whiting	1400 MT
Capelin	1200 MT
Sablefish	900 MT
Eulachon	600 MT
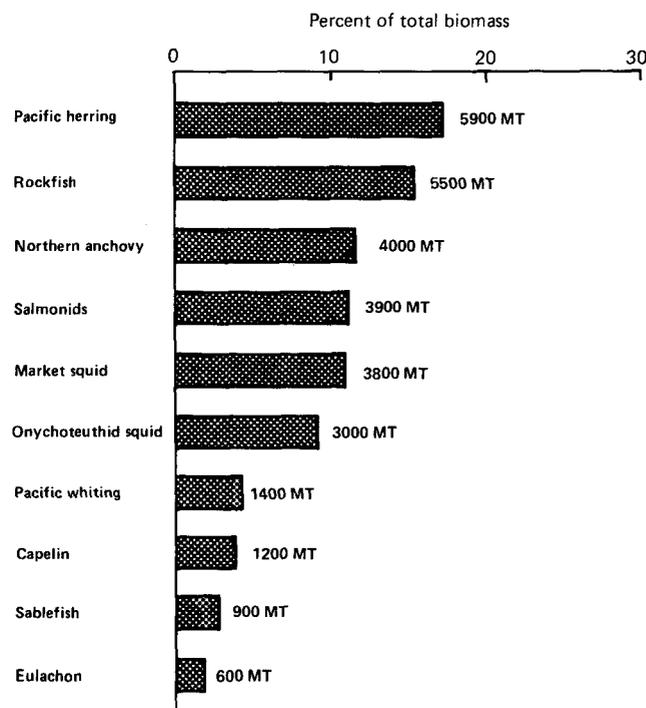
Figure 6. Relative importance of prey species consumed by northern fur seals in coastal waters of Oregon-Washington expressed as a percentage of the total biomass consumed (December-June).

during winter and spring, assuming there has been no significant change in this behavior during the past 30 years. In other words, the estimated values may change over time, but the migrating patterns as shown in Figure 2 should be similar during the foreseeable future.

Our peak estimate of 309,000 fur seals migrating south of 49°N latitude during the month of February is lower than the estimate of 500,000 given by Fiscus (1980). This is probably due in part to the decline in the fur seal population that has occurred in recent years. Additionally, Fiscus based his estimate on the number of fur seals that occurred within the range of the Pacific whiting, an area that included some seals north of our area of interest.

In a more recent study of the distribution of pinnipeds off the central and northern California coast, Bonnell et al. (1983) estimated the peak abundance of northern fur seals at 25,000 (± 8,500) during February–March. Although their report is consistent with previous reports on the occurrence of peak fur seal abundance (Kajimura 1980; Bigg 1982) off California, their estimated numbers are 87% lower than our peak estimates. The apparent reason for this discrepancy is that we examined a larger study area, extending offshore 300 km, whereas they surveyed the coastal waters only to 185 km.

Our estimate of food consumption by fur seals off California at 12,200 MT. Our estimate (8,600 MT) MT reported by FAO (1978). We assume the FAO estimate is higher than ours because it treated the entire population of migrants as a single unit, presumed to be present during all winter and spring months. Furthermore, their population estimates were made
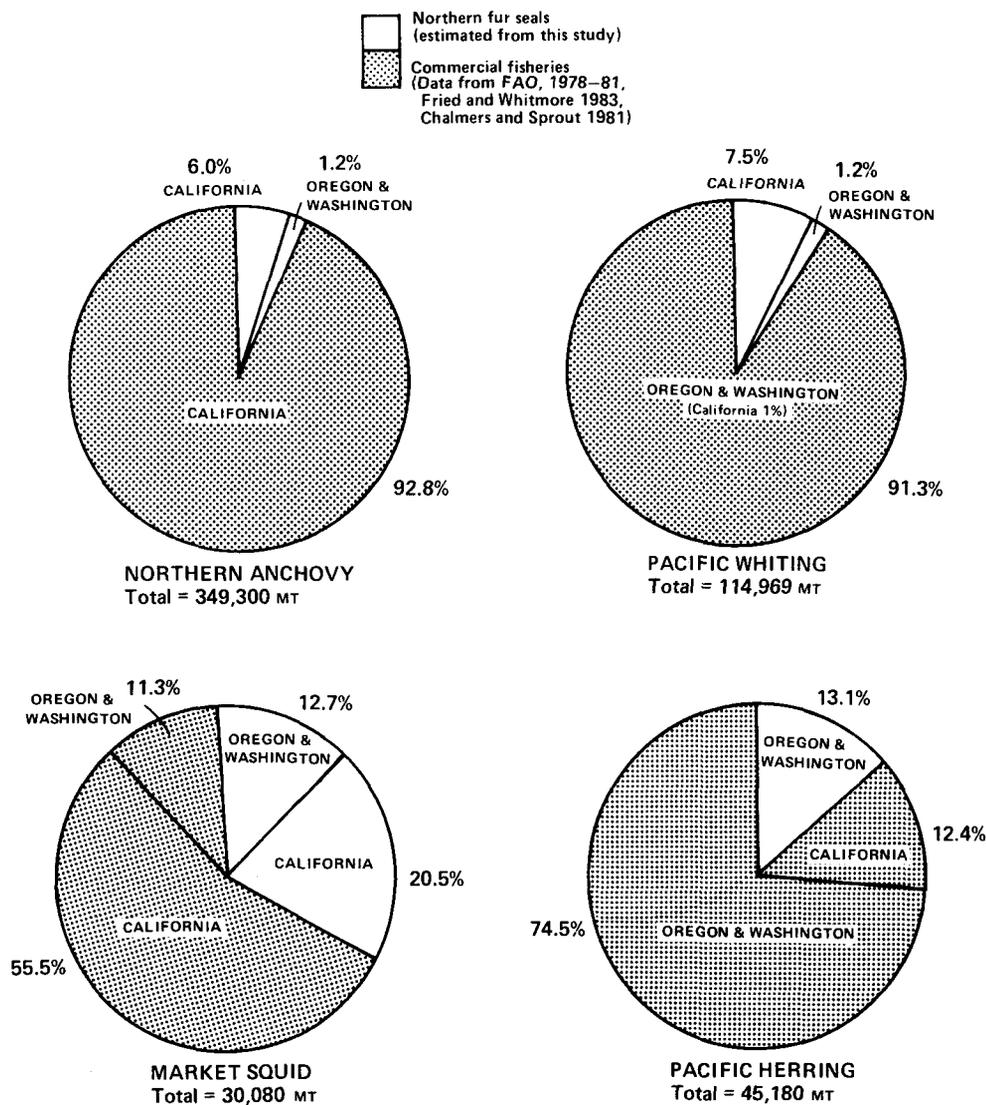
Figure 7. Annual take of biomass (MT) by northern fur seals and commercial fisheries off California, Oregon, and Washington.

several years before the recent 20% decline in the population was reported (NPFSC 1983).

In another study, Bailey and Ainley (1982) estimated the Pacific whiting consumption by fur seals off California at 12,200 MT. Our estimate (8,600 MT) was 70% of their value, because of differences in estimating the percentage of Pacific whiting in the diet and the time northern fur seals remain in the waters off California.

Potential Competition between Fur Seals and Man

Figure 7 illustrates the proportion of four prey species (northern anchovy, Pacific herring, Pacific whiting, and market squid) taken by fur seals and commercial fisheries. It is apparent that fur seals remove only a small percentage of the total anchovy taken in this comparison, yet this is their most important prey off the coast of California. It should be noted, moreover,

that the majority of fur seals forage in areas north of the important commercial southern California fishing grounds for northern anchovy, further reducing the potential for direct competition.

The most important commercial harvest of Pacific whiting is off Oregon-Washington, whereas central California is the area with the most significant take by northern fur seals. Pacific whiting, like the northern anchovy, appears to be most heavily preyed upon by northern fur seals in areas that have the least commercial fishing activity.

There are also differences in the location of Pacific herring taken by commercial fisheries and northern fur seals, even though both take greatest quantities from Oregon-Washington waters. Commercial fisheries concentrate their harvest in nearshore waters, including bays and estuaries; northern fur seals forage most frequently in offshore waters. The seals forage most

143

heavily on Pacific herring in the northern portion of the Oregon-Washington region, around the U.S.-Canadian border (Taylor 1974).

Market squid is the only species in our comparison whose overall take by fur seals approaches that of the commercial fisheries. However, this relationship could change in the future because market squid is currently considered an underutilized fisheries resource (Kato and Hardwick 1976). Like Pacific herring, market squid are primarily taken in the offshore waters by fur seals and nearshore by commercial fisheries.

Considering these four prey species, it appears that the potential for direct competition between fisheries and fur seals is low because of the geographical separation in the main areas of harvest. It should be pointed out, however, that there may be a slight bias in the commercial fisheries information resulting from an underestimation of the take off California and an overestimation of the take off Oregon and Washington. This resulted when FAO catch statistics off the west coast of North America were summarized into only two regions (the area north of Eureka, California, is included with Oregon in one region, whereas the rest of California is in a second region). Nevertheless, we believe our comparisons are not compromised by this bias.

Implications of Dietary Habits

The northern fur seal is not a specialized predator (Bonner 1982) and feeds on a wide range of seasonally abundant prey species (Antonelis and Fiscus 1980; Kajimura 1982). However, it routinely forages on a relatively small number of these prey within a specific region at any given time (Kajimura 1982; Perez and Bigg 1984). Monthly, and possibly interannual, changes in the proportion of different prey in the diet are primarily due to availability and abundance. This might result from a variety of factors such as depletion of resources by commercial fisheries, interspecific competition, disease, or climatic changes (MacCall 1983; Moyle and Cech 1982).

It has been suggested by Perez and Bigg (1984) that some food types may be more important than others because of their energy content. Consequently, in addition to the quantity, the "quality" (energy content) of various prey may affect the foraging success of fur seals. The importance of quality food has also been discussed by Geraci (1975). This may be especially important if we consider the large numbers of pregnant females that migrate to the coastal waters off California, Oregon, and Washington. The level of nutrition obtained by these females should have a physiological effect on their fetuses. For fur seals,

such an effect could result in reduced size of the fetus or inability to bring the offspring to full term, phenomena which have been reported for other mammals (Sadleir 1976; Millar 1977; Payne and Wheeler 1968).

Future studies on fur seals should closely investigate factors affecting their migratory patterns and food habits. This kind of research is important because fur seals spend at least 88% of their life at sea. Thus the quality and quantity of food available to pregnant northern fur seals foraging in the eastern North Pacific is of great importance to the growth of the population, and any perturbation in the ecosystem, including overexploitation from commercial fisheries or major climatic disturbance (e.g., El Niño), could directly or indirectly affect their reproductive success.

ACKNOWLEDGMENTS

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GROWTH OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, IN CAPTIVITY

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ABSTRACT

Fishery data indicate that jack mackerel captured from inshore waters are seldom more than 380 mm in fork length (FL). This laboratory study shows that the inshore fish have the potential to grow as large as 425-450 mm FL. During a 2-year period laboratory-held mackerel grew more than three times faster in length and more than five times faster in weight than fish in the wild. Most of the surplus weight (65%) was fat, but a significant portion (26%) was fat-free dry weight, indicating that protein as well as fat was stored. The high levels of fat and protein accumulated by the laboratory fish indicate that the growth in length (skeletal growth) may have been near the maximum rate. The excess fat was deposited in the red and white muscles and viscera in different proportions.

RESUMEN

Los datos de pesca indican que los *Trachurus symmetricus* capturados en aguas costeras raramente alcanzan más de 380 mm de longitud a la horquilla. Los estudios en el laboratorio señalan que los peces costeros tienen un potencial de crecimiento que llega a los 425-450 mm de longitud de horquilla. Los charritos mantenidos en el laboratorio durante dos años, incrementaron su longitud y peso con una rapidez tres y cinco veces mayor respectivamente, que los peces que habitan su medio natural. La mayor parte del exceso en peso estaba constituido por grasas (65%) pero una porción significativa (26%) corresponde a peso seco sin grasas, lo cual indica que almacenan tanto proteínas como grasas. Los altos niveles de grasa y proteínas acumulados por los peces mantenidos en el laboratorio indican que el crecimiento en longitud (crecimiento del esqueleto) debió alcanzar un valor cercano a la tasa máxima de crecimiento. El exceso de grasa se depositó en diferentes proporciones en los musculos blancos y rojos, y en las vísceras.

INTRODUCTION

Reports by MacCall et al. (1980) and MacCall and Stauffer (1983) on the biology of the jack mackerel, *Trachurus symmetricus*, indicate that little is known about the structure of the jack mackerel population.

The reports state that the catch consists of two size groups; the inshore purse seine fishery off southern California takes fish ranging from 100 to 300 mm FL, whereas the offshore fishery, largely foreign trawlers, takes fish from 500 to 600 mm FL. Intermediate-sized fish are conspicuously absent in both fisheries. Mid-sized fish are sporadically caught (Blunt 1969) but have never been observed in numbers to support the hypothesis that the small inshore fish grow and eventually join larger fish offshore. The difference in length could be due to disparate fishing methods but may also indicate inshore-offshore populations with different growth patterns. To better understand the growth potential of the inshore mackerel, I held a school in captivity for two years to observe growth. Some adjunct observations on maturation and the accumulation of energy reserves during captivity were also made, since these aspects of mackerel biology are still inadequately known. This report presents the results of these observations and compares them with observations made on fish in the wild.

METHODS

The observations on jack mackerel growth were made at the National Marine Fisheries Service, Southwest Fisheries Center in La Jolla, California. The fish were held in an outdoor circular swimming pool 7.3 m in diameter with 1 m of water (42 m³ water volume). The pool had a fresh seawater inflow of 25 liters per minute and a recirculating pump with a capacity of 250 liters per minute. An overhead canopy shielded the pool from direct sunlight to reduce solar heating. The temperature ranged from 14.0° to 22.5°C and averaged 17.8° during the 2-year period. The fish were purchased from a bait dealer who caught them with a purse seine approximately 5 km southwest of La Jolla. The fish were fed daily until satiation with either chopped anchovy or squid and occasionally frozen euphausiids. The fish, about 200 in number, were feeding well and appeared adapted to captive conditions by the end of two weeks, when observations began.

I observed growth by sampling the school at various elapsed times and noting the change in fork length. The number of fish sacrificed and the elapsed times from the beginning were:

Elapsed time in days	0	62	121	180	240	322	411	505	600	733
Number of fish sacrificed	24	22	20	10	10	10	11	10	11	23

No fish were added or replaced after removal of samples. Routine data on individual fish included fork length (FL) to the nearest 1 mm, body weight to the nearest g, sex, and gonad weight to the nearest g. I calculated the gonosomatic index—gonad weight/body weight x 100—for all fish. Observations were terminated after two years because some of the fish appeared to be in declining health and were not feeding well, possibly because of long-term stress.

The von Bertalanffy growth equation,

$$l_t = L_\infty [1 - e^{-k(t - t_0)}]$$

where

l_t = fork length at time t in mm,
L_∞ = maximum expected fork length,
t_0 = hypothetical time of zero length,
t = elapsed time in years after start of experiment,
k = a constant pertaining to metabolism

was applied to the length-time data to describe the growth and estimate L_∞, the length the fish would have reached had they remained indefinitely under laboratory conditions. I used a computer program (Abramson 1971) utilizing the least squares procedure of Tomlinson and Abramson (1961) to estimate the parameters.

The weight-length relation was determined by fitting the weight-length data to the equation $W = aL^b$

where

W = weight in g,
L = fork length in mm,
a = a constant,
b = slope of line after log transformation.

After growth observations, I measured the fat and water content in the red muscle, white muscle, viscera, and body as a whole of some of the laboratory fish and also of some sea-caught fish. The sea-caught fish were captured by a Russian trawler about 250 km from the California coast and were frozen. I used five fish from each group for whole-fish fat analysis. Each fish was passed through a meat grinder several times for homogenization and dried to constant weight at 55°C in a vacuum oven. Fat extraction was accomplished with a Soxhlet apparatus using chloroform and methanol as suggested by Kvaric and Muzinic (1950). Prior to homogenization, I measured the cross-sectional areas of the fishes' red and white muscle bundles. The measurements were made from a transverse steak taken one-third of the fish length anterior to the tail, as sug-

gested by Greer-Walker and Pull (1975). I traced the outlines of the muscle areas onto a sheet of clear plastic and measured them with a planimeter.

Seven laboratory and seven wild fish were used for red muscle, white muscle, and visceral fat analysis. I dissected the red and white muscle tissues from the musculature at mid-fork length near and above the lateral line. The viscera included all the organs in the body cavity except the kidneys, which were inadvertently excluded. The procedure for fat analysis was the same as for whole fish.

RESULTS

The distribution of fish lengths at the various elapsed times and the von Bertalanffy growth curves for the captive and wild fish are given in Figure 1. The parameters describing the growth of the captive and wild fish are presented in Table 1. Figure 1 shows the two curves beginning at a time when the captive and wild fish were 243 mm FL, ($t = 0$; equivalent age is 2.26 years for wild fish). The curves show that an average fish in the laboratory grew to 408 mm FL for an increase of 165 mm during the 2-year period, while a typical wild fish would have grown to 304 mm FL for an increase of only 61 mm. Calculations with the Wine-Knaggs equation indicate that the time required to grow from 243 to 408 mm FL is 6.55 years. Hence the captive fish put on more than 6 years of growth in 2 years.

The estimate of L_∞ (Table 1) for captive fish suggests that they could have grown to an average fork length of 463.9 mm had they remained indefinitely under laboratory conditions. The L_∞ value for captive fish is much lower than that for wild fish (602.9 mm FL), although the captive fish had a higher growth rate during the 2 years under observation. Mackerel in the sea attain lengths slightly over 600 mm FL (MacCall and Stauffer 1983) and live over 30 years (Fitch 1956). The relatively high K value for captive fish indicates that their growth rate was declining rapidly. The t_0 values are not directly comparable because of differences in computation.

Many of the captive fish grew significantly larger than fish taken in the inshore southern California

TABLE 1
Estimated Growth Parameters in the von Bertalanffy Equation for Captive and Wild Jack Mackerel

	L_∞ (mm FL)	K	t_0 (years)
Captive fish	463.9	0.6836	−1.08
S.E.	16.1	0.0919	0.10
Wild fish	602.9	0.0935	−3.25
(Wine and Knaggs 1975)			
S.E.	5.9	0.0027	0.11
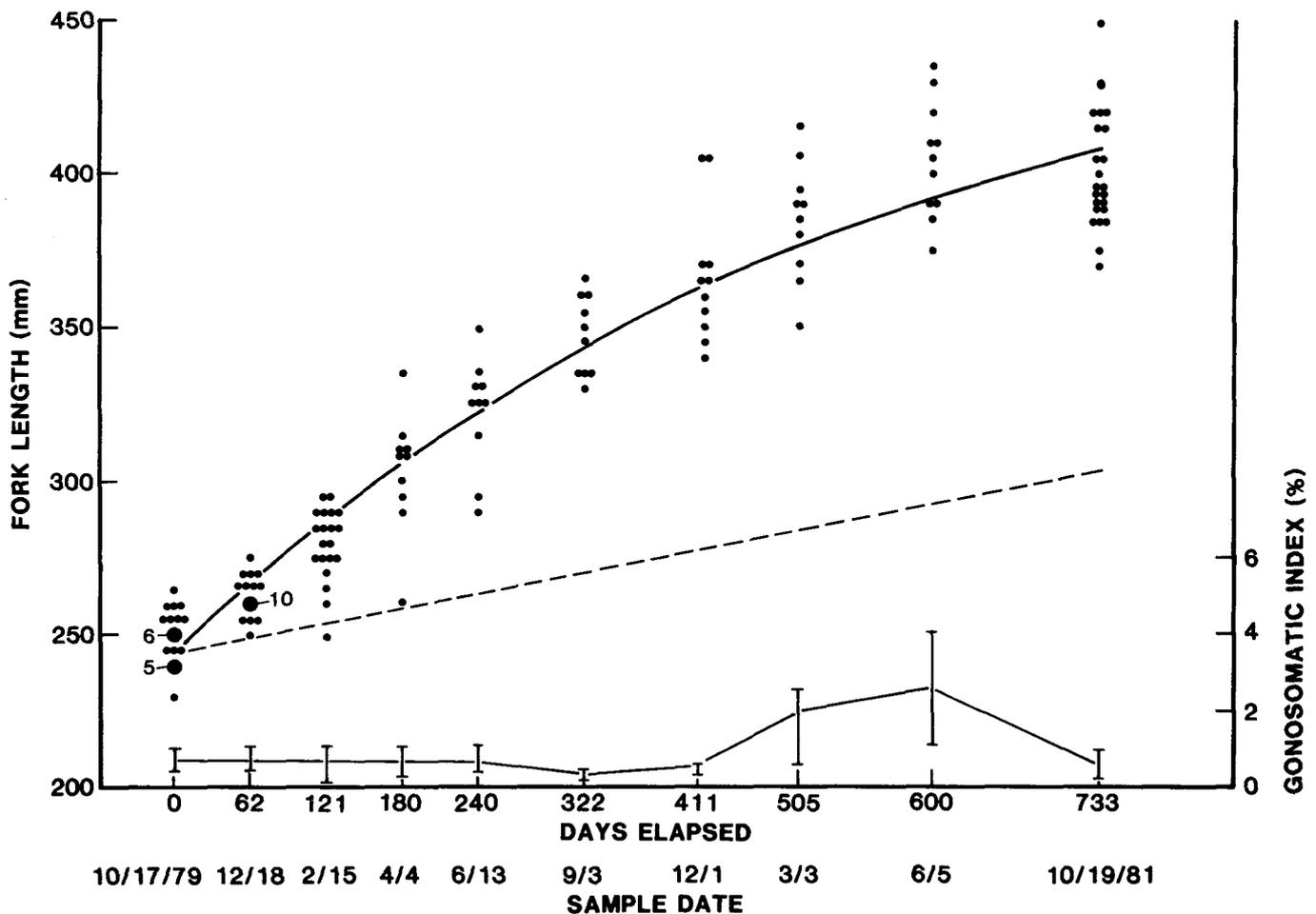
Figure 1. Growth of jack mackerel in the laboratory compared to growth of mackerel in the sea, and female ovarian development during captivity. Upper scale shows the distribution of fork lengths at elapsed times, the growth curve for fish in the laboratory (solid line), and the growth curve for fish in the sea (dashed line). Lower scale gives the ranges and means of female gonosomatic indices at sampling dates.

fishery. Data from Mallicoate and Parrish (1981) reveal that only a few mackerel of more than 20,000 sampled were over 350 mm FL, and none were over 380 mm FL during the years 1966-70. Most of the laboratory fish were larger than 350 mm FL in the 411-day sample (Figure 1), and none were less than 350 mm FL in the last three samples. The largest captive fish sampled was 450 mm FL. The sample of offshore fish in the present study contained 24 of 100 fish measuring less than 450 mm FL, with the two smallest between 300-350 mm FL. The remaining fish were larger, and two of the fish were over 600 mm FL.

The parameters describing the weight-length relationship for captive and wild fish are given in Table 2. The Wine and Knaggs equation is applicable to fish measuring 100-300 mm FL, according to MacCall et al. (1980), whereas their equation is more applicable to the entire range of lengths.

The weights (g) for some selected lengths calculated from these equations are:

Length (mm FL)	250	300	350	400	450
MacCall et al. (1980)	171	294	465	692	982
Wine and Knaggs (1975)	177	319	524	807	1179
Captive fish this study	179	356	635	1048	1632

The calculated weight, 179 g, for the captive fish at 250 mm FL is not very different from the values obtained with the other equations. This difference increases markedly with length, however, and captive fish of 450 mm FL would weigh nearly 1.4 times as much as wild fish of similar length from the Wine-Knaggs equation and over 1.6 times as much as fish from the other equation. Calculations with the weight-

TABLE 2
Estimated Parameters in the Weight-Length Equation, $W = aL^b$, for Captive and Wild Jack Mackerel

	a	b
Wild fish (Wine and Knaggs 1975)	0.0000033101	3.223229
Wild fish (MacCall et al. 1980)	0.000012338	2.97785
Captive fish this study	0.000000176	3.75670

length equation for captive fish indicate that the weight should have increased from 161 to 1130 g as the mean length increased from 243 to 408 mm FL during the 2-year holding period. Calculations with the Wine-Knaggs length-growth equation and the weight-length equation from MacCall et al. (1980) indicate that mackerel in the sea would require 10.8 years to grow from 161 g to 1130 g. It thus appears that the captive fish gained weight about five times faster than fish in the wild.

The average whole laboratory fish contained less water (50.2% vs 70.7%) but more fat per unit wet weight (25.7% vs 6.4%) than the average sea-caught fish (Table 3A). The values for the sea-caught fish were close to those found for *Trachurus trachurus*, which had an estimated moisture content of 76.7% and fat content of 6.8% (Sidwell et al. 1974). The average laboratory fish used in whole-fish fat analysis was slightly longer—433 vs 426 mm—but much heavier—1332 vs 850 g—than the average sea-caught fish. For a further comparison of the wet and component weights, I calculated the expected wet weight of a 430 mm FL fish from the weight-length relationship for both groups. I then estimated the water, fat, and fat-free dry weights with the percentages in Table 3A. The calculations (Table 3B) show that fat accounted for 65.2% of the difference in wet fish weight, water only 8.4%, and fat-free dry weight 26.4%. The large difference in fat-free dry weight is of particular in-

terest because it implies that the laboratory fish stored a substantial amount of protein in addition to fat.

The red muscle, white muscle, and viscera of the laboratory fish all contained much more fat per unit wet weight than did the sea-caught fish (Table 4). The viscera and white muscle of the laboratory fish had about 7.1 and 8.6 times more fat per unit wet weight than those of sea-caught fish. The percentage of fat in the red muscle of the laboratory fish was only 4.5 times higher, suggesting that the increase in fat was not distributed proportionately to the three body areas. The viscera were highest in fat content, followed by red muscle and white muscle in captive as well as sea-caught fish. Although lower in relative fat content, the white muscle tissues probably contain more total fat because they occupy a much greater portion of the body volume. The water content was higher in sea-caught fish for the three types of tissues examined.

The red and white muscle bundles appeared to have enlarged proportionately with fish girth, because the percentage of red muscle to total muscle was nearly the same at 11.1% and 10.8% (Table 3). These percentages were much lower than the 18.3% recorded for *Trachurus trachurus* by Greer-Walker and Pull (1975). Much of the difference may be due to technique and the exact position of the transverse cut. The same technique was applied to both laboratory and sea-caught groups of jack mackerel.

The ovaries of the captive females were most highly developed during June 1981 (Figure 1). The eggs in the more mature ovaries were heavily yolked, and measured 0.5-0.7 mm in diameter, about the maximum size found by MacGregor (1966 and 1976) in his fecundity studies. Ichthyoplankton surveys indicate that June is one of the peak spawning months (Ahlstrom 1956; Farris 1961). The gonosomatic indices for the males were all under 1% except in June 1981 when two of the five males sampled had indices above 2%.

TABLE 3
A. Comparison of Water, Fat, Red Muscle, and Size of Five Laboratory and Five Sea-Caught Mackerel

	Laboratory		Sea-caught	
	Mean	S.E.	Mean	S.E.
Percent water[a]	50.2	1.4	70.7	1.4
Percent fat[a]	25.7	3.9	6.4	1.7
Percent red muscle to total muscle[b]	11.1	0.5	10.8	0.5
Fork length mm	443	4.8	426	4.5
Wet weight g	1332	49	850	46

B. Comparison of Wet and Component Weights (g) of Laboratory and Sea-Caught Fish[c], Applying above Data

	Laboratory	Sea-caught	Difference	Percent of 428-g wet weight difference
Weight of Water	655	619	36	8.4
Weight of fat	335	56	279	65.2
Fat-free dry weight	314	201	113	26.4
Wet weight of 430-mm mackerel[d]	1304	876	428	100.0

[a]Percent based on wet weight.
[b]Percent red muscle measured from transverse cut.
[c]Standardized to 430 mm.
[d]Wet weight obtained from weight-length relationship within each sample.

TABLE 4
Comparison of Seven Laboratory and Seven Sea-Caught Mackerel

	Laboratory		Sea-caught	
	Mean	S.E.	Mean	S.E.
Red muscle				
Percent water	48.4	1.7	71.2	0.8
Percent fat[a]	31.9	2.5	7.1	1.1
White muscle				
Percent water	63.5	1.9	75.0	0.8
Percent fat	12.7	1.9	1.5	0.3
Viscera				
Percent water	25.4	2.6	75.2	1.4
Percent fat	67.5	9.1	9.6	1.5
Length (mm)	394	3.0	395	16.2
Weight (g)	907	55	593	85

[a]Percent water based on wet weight.

These two males produced sperm upon stripping and appeared capable of spawning. The water in the tank was checked regularly for eggs but no sign of actual spawning was detected. The females did not show signs of advanced ovarian development during June of 1980, although they were large enough to be sexually mature (235 mm FL) according to Wine and Knaggs (1975).

DISCUSSION

The abundant food supply and lack of predators undoubtedly contributed much to the high growth rate observed in this study. The temperature and the absence of spawning may also have been important in increasing growth. The large increase in growth by fish in the laboratory over fish in the sea has been observed for other pelagic species including the Japanese jack mackerel, *Trachurus japonicus* (Ochiai et al. 1983) and northern anchovy, *Engraulis mordax* (Hunter and Leong 1981). In spite of the rapid growth rate observed, the ultimate length, L_∞, attainable by the captive fish appeared to be relatively small. The stress of confinement in a small volume of water and missing elements in the diet over an extended period are factors that can limit growth.

The captive fishes' growth in length exceeded that of the wild population by about three times. The captives' greater growth in body weight—about five times—suggests that the food ration exceeded that needed for skeletal growth and that growth in length may have been near the maximum for the given conditions. It is not surprising that a large food supply increased fat deposition, but the finding that it also resulted in a substantial increase in fat-free dry weight suggests that excess rations are stored not only as fat but also as protein.

That fact that some of the captive fish grew beyond 425 mm FL and one reached 450 mm FL indicates that the small jack mackerel in the inshore regions off southern California have the potential to reach those lengths. Observations in the present study do not exclude the possibility that these inshore fish have the potential to grow even larger.

ACKNOWLEDGMENT

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Manuscript should be typed (no dot-matrix printouts, please) DOUBLE-SPACED with wide margins, and submitted complete with figures, figure captions, and tables, in triplicate (good copies but not carbons) to

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California Department of Fish and Game
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In addition to the manuscript, contributors should submit the names of three suggested *reviewers* who would be knowledgeable about the contents and who would be available and willing to give their time and effort.

Sequence of the material should be TITLE PAGE, ABSTRACT, RESUMEN, TEXT, LITERATURE CITED, APPENDIX (if any), TABLES, LIST OF FIGURES with entire captions, and FIGURES.

Title page should give:
a running head of no more than 60 letters and spaces,
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Text style will in general follow that of the U.S. Department of Commerce (NOAA) *Fishery Bulletin*. Contributors who are not familiar with this publication will do well to follow the *U.S. Government Printing Office Style Manual* (1973). Authors are strongly urged to compare their typewritten equations with similar expressions in the printed literature, with special attention to ambiguity of the symbols for "one" and for "el," before submitting. Whenever possible, write in the first person, and use active verbs.

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(book):
Odum, E.P. 1959. Fundamentals of ecology. 2nd Ed. Saunders, Philadelphia, 546 p.

(chapter):
Wooster, W.S., and J.L. Reid, Jr. 1963. Eastern boundary currents. *In* M.N. Hill (ed.), The sea. Interscience Pub., New York, p. 253–280.

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Figures, whether drawings or halftones, should be submitted in a format not larger than 8½ x 11". Submit one set of camera-ready figures plus 2 sets of copies. Photographs should be printed on glossy paper. Drawings should be reduced photographically. A composite figure should be submitted as a single photograph or at least as a single careful paste-up. Figures will appear as either single-column (85-mm-width limit), or double-column (178-mm-width limit; maximum height for either, 115 mm), or as full page. Special cases should be discussed with the editor before submittal. After reduction, no letter or number should be smaller than 1 mm. Special note should be taken of the disappearance of decimal points during reduction. If commercially prepared shading is used, make a trial reduction to ensure that the patterns do not merge at the required reductions. The determining factor for size should be the complexity of detail to be shown.

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Acknowledgments, if included, should be placed at the end of the text and should include funding source.

Reprint orders will be mailed (to senior author only) on publication of the completed book. No covers will be supplied, and there will be no further reproduction.

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The CalCOFI Editorial Board will consider for publication in the section entitled "Scientific Contributions," manuscripts not previously published elsewhere that bear some relationship to the following with respect to the Californias, the California Current, and the Gulf of California:
marine organisms
marine chemistry, fertility, and food chains
marine fishery modeling, prediction, policy, and management
marine climatology, paleoclimatology, ecology, and paleoecology
marine pollution
physical, chemical, and biological oceanography
new marine instrumentation and methods.

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CONTENTS