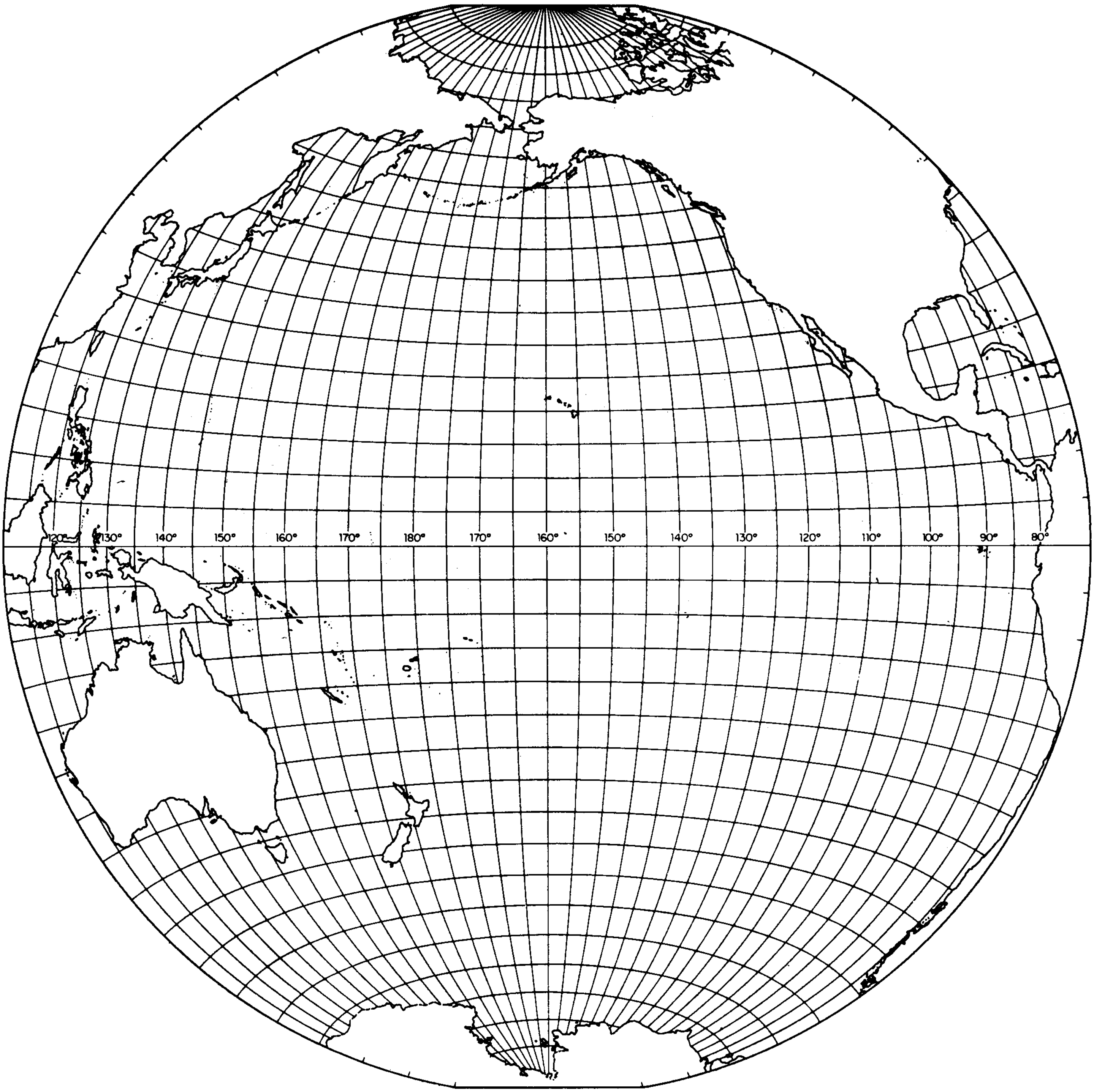

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

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CALIFORNIA
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NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL MARINE FISHERIES SERVICE

EDITOR Julie Olfe

SPANISH EDITOR Patricia Matrai

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

The member agencies of CalCOFI remain strongly committed to cooperative partnership as a means of making optimal use of public resources, sharing ideas in research, and providing a public forum to examine and discuss fisheries problems that concern the people of California. The pelagic ecosystem off the coast of the Californias is multidimensional, dynamic, and complex, and research on that system requires openness to new ideas and approaches, with assurance of the continuity of fundamental CalCOFI data bases. As a result, CalCOFI scientists' work follows two major trajectories. First, quarterly cruises are made off the coast of California to measure the same physical, chemical, biological, and meteorological variables year after year. On these cruises, new technologies, including satellite-mediated information gathering, are employed. Second, this information is used to form hypotheses and test them ashore and at sea, using state-of-the-art methods such as satellite-tracked drogues, very high-frequency sonar, automated sampling devices, and satellite imaging.

The 36-year time series of physical, chemical, biological, and meteorological data from the California Current, collected and processed by the CalCOFI team, constitutes an enormous challenge in data-base management and data access. The Southwest Fisheries Center has continued to develop a user-friendly system for access to the entire data suite. In addition to the development of software, the process has required the verification of some earlier larval identifications in the light of later knowledge. The system, when completed, will make a large body of data readily accessible to qualified researchers, and will greatly increase the knowledge available from CalCOFI's extensive collections.

Determining the spawning biomass of sardines, when their biomass is very low, has been a problem in the past. During the last year, Patricia Wolf of the California Department of Fish and Game, and Paul Smith of the National Marine Fisheries Service (NMFS) used the newly developed egg production method to make a cost-efficient, quantitative determination of the relative magnitude of sardine spawning biomass during times of low biomass levels. This method was employed during May 1985 to determine that the spawning biomass was at least 20,000 short tons, permitting the opening of a 1,000 ton sardine fishery on January 1, 1986. The 1986 sardine fishery is the first since the moratorium took effect in 1974.

CalCOFI was organized in 1949 as a response to the needs of California's fishing industry, and has a long-standing relationship of cooperation with and service to the industry and to governmental managers. In 1985, CalCOFI researchers from the Southwest Fisheries Center and from the California Department of Fish and Game consulted with industry scientists to discuss management options for Pacific mackerel. Their recommendations resulted in the adoption, by the state legislature, of new law for managing this stock.

The CalCOFI Committee sponsors a conference each October to discuss the status of knowledge about fisheries; the biology of fishes; their environment, including physics, chemistry, meteorology, and—from time to time—fishing gear; and the industry and its politics. The 1985 conference at Idyllwild, California, included a symposium convened by John Grant of the California Department of Fish and Game, entitled "Southern California Nearshore Waters: Selected Patterns and Processes." Some of the papers presented at that symposium are included in this volume.

During the past year, CalCOFI personnel of NMFS's Southwest Fisheries Center, the Marine Life Research Group at Scripps Institution of Oceanography, and the California Department of Fish and Game have fielded four CalCOFI survey cruises of 15 days' duration, two trawl survey cruises, one biomass cruise, two Sardine-Anchovy Program cruises, and one Dover sole trawl-survey cruise. The CalCOFI Committee wishes to acknowledge the officers and crews of NOAA research vessels *David Starr Jordan* and *McArthur* and the University of California's R/V *New Horizon* for their support. The data have been reported in the Scripps Institution of Oceanography Reference Series, the CalCOFI Data Report Series, and other data reports and documents.

The Committee wishes to thank Herbert Frey of the California Department of Fish and Game for his many years of service to the CalCOFI Committee. Herb has served as alternate to the Committee, as a member for two terms, and as CalCOFI Coordinator. He has also served as editor of *CalCOFI Reports* and as executive secretary of the Marine Research Committee of the State of California—the parent committee of CalCOFI. Richard Klingbeil has been appointed as the new Committee member representing the California Department of Fish and Game.

Finally, the CalCOFI Committee wishes to thank the dozens of reviewers who suggested substantial improvements to the scientific contributions in this volume, Julie Olfe for her very competent and efficient services as editor, the staff who provided translating services and scientific consultation, and to George Hemingway, our current CalCOFI Coordinator.

Copies of this report and other CalCOFI documents may be obtained gratis by addressing a request to: CalCOFI Coordinator, Scripps Institution of Oceanography, A-027, La Jolla, CA 92093.

The CalCOFI Committee:
Izadore Barrett
Richard Klingbeil
Joseph Reid

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1985

California Department of Fish and Game
Marine Resources Region
245 West Broadway
Long Beach, California 90802

Total 1985 landings of fishes, crustaceans, and mollusks declined for the fifth straight year. Landings declined 21% from 1984 to a level 52% below the average for the last ten years. Continuing closures of California tuna processing plants were the primary reason for the persistent decline.

Landings of pelagic wetfishes increased slightly for the first time in four years (Table 1). Both the Pacific herring and market squid fisheries rebounded from the low levels recorded during the recent warm-water period. While mackerel landings remained relatively stable, and the anchovy reduction fishery faded, the Pacific sardine resource continued a modest trend of apparent increased abundance.

Groundfish landings increased somewhat over 1984 levels, with significant gains for flatfishes and Pacific whiting almost offset by declines for rockfishes. Swordfish landings set a new high; for the first time in several years harpoon vessels contributed considerably, augmenting the catches of the drift gill net fleet. Pacific ocean shrimp landings increased for the second straight year.

Moderate decreases were recorded for the Dungeness crab and lobster fisheries, while albacore decreased by almost 50% from 1984 landings.

Sportfish landings were more comparable to those years with "normal" water temperatures: there were fewer exotics, and salmon were healthier.

PACIFIC SARDINE

The moratorium on commercial fishing for Pacific sardines (*Sardinops sagax caeruleus*) remained in effect during 1985 because the spawning biomass was assessed as remaining below the 20,000 tons required before a fishery may be allowed. However, recent occurrences of sardines in mackerel and live bait catches, in California Department of Fish and Game (CDFG) sea surveys, and in CalCOFI ichthyoplankton surveys, as well as observations by aerial fish spotters indicated that the biomass might be approaching 20,000 tons. CDFG and the National Marine Fisheries Service, Southwest Fisheries Center designed and conducted a survey in May to determine whether the sardine spawning biomass had exceeded this level. The

TABLE 1
Landings of Pelagic Wet Fishes in California in Short Tons

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	106,307
1970	221	96,243	311	23,873	158	12,295	133,101
1971	149	44,853	78	29,941	120	15,756	90,897
1972	186	69,101	54	25,559	63	10,303	105,266
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	160,111
1977	6	111,477	5,975	50,163	5,827	14,122	187,570
1978	5	12,607	12,540	34,456	4,930	18,899	83,437
1979	18	53,881	30,471	18,300	4,693	22,026	129,389
1980	38	47,339	32,645	22,428	8,886	16,958	128,294
1981	31	57,659	42,913	15,673	6,571	25,915	148,762
1982	145	46,364	31,275	29,110	11,322	17,951	136,167
1983	388	4,740	35,882	20,272	8,829	2,010	72,121
1984	259	3,258	46,531	11,768	4,241	622	66,679
1985*	652	1,792	38,100	10,316	8,801	10,881	70,542

*Preliminary

survey used the presence of sardine eggs to assess the extent of spawning area in southern California waters. Sardine spawning covered an estimated 670 n.mi.^{2}, which was determined to be characteristic of a biomass of at least 20,000 tons. As provided by current law, CDFG announced the opening of a 1,000-ton fishery to begin January 1, 1986. Apart from the 75-ton live bait quota initiated last year, this is the first directed take of sardines allowed in California since the moratorium took effect in 1974.

The trend of increasing occurrences of sardines in the mackerel fishery, which slowed last year, appears to have resumed. An estimated 652 tons of sardines were landed incidentally with mackerel during 1985 (Table 1). This is the largest annual take in 20 years. Monterey landings accounted for 6% of the incidental catch, and local fishermen reported sighting large schools of sardines in Monterey Bay on several occasions. The proportion of observed mackerel landings containing sardines increased from 30% in 1983 and 1984 to over 57% during 1985. Sardines constituted 1.3% of the overall 1985 "mackerel" catch; during March-April sardines were nearly 3% of the catch. Length frequencies of incidentally caught sardines show an increasingly broader distribution from 1983 through 1985, indicating that recruitment has continued.

Sardine landings in live bait declined to roughly 25% of the 1984 estimated landings, and failed to reach the 75-ton annual quota. This probably resulted from a decreased demand for sardines rather than a decline in availability. Live bait fishermen often targeted instead on squid, which were available for the first time in recent years and are often preferred as bait for certain big game fish. Legislation passed in 1985 increases the annual live bait quota for sardines from 75 to 150 tons, effective January 1, 1986.

During CDFG experimental young fish surveys in July and August, only adult sardines were captured. Evidence of sardine recruitment was not observed until September, when young-of-the-year fish appeared in both the live bait catch and sea survey trawls. Adult and juvenile catch frequencies during the September cruise were lower than last year's; however, the catch frequency of juveniles suggests that the 1985 year class is similar in strength to the 1984 year class and considerably weaker than the 1983 year class. Adult fish captured during the sea survey cruises were in progressively more advanced stages of prespawning condition from July through September. Also, a greater proportion of adult sardines occurring in the mackerel fishery were nearing spawning in the late summer than in the spring. These observations suggest that a large portion of spawning occurred during late summer and early fall this year; the historical sardine population spawned mostly in spring.

Current state law provides for the rehabilitation of the sardine resource. During the process of rehabilitation a small fishery is allowed. If the spawning population increases beyond 20,000 tons, CDFG may increase the seasonal quota, but at such a rate as to allow for the continued recovery of the population. Only limited markets exist now for sardines, and it remains to be seen whether new markets and uses will develop as the resource recovers.

NORTHERN ANCHOVY

At least one processor in both the northern (north of Point Buchon) and southern permit areas issued orders for northern anchovy (*Engraulis mordax*) for reduction during the 1984-85 season. Fishermen, however, found anchovies unprofitable and concentrated their efforts on mackerel. The anchovy price per ton dropped from $38 to between $25 and $30, and fishermen reported that large anchovy schools were not locally available in either permit area.

A single landing of 77 tons was made during the 1984-85 reduction season (Table 2). This landing occurred at Terminal Island in November 1984, against the southern area quota of 6,250 tons. No landings for reduction purposes were made toward the northern area 1984-85 season quota of 694 tons.

Using an egg production biomass assessment method, the National Marine Fisheries Service esti-

TABLE 2
Anchovy Landings for Reduction Seasons in the Southern and Northern Areas, 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	1,374	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
1983-84	70	1,765	1,835
1984-85*	77	0	77

*Preliminary

mated the 1985 northern anchovy spawning biomass at 574,421 tons (521,000 metric tons). The U.S. optimum yield for the 1985-86 season was set at 159,750 tons, and the harvest quota for reduction purposes was set at 154,350 tons. Allocations established were 10,000 tons for the northern permit area, and 144,350 tons for the southern area.

The 1985-86 reduction season opened on August 1 in the north and September 15 in the south. Approximately 909 tons of anchovy were landed between November 15 and December 30, 1985. All landings were made in the northern permit area by two boats fishing just outside the Monterey Bay breakwater. Efforts to fill reduction orders dropped off as fish moved out of the area.

Statewide reduction landings of northern anchovy for 1985 were 909 tons. Nonreduction landings totaled 883 tons. The live bait catch was estimated at 5,055 tons. Bait was highly available year-round.

Trawl surveys during 1985 indicate dominance by the 1984 and 1983 year classes (66% and 22% by number, respectively, in survey samples). Although young-of-the-year (1985 year-class) fish made a strong showing in live bait hauls from June through December, reports of poor catches of young fish in the 1985 Mexican reduction fishery, and their poor representation in CDFG recruitment surveys indicate that the 1985 year class may actually be weak.

JACK MACKEREL

Approximately 10,320 tons of jack mackerel (*Trachurus symmetricus*) were landed during 1985. Jack mackerel constituted roughly 21% of total mackerel landings. This marks the seventh consecutive year that jack mackerel have contributed less than Pacific mackerel to the California mackerel fishery. It is the second consecutive year that jack mackerel have contributed such a low proportion of the mackerel fishery since this species first supported a fishery in the late 1940s.

Jack mackerel dominated landings only during January, when landings of Pacific mackerel were limited by interseason restrictions, and overall mackerel landings were the lowest of the year. Jack mackerel were mostly unavailable or not sought after in southern California during the last four months of the year. The composition of northern California catches varied greatly throughout the year, with jack mackerel constituting less than 1% of the catch in October and more than 95% of the catch in January and February. Calculated throughout the year, jack mackerel made up 23% of the northern California mackerel catch and 20% of the southern California catch. This is in contrast to 1984 and 1983, when jack mackerel contributed a considerably larger proportion of the mackerel landings in the north than in the south.

Sea surveys conducted during 1985 indicate fair to good recruitment for the 1985 year class of jack mackerel.

PACIFIC MACKEREL

The 1984-85 season (July 1-June 30) for Pacific mackerel (*Scomber japonicus*) was closed on December 20 because the adjusted season quota of 26,000 tons has been landed. Interseason restrictions were in effect through January, limiting the take of Pacific mackerel to 50% or less by number, or pure loads of 3 tons or less. The season reopened on February 5 after the California Fish and Game Commission (FGC), as recommended by CDFG, augmented the quota with 5,000 tons per month for February, March, and April, with uncaught portions of the monthly allotments to be added to the next month's quota. The quota increase resulted from a reevaluation of the 1984-85 Pacific mackerel total biomass, finally estimated to range between 131,000 and 242,000 tons. For the first time this estimate included consideration of Mexican commercial and U.S. recreational catches in cohort analysis.

Landings continued to be low despite quota increases, because southern California processors imposed a landing limit of approximately 70 tons per boat per month through March. In April the landing limit was increased to 50-60 tons per boat per week, but the price per ton was lowered from $190 to $163. On April 24, the FGC added another 15,000 tons to the season's allowable catch, bringing the 1984-85 season quota to 56,000 tons. Fishing for the remainder of the season was slow. Although the price was increased to $170 per ton, landing limits were decreased to 25 and 50 tons per boat per week, because inventories of frozen mackerel reportedly exceeded last year's by 60%. In Monterey only about 1,600 tons of mackerel were landed from January through June, because fishermen concentrated their efforts on squid. The National Marine Fisheries Service (NMFS) began to investigate the use of Pacific mackerel in a federal surplus commodities program to help ease poor local market conditions, which were partly caused by competition from foreign countries.

The 1984-85 season ended with a total catch of 43,270 tons of Pacific mackerel. Approximately 83% was landed in southern California. Pacific mackerel constituted an average 93% of total mackerel landings from January through June 1985, and 81% of total landings for the 1984-85 season. Areas where fish were caught from February through June ranged from off the Santa Barbara coast to outside Santa Monica Bay, and out to Santa Cruz, Anacapa, and Santa Catalina islands.

The 1985-86 season opened July 1, 1985. The Pacific mackerel biomass was estimated to range between 178,000 and 260,000 tons, providing a season fishery quota of 40,000 tons. The season started off slowly, because Terminal Island processors were closed for much of July. Southern California purse seiners fished up the coast to Morro Bay in August, when landings increased substantially.

On September 9, urgency legislation (AB 1197) was passed. This law (1) requires CDFG, by February 1 of each year, to estimate the total Pacific mackerel population size for the current season, and the expected size at the beginning of the next season; (2) sets the quota at 30% (up from 20%) of the population above 20,000 tons when the total biomass is between 20,000 and 150,000 tons; (3) allows for no quota restrictions (open fishery) when the biomass is greater than 150,000 tons; (4) allows CDFG to adjust quotas during any portion of the season; (5) increases the pure-ton interseason restrictions from 3 to 6 tons; and (6) eliminates the 10-inch size limit. Quota restrictions for the remainder of the 1985-86 season were subsequently lifted upon consideration of the estimated biomass range.

Landings were high in September, but declined in October during a dispute over landing limits and prices. Fishing resumed in November, with landing limits remaining in place and the price reduced to $155 per ton. Landings were limited by a lack of orders, particularly in northern California. December landings were high, for fish were locally abundant, and orders increased.

By the end of December approximately 22,870 tons of Pacific mackerel had been landed for the 1985-86 season. Landings for 1985 reached 38,100 tons, of which only 7% was landed in northern California. This is a decrease from the 18% northern California contributed to mackerel landings last year. As in 1984, the 1980 and 1981 year classes of Pacific mackerel accounted for the majority of landings. Fish 3 years of age and younger showed better recruitment than in 1984, but the 1982 and 1983 year classes still appear very weak. The strong showing of the 1984 year class, as 1-year-olds, is encouraging. Young-of-the-year fish did not enter the fishery during 1985, and sea survey experimental cruises to assess recruitment of Pacific mackerel off southern California gave preliminary indications that the 1985 year class may be weak.

MARKET SQUID

The California market squid (*Loligo opalescens*) fishery landed 10,881 tons during 1985, a very large increase over the last two years' landings (Table 1). However, this was still 23% below the last ten-year average. The California squid fishery is best described as two separate fisheries: the northern California (or Monterey) fishery, and the southern California fishery.

In Monterey the fishery normally follows a summer-fall season, but has been atypical the last three years. This year the fishery started earlier than normal. Large squid (seven to eight per pound) were caught in April, although there were signs that they were not abundant. In good years the boats are usually at the dock unloading their catch shortly after sunrise. This year, boats spent more time looking for squid and arrived at the dock as late as noon, with highly variable fishing success. The initial price was $600 per ton.

Fishermen voluntarily increased the spawning escapement by giving the squid two weeks to spawn undisturbed in May. Squid landed during May were still large, but many were spent, and the overall quality was poorer than two weeks earlier. The price dropped to $400 per ton.

During the summer, fishing moved northerly, away from the traditional grounds near Monterey to the area between Año Nuevo and Pigeon points. Fishing ranged from excellent to spotty, with landings through mid-September. Despite continued effort, commercial boats were unable to catch squid after that time. Partyboats, however, were still successfully jigging squid for bait in November.

For the Monterey fishery, squid were scarce throughout the year. Although demand was strong, only 4,286 tons were landed. This is a great improvement over the past two years, but is still only 30% of the 14,000 tons landed in 1981, the best single year in the past 40 years.

The southern California squid fishery typically has a fall-winter season, running from early November through February. This pattern had not been followed since 1982, because of a lack of squid, which was probably related to El Niño. This year, however, the pattern resumed; significant landings began in October and continued through the winter. Early in the year, squid were very large, averaging about 5 per pound; later in the year, they ranged from 8-11 per pound.

Southern California landings totaled 6,595 tons, 75% of which were landed during the last quarter of the year. The price at the beginning of the year, when squid was still in very strong demand, went as high as $700 per ton. The price then dropped steadily until the end of the year, stabilizing at $200 per ton.

PACIFIC HERRING

The Pacific herring (*Clupea harengus pallasi*) fishery recovered in 1985 from the transitory effects of the 1982-84 El Niño. The 1984-85 seasonal (December-March) catch of 8,264 tons exceeded the 7,590-ton statewide quota and nearly tripled the 1983-84 seasonal catch of 3,000 tons. Annual catch figures for 1985 also improved, more than doubling the 1984 catch (Table 1). There was a corresponding economic improvement in the fishery. The base price for 10% roe recovery increased to $1,000 per ton and resulted in an ex-vessel value for the 1984-85 fishery of over $9 million.

Population estimates from 1984-85 spawning-ground surveys in Tomales and San Francisco bays paralleled the improvement in the fishery. After the poor 1983-84 season, almost 6,600 tons of herring returned to Tomales Bay this past season, and in San Francisco Bay the population increased 15%, to 46,000 tons.

Herring exhibited good growth characteristics during 1984; weight lost during the period of poor growth caused by El Niño was regained. The generally good condition of herring this year contributed to the success of the 1984-85 fishery.

Based on the 1984-85 population estimates, the statewide herring quota for 1985-86 was increased to 8,690 tons. Early 1985-86 season catches have been excellent. This, coupled with an increase in the ex-vessel price for 10% roe recovery to $1,200 per ton, should result in another very good herring season.

GROUNDFISH

California's 1985 commercial groundfish landings (Table 3), including California halibut (*Paralichthys californicus*), were 43,730 metric tons (MT) with an ex-vessel value of $28 million. This represents an increase of 2,658 MT or 6% from the previous year, but is still 18% less than the record 1982 catch of 52,152 MT. California landings constituted 38% of the total 1985 Washington-Oregon-California (WOC) commercial groundfish harvest. Trawl vessels continued their historical domination of the fishery, landing 81% of California's 1985 commercial catch.

Trawl landings of the principal groundfish species, with the exception of lingcod (*Ophiodon elongatus*) and Pacific ocean perch (*Sebastes alutus*), increased from 4% to 41% over 1984 levels. Dover sole (*Microstomus pacificus*), sablefish (*Anoplopoma fimbria*), and Pacific whiting (*Merluccius productus*)—species of particular sensitivity to market fluctuations—registered increases due in part to robust market demand and, in the case of Dover sole, to the continued expansion of the Morro Bay flatfish fishery. Trawl-caught rockfish (*Sebastes* spp.) landings remained relatively stable. The setnet fishery for rockfish and lingcod continued its expansion.

Federal and state management regulations for the WOC area restricted the harvest of sablefish, widow rockfish (*S. entomelas*), and other rockfishes during the year. The coastwide widow rockfish optimum yield (OY) was set at 9,300 MT, and the sablefish OY was set at 13,600 MT. Vessel trip and frequency limits were the regulatory measures used to provide a year-round fishery without exceeding harvest quotas or guidelines. The year began with a coastwide widow rockfish trip limit of 30,000 pounds once per week, but with the option to land 60,000 pounds biweekly. For the third consecutive year, a 40,000-pound trip limit without a frequency restriction was retained for the rockfish complex for the waters from Cape Blanco, Oregon, to the Mexican border. Unrestricted landings of sablefish were allowed, with the provision that landings of fish less than 22 inches total length could not exceed 5,000 pounds per trip in all areas north of Point Conception.

TABLE 3
California Groundfish Landings (Metric Tons)

Species	1984	1985*	Percent change
Dover sole	9,774	12,159	24%
English sole	952	1,073	13%
Petrale sole	590	863	46%
Rex sole	568	906	60%
Thornyheads	2,124	2,975	40%
Widow rockfish	2,781	3,065	10%
Other rockfish	14,727	11,812	−20%
Lingcod	950	696	−27%
Sablefish	4,823	5,167	7%
Pacific whiting	2,335	3,023	29%
Other groundfish	1,448	1,991	38%
TOTAL	41,072	43,730	6%

*Preliminary

The rapid pace of the WOC fishery necessitated in-season regulatory measures. On April 28 the biweekly widow rockfish trip limit was rescinded to reduce the rate of landings. This proved to be insufficient, and on July 21 the widow rockfish trip limit was reduced to 3,000 pounds per trip without a frequency limitation. The latter measure sustained the fishery throughout the year. It became necessary to impose a sablefish trip limit of 13% of a trawl vessel's total weight of fish landed per trip, effective November 25, by which time 90% of the OY had been harvested. Sablefish harvests by other gear types were unaffected. This limit remained in effect until December 5, when the sablefish OY of 13,600 MT was captured, and landings were prohibited.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1984-85 commercial season totaled 4.75 million pounds. This was 0.58 million pounds less than the previous season.

In northern California, fishing began on December 4, after a price settlement of $1.25 per pound. The price was increased shortly thereafter to $1.75 per pound. Weather during the season was generally good, and 347 vessels trapped 92% of the season's catch by the end of January. As in the 1983-84 season, few sublegal crabs were observed. The season closed on July 15.

Landings for Crescent City, Trinidad, Eureka, and Fort Bragg were 2.29, 0.33, 1.38, and 0.17 million pounds, respectively.

A high opening price of $2.00 per pound and low volume catches greeted San Francisco crabbers on opening day, November 12. Many fishermen stopped fishing in December because of low production. The season closed on June 30 with a total catch of 0.58 million pounds. It was a disappointing season after the previous season's landings of 0.86 million pounds.

PACIFIC OCEAN SHRIMP

Statewide landings of ocean shrimp (*Pandalus jordani*) in 1985 totaled 3.3 million pounds, increasing for the second straight year. Areas of production were Area A (False Cape to the Oregon border) and Area C (Pigeon Point to the Mexican Border). The ex-vessel price of $0.35 per pound was uniform statewide.

Area C landings of 39,000 pounds resulted from a combination of targeted trips for ocean shrimp and incidental catches in fisheries for spot and ridgeback prawns. The Area C total represents the lowest annual catch since 1979. The low price and a scarcity of shrimp discouraged all but one vessel (double-rigged) from fishing. Inexpensive shrimp imports and improved catches in other areas also contributed to the low effort for ocean shrimp in the Morro Bay and Avila areas.

Landings from Area A (California-Oregon border to False Cape) totaled 2.9 million pounds, more than double the 1.1 million pounds landed during 1984 but still well below the 1973-82 average of 4.6 million pounds. Shrimpers landed an additional 0.45 million pounds in Area A; these were caught in Oregon waters. The $0.35 per pound price received throughout the season was the lowest ex-vessel price since 1979.

Only 31 boats (16 single-rigged and 15 double-rigged) delivered shrimp to Area A ports during the season (April 1 through October 31); this was the lowest number of boats since 1977 (excluding 1983). Single-rigged vessels had an average seasonal catch rate of 398 pounds per hour; double-rigged vessels averaged 573 pounds per hour.

One-year-old shrimp constituted 87.1% of all shrimp sampled. The incoming year class (1985) made up only 2.4% of the samples, but during October they constituted 13.9% of the samples. This indicates good recruitment. Average counts per pound ranged from 152.8 in May to 105.3 in October and averaged 123.6 for the season.

PELAGIC SHARK AND SWORDFISH

During 1985, 245 permits were issued for harpooning swordfish (*Xiphias gladius*), and 227 drift gill net permits were issued for taking pelagic sharks and swordfish. In addition, 33 permits were issued in a special category authorizing swordfish to be taken by drift gill nets north of Point Arguello.

Harpoon fishermen enjoyed their most successful season since the record year of 1978, landing approximately 0.5 million pounds of swordfish. During 1978 an unprecedented 3.8 million pounds were landed. It is still not clear why record numbers of swordfish moved into waters off southern California in 1978, since nothing even close to this has occurred before or since. The success achieved in 1985, however, may be attributable to the use of spotter aircraft. An eight-year ban on the use of spotter aircraft was lifted by the California Fish and Game Commission late in 1984.

Reported swordfish landings by drift gillnetters fell slightly in 1985. Logbook submittals indicated 23,129 fish caught for the 1985-86 season (May through January), as opposed to 25,367 fish reported for the same period during the 1984-85 season. A reduction in fishing effort during the month of January, due mainly to inclement weather, probably accounts for the decrease in total reported landings this past season. Waters adjacent to the escarpment bordering the Southern California Bight, and the seamounts—particularly Rodriguez and San Juan—remained the most productive fishing grounds during the 1985-86 season.

Preliminary 1985 landings of swordfish will once again set a new high mark. Because of the combined success of harpooners and gillnetters, 5.25 million pounds of swordfish were reported, with an ex-vessel value of $13.4 million.

Common thresher shark (*Alopias vulpinus*) landings amounted to 1.5 million pounds, equaling the previous season's mark. The mean length of fish taken in this fishery continued to decline in 1985. The 1986-87 season will be shortened by a 2.5-month closure (June 1-August 14) in an attempt to take the pressure off what is believed to be a depressed thresher shark stock.

CALIFORNIA SPINY LOBSTER

Daily log returns from the 1984-85 (first Wednesday in October to first Wednesday after March 15) commercial California spiny lobster (*Panulirus interruptus*) fishery documented a precipitous decline in legal lobster catch. The level was the lowest in 12 years.

A spirited anticipation pervaded the fishery; the 440 authorized fishermen represented the largest participation in the 15 years since an application fee was initiated. But enthusiasm dwindled, and the 474,000 trap-hauls from 200 boats made up the lowest reported effort since the 1980-81 season, 12% below the peak established during the 1983-84 season.

Log entries tallied a total sublegal ("short") retention of 419,000 animals at a 0.89 catch-per-trap (CPT) rate. Sublegal CPT levels have steadily increased during the nine years since sublegal escape ports were first required.

A total of 245,000 legal-sized lobsters was logged. Commercial fishery landing receipts documented a total weight of 400,000 pounds, and an average ex-vessel price of $4.00 per pound. Thus the 1984-85 fishery was valued at $1.6 million, 16% below the previous season's estimate. The 0.52 legal CPT rate tied 1973-74 as the poorest season, and catch rates for the months of November (0.42 legals) and December (0.39 legals) were the poorest ever in the 12-year history of logbook records.

Catch success, as measured by pounds-per-hundred-trapping-hours (PPHTH) averaged 1.4, compared to 1.7 the previous season. Monthly catch success was highest in October (2.0), declined to 0.9 in December, and recovered modestly to 1.3 in February and March.

Depressed catch success was largely restricted to southern California's mainland coast. The lightly trapped northern mainland (8% of the state's trapping effort from Malibu Point to Point Arguello) took 8% of the state catch and averaged just under 1.0 PPHTH. South of Santa Monica Bay a concentrated 64% of the trapping effort took 47% of the state catch at a success rate of 1.1 PPHTH.

The Channel Islands portion of the fishery was least affected during this off season. Indeed, the effort here increased slightly from the previous season. Twenty-seven percent of the state's trapping effort captured 44% of the catch at a success rate double that of the mainland.

Although the 1984-85 season was disappointing to a large sector of the fishery—specifically those concentrating their efforts along the mainland coast—the outlook is not all bad. A continuation of the high sublegal retention should initiate a rapid recovery of legal recruitment from a presumably recovering standing stock of late juveniles/young adults. Preliminary log returns indicate that catch success for the 1985-86 season has improved, especially along the northern mainland coast.

The highly productive but densely trapped southern mainland coast continues to foster unrest among veteran lobster fishermen. Although logbook records indicate the most strongly recovering sublegal stock levels in the state, saturation trapping of the nearshore waters off populous San Diego, Orange, and Los Angeles counties effectively limits most fishermen's economic gain to the high catchability months of October and November. High competition for the early season profits has created a spiraling escalation of trap deployment. Overcapitalized fishermen can incur disastrous losses from sudden storms, poaching, theft, or concurrent boating activity. Turnover among participants is high.

Stock conservation management seems to be perpetuating biologically sound harvest rates, and gradual increase is expected in the near future. However, socioeconomic considerations may shift the fishery to limited-entry management. Preliminary legislation has been initiated by San Diego-based veteran fishermen and processors in this regard.

ALBACORE

The 1985 albacore (*Thunnus alalunga*) season had a fairly traditional start, with an excellent bite near Midway Island at the end of May, and fish appearing off southern and Baja California in June. By the end of June, fish had been spotted as far north as Mendocino Ridge (about 150 miles west of Cape Mendocino). During the last half of July, commercial boats were fishing from northern Baja California to the Oregon-Washington border. By the end of August, the best albacore fishing was along the Mendocino Ridge. Much of September's fishing was hampered by rough weather, but most vessels concentrated their efforts off Point Arena and Bodega Bay when weather permitted. During early and mid-October, many boats were working their last trip of the season.

The 1985 season total for California was about 7,200 tons. Approximately 1.5% of this was accounted for by fishermen retailing their catch directly to the public. The season total was a little more than half the previous season's landings. The 1985 landings also fell 17% below the last 10-year average and 36% below the last 25-year average (11,182 tons). During 1984 the southern California purse seine fleet contributed significantly to the catch. This year, as is more typical, the fish were not readily available and schooling at the surface, and so were not vulnerable to round haul nets.

As in the recent past, there were very low landings in Oregon and Washington this season. Approximately 750 tons were landed in Oregon and 150 tons in Washington. This brought the WOC fishery landings to about 8,100 tons, or 60% of the last ten-year coastwide average. California has historically landed about 60% of the albacore caught in the WOC fishery, but over the last few years this percentage has shifted. Last year California contributed 93% of the total tonnage, and this year about 85%. To help put this in perspective on an ocean-wide scale, the WOC fishery lands roughly 10%-20% of the annual Pacific-wide catch.

A 1985 price agreement of $1,300 per ton for fish weighing 9 pounds or more, and $950 per ton for fish less than 9 pounds was reached in June between Pan Pacific Cannery and the Western Fishboat Owners Association. During the summer the price dropped twice, bringing the rate down to $1,000 per ton for fish sold directly to the cannery. This price was as low as the rates in the mid-1970s. Shipping charges continued to be deducted from albacore sales at other locations. In 1984, the prices opened at $1,400 per ton for fish 9 pounds or more and $1,125 per ton for fish less than 9 pounds. By the end of the season, prices had declined to $1,150 per ton and $875 per ton.

Market demand has been one of the most significant influences on the fishery. Pan Pacific at Terminal Island was the only cannery to process and can albacore this season. The other major cannery, Starkist, stopped processing tuna in the United States in October 1984. This year it did continue, however, to purchase albacore, shipping it to Puerto Rico for processing. Fewer buyers and low prices, combined with occasional wholesaler buying limits, discouraged many fishermen. Considering that southern California sport boats reported fair to excellent fishing this season, the low commercial landings are probably due more to reduced fishing effort than fish availability.

In the fall of 1983, U.S. and Japanese scientists met to discuss the status of the Pacific-wide population. They concluded that the stock appears to be well exploited, and is being fished near the estimated ranges of maximum sustainable yield.

RECREATIONAL FISHERY

The catch record of sport anglers fishing on commercial passenger fishing vessels (CPFVs or partyboats) roughly reflects the success of ocean-going anglers on private boats. These two groups account for the vast majority of the marine sportfish catch. During the past four years, this catch record has demonstrated wide fluctuations in relative catch success for many species as a result of the 1982-84 El Niño phenomenon. Even though the onset of El Niño was in 1982, the coastal water temperatures along California in 1982 were "normal" or within normal limits of a ten-year mean, and relative abundance of many species caught by CPFV anglers was also normal. However, the 1983 and 1984 warm-water phenomenon caused wide fluctuations in catch rates. This report compares catch rates of CPFVs from 1982 through 1985, when coastal water temperatures returned to normal.

The catch of a number of species rose markedly in 1983, increased again in 1984, and returned to near normal in 1985 (Table 4). These species include California barracuda (*Sphyraena argentea*), Pacific bonito (*Sarda chiliensis*), dolphinfish (*Coryphaena hippurus*), jack mackerel, and striped marlin (*Tetrapturus audax*). One species, bluefin tuna (*Thunnus thynnus*), supported increased catches in 1983, 1984, and 1985. Catches of California sheephead (*Pimelometopon pulchrum*), skipjack tuna (*Euthynnus pelamis*), yellowfin tuna (*Thunnus albacares*), and yellowtail (*Seriola lalandei*) increased strikingly in 1983, then decreased in 1984 and again in 1985 to levels similar to those of 1982. Although the catch record includes landings from long-range boats that fish off Mexico and operate from San Diego, many of the above fishes are subtropical species that increased in California waters as far north as Santa Barbara during 1983 and 1984. In addition, bonito were caught as far north as Crescent City, and barracuda as far north as San Francisco Bay.

A number of species had declining catches in both 1983 and 1984 but increased to levels approaching "normal" in 1985. This group includes barred sand bass (*Paralabrax nebulifer*), kelp bass (*P. clathratus*), California halibut, Pacific mackerel, and white seabass (*Cynoscion attractoscion*). The rockfish complex (*Sebastes* spp.) followed a similar pattern, but did not increase to the same extent in 1985. Some species did not follow the same patterns, but still demonstrated strong fluctuations. For example, albacore catches declined in 1983 then rose in 1984 to provide a record second only to the 230,000 fish taken in 1962. The least desirable pattern is that of lingcod (*Ophiodon elongatus*); the catch has declined every year since 1982.

While the catch data of fish taken from CPFVs might be considered a reflection of abundance, other factors detract from this belief. One is the 1982-84 disruption in water temperature patterns that could have altered the feeding habits of some species like rockfishes in northern California. CPFV operators claim that these species were present, but were in very poor condition and would not take a baited hook. Another factor that may account for lower catches of southern California resident fishes like kelp bass, sand bass, and halibut is that fishing effort was largely directed toward migrant game fishes (e.g., tunas and yellowtail) from more southerly waters.

In summary, the 1982-84 El Niño phenomenon provided exceptionally good fishing for recreational anglers in the Southern California Bight and exceptionally poor fishing north of Point Conception.

TABLE 4
Reported Catch and Nominal Effort of Selected Species Landed by California-Based Commercial Passenger Fishing Vessels

Species	Numbers of fish			
	1982	1983	1984	1985
California barracuda	73,135	81,989	87,414	75,448
Barred sand bass	273,828	158,353	136,612	299,152
Kelp bass	312,891	304,645	222,771	273,299
Striped bass	3,646	14,206	13,524	9,686
Pacific bonito	219,478	348,050	377,678	120,139
Dolphinfish	1,099	4,992	6,532	1,307
California halibut	11,804	5,682	3,209	7,090
Lingcod	49,791	30,543	23,797	20,603
Pacific mackerel	914,238	630,003	604,324	695,708
Jack mackerel	4,404	5,308	13,261	6,825
Marlin, unspecified	33	65	287	68
Rockfishes	3,089,655	2,346,270	2,015,791	2,043,129
Sablefish	1,578	15	568	3,928
Salmon, unspecified	103,576	55,560	71,491	108,851
White seabass	1,899	1,003	973	1,045
California sheephead	37,242	68,972	38,522	35,934
Albacore tuna	36,690	17,161	211,285	172,493
Bluefin tuna	665	1,912	2,834	4,980
Skipjack tuna	32	103,040	30,357	238
Yellowfin tuna	2,035	116,298	8,648	3,898
Ocean whitefish	22,604	22,095	64,241	84,381
Yellowtail	37,308	178,688	96,018	45,509
All others	174,014	130,146	142,256	135,985
Total fish	5,370,645	4,624,996	4,172,393	4,149,696
Total anglers	775,473	691,792	701,737	711,787

Contributors:
Dennis Bedford, pelagic shark, swordfish
Patrick Collier, Pacific ocean shrimp
Terri Dickerson, albacore, market squid
Paul Gregory, recreational fishery
Jim Hardwick, pelagic wetfishes (central California)
Frank Henry, groundfish
Kenneth Miller, California spiny lobster
Sandra Owen, Pacific ocean shrimp
Cheryl Scannell, northern anchovy, Pacific mackerel
Jerome Spratt, Pacific herring
Ronald Warner, Dungeness crab
Patricia Wolf, Pacific sardine, jack mackerel

Compiled by Richard Klingbeil

THE 1985 SPAWNING BIOMASS OF THE NORTHERN ANCHOVY

ANDREW G. BINDMAN
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The 1985 spawning biomass of the central subpopulation of the northern anchovy (*Engraulis mordax*) is 522,000 metric tons (MT). This estimate was made using the egg production method, which computes the spawning biomass as the ratio of the daily egg production rate (eggs per day for the entire population) and the daily specific fecundity (eggs per day per metric ton). For the entire population, the egg production rate was 16.95×10^{12} eggs/day, and the daily specific fecundity was 37.00×10^{6} eggs/day/MT. In 1985 anchovy eggs were found farther offshore than in any survey since the egg production method was first employed in 1980. A significant number of eggs spawned far offshore may have been missed by the survey, thus biasing the estimate downward.

RESUMEN

En 1985, la biomasa de desove de la subpoblación central de la anchoveta norteña (*Engraulis mordax*) es 522,000 toneladas métricas (TM). Esta estimación fue calculada por medio del método de producción de huevos, él cual calcula la biomasa de desove como la proporción entre la tasa diaria de producción de huevos (huevos por día para toda la población) y la fecundidad específica diaria (huevos por día por tonelada métrica). La tasa de producción de huevos de la población total fue 16.95×10^{12} huevos/día, y la fecundidad específica diaria 37.00×10^{6} huevos/día/TM. Los huevos de anchoveta fueron encontrados más alejados de la costa en 1985 que en cualquiera de los estudios anteriores desde que el método de producción de huevos fuera inicialmente empleado en 1980. Es posible que un número significativo de los huevos puestos mar afuera haya sido obviado por el presente estudio implicando una subestimación de la biomasa.

INTRODUCTION

This estimate of the 1985 spawning biomass of the central subpopulation of the northern anchovy (*Engraulis mordax*) fulfills the requirements of the Anchovy Management Plan adopted by the Pacific Fishery Management Council (PFMC 1983). In the past, anchovy biomass has been estimated using a larval census method (Smith 1972; Stauffer and Parker 1980; Stauffer and Picquelle 1981) and an egg production method (Parker 1980; Stauffer and Picquelle 1980; Picquelle and Hewitt 1983, 1984; Hewitt 1984; Lasker 1985). In 1985 only the egg production method was used to estimate the anchovy spawning biomass.

With the egg production method (EPM), we compute the spawning biomass as the ratio of the daily production of eggs (eggs per day for the entire population) and the daily specific fecundity (eggs per day per metric ton) of the adult population. The daily production of eggs is estimated from the density and embryonic developmental stages of egg samples from an ichthyoplankton survey. The developmental rates of anchovy eggs are measured in the laboratory under various temperature regimes. The daily specific fecundity of the anchovy population is estimated from adult fish sampled during a trawl survey. The parameters used to produce the average specific fecundity are average female weight, batch fecundity, sex ratio, and the proportion of females spawning each night. Variance and covariance values are also produced for the parameters.

The survey results, the EPM estimate of spawning biomass, and the variance of the estimate are presented in the following sections.

DESCRIPTION OF THE SURVEY

The 1985 EPM survey of the central subpopulation of northern anchovy was conducted with the NOAA ship *David Starr Jordan* from January 28 through March 8, 1985. The survey (Figure 1) ran from north to south starting approximately 50 miles south of Monterey, California, (CalCOFI line 71.7) and ending at Bahía del Rosario, Baja California, (CalCOFI line 110.0). Several survey lines were extended farther offshore than planned because of the unexpected extent of positive samples. The survey lines directly north of the greatest concentration of anchovy eggs (northwest of San Diego) may not have extended far enough offshore to sample the northern extent of this concentration. Thus a significant number of anchovy eggs may have been missed.

We used a 25-cm-diameter vertical egg net with a 0.15-mm mesh to take plankton samples from 70-m-

[Manuscript received January 29, 1986.]

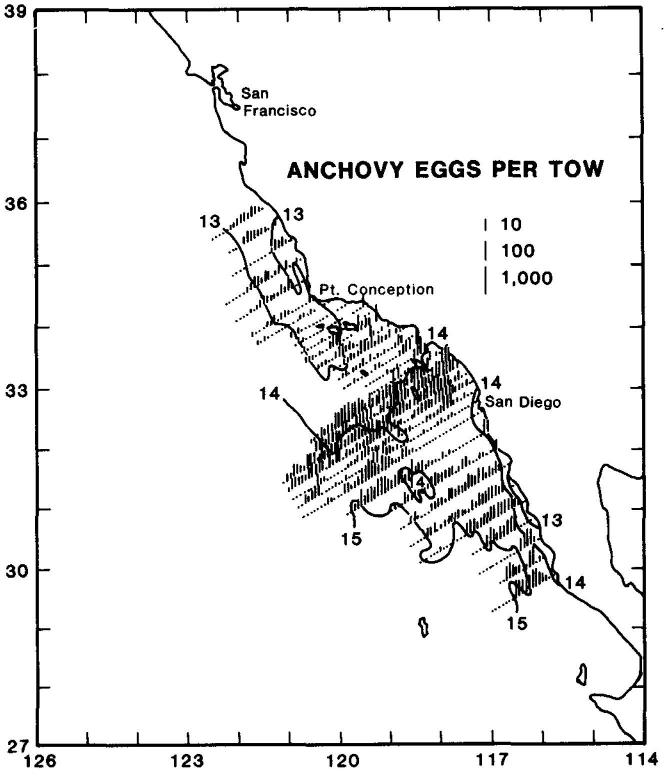

Figure 1. Geographic distribution of ichthyoplankton stations, anchovy eggs, and surface isotherms.

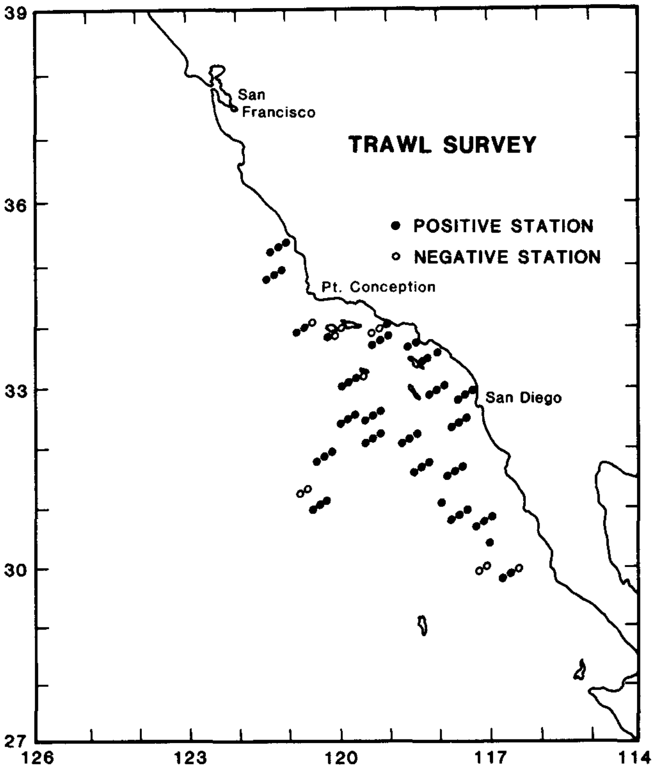

Figure 2. Geographic distribution of trawl stations.

deep water at 492 stations, and 210-m-deep water at 417 stations. Of these 809 samples, 547 contained anchovy eggs (Figure 1). A 15-m^2 pelagic trawl with a 2-mm-mesh liner was towed at 74 stations. Adult anchovies were caught at 64 stations (Figure 2). (For a more complete description of the field operations, see Cruise Report 8502-JD, dated April 29, 1985, William Flerx, Southwest Fisheries Center, La Jolla, California.)

Anchovy eggs extended much farther offshore than in any other year since egg production surveys began in 1980. Spawning activity, as in previous years, was correlated with sea-surface isotherms (Lasker et al. 1981) (Figure 1). South of Point Conception, spawning was generally constrained within the 15°C isotherm. North of Point Conception, spawning occurred in colder water. The cruise report of the USSR research vessel *Mys Babushkina* (Cruise Report 8503-MB, dated June 7, 1985, D. Abramenkoff, Southwest Fisheries Center, La Jolla, California) gave quantitative evidence of spawning in the area north of our survey area up to the San Francisco Bay area (Figure 3). On the Soviet cruise, ichthyoplankton samples were visually "scanned" (the number of larvae per tow roughly estimated) to estimate the number of anchovy larvae taken at each station. We used the scanned estimates to estimate the anchovy spawning biomass in the area north of our survey.

In summary, in the late winter of 1985, anchovies were spawning from Baja California to the San Francisco Bay. This spawning was concentrated in the Southern California Bight and extended farther offshore than usual. Because some of our survey lines may not have extended far enough offshore, many anchovy eggs may not have been counted. This would bias our biomass estimate downward. South of San Diego and north of Point Conception the population was closer to shore, but generally not present in the colder, upwelled water adjacent to the coast.

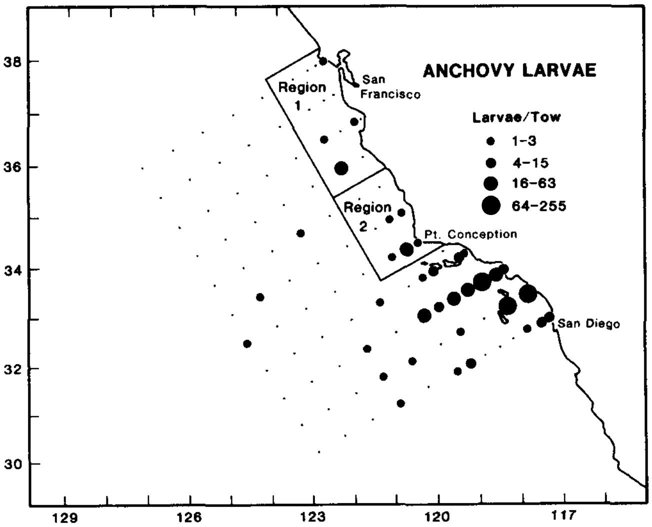

Figure 3. Geographic distribution of ichthyoplankton stations and anchovy larvae from the Soviet cruise (*Mys Babushkina*).

BIOMASS MODEL

The egg production method estimate of spawning biomass (Parker 1980; Stauffer and Picquelle 1980) is:

$$B = PA\frac{k\,W}{R\,F\,S} \qquad (1)$$

where B = spawning biomass in metric tons,
P = daily egg production rate in number of eggs per day per 0.05 m^2,
W = average weight of mature females in grams (g),
R = female fraction of the population by weight,
F = batch fecundity in number of eggs,
S = fraction of mature females spawning per day,
A = area of survey in units of 0.05 m^2, and
k = conversion factor from grams to metric tons (10^{-6} MT/g).

An estimate of an approximate variance for the biomass estimate, derived using the delta method (Seber 1982), is:

$$\mathrm{var}(B) \cong B^2\{\mathrm{var}(P)/P^2 + \mathrm{var}(W)/W^2 + \mathrm{var}(R)/R^2 + \mathrm{var}(F)/F^2 + \mathrm{var}(S)/S^2 + 2[\mathrm{cov}(PW)/PW - \mathrm{cov}(PR)/PR - \mathrm{cov}(PF)/PF - \mathrm{cov}(PS)/PS - \mathrm{cov}(WR)/WR - \mathrm{cov}(WF)/WF - \mathrm{cov}(WS)/WS + \mathrm{cov}(RF)/RF + \mathrm{cov}(RS)/RS + \mathrm{cov}(FS)/FS]\}.$$

DAILY PRODUCTION OF EGGS

The daily production of eggs in the sea, P, is the number of eggs spawned per night per unit area (0.05 m^2, the area of the ichthyoplankton net) averaged over the range and duration of the survey. The density of eggs was determined from an ichthyoplankton survey, and the embryonic developmental stage of each egg was determined by microscopic inspection. The ages of the eggs in hours from spawning were computed from the embryonic developmental stage by a FORTRAN program (Hewitt et al. 1984; Lo 1985) which assumes that the daily spawning of anchovy eggs occurs at 2200 hours. An exponential mortality curve for the eggs was fit to the egg age data. I estimated the daily production of eggs as the value of the predicted curve at the time of spawning.

In order to reduce the variance of the estimate of P, I used a two-step sampling scheme with postsurvey stratification. The first step was the systematic ichthyoplankton sample of the survey area. Each sample was assigned a weighting factor proportional to the area the station represented. The second step was to divide the survey area into two strata: stratum 1 was defined as the area where eggs were found or were likely to be found based on incidence in surrounding locations, and stratum 0 was the area devoid of eggs (Figure 4).

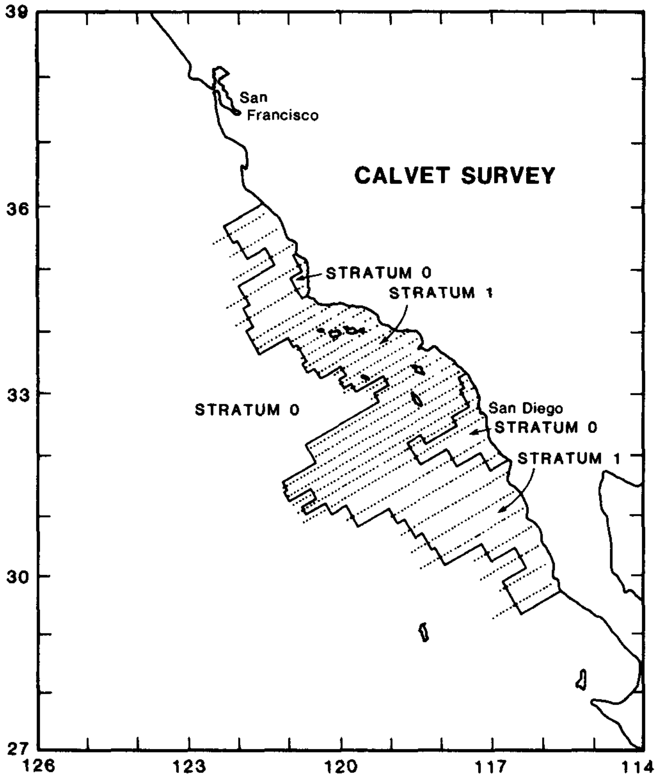

Figure 4. Subdivision of 1985 survey into strata (stratum 1 is the spawning area; stratum 0 is devoid of eggs).

The egg mortality model

$$P_{ijt} = P_i e^{-Zt} \qquad (3)$$

was fit to the data by a weighted nonlinear least-squares regression, with station-weighting factors used as the weights,

where P_{ijt} = the number of eggs of age t from the j^{th} station in the i^{th} stratum,
t = the age in days measured as the elapsed time from the time of spawning to the time of sampling at the j^{th} station (because spawning occurs once a day and because the incubation period was 3 days or less, as many as 3 cohorts of eggs could be found at each station),
Z = the instantaneous rate of mortality on a daily basis,
P_0 = the daily egg production rate in stratum 0; it is zero by definition, and

P_1 = the daily egg production rate in stratum 1.

Mean half-day frequencies for the age data along with the fitted curve and a 95% confidence region for the regression line are described in Figure 5. By definition, the number of eggs produced in stratum 0 is zero. The daily egg production rate for the total survey area and its variance (Jessen 1978) is:

$$P = (A_1/A)\,P_1 \qquad (4)$$

$$\mathrm{var}(P) = (1 + 1/n)[(A_1/A)\,\mathrm{var}(P_1)] \qquad (5)$$

where n = the total number of stations,
A_1 = the area of stratum 1, and
A = the total survey area.

The estimates used to compute P, and their variances are given in Table 1. P was found to be 6.41 within stratum 1. For the entire 51,720 n.mi.^{2} survey area, the estimate of P is 4.78 eggs per day per 0.05 m^2 with an approximate variance of 0.33. This gives a coefficient of variation of 12.0%

ADULT PARAMETERS *W, F, S,* AND *R*

The parameters W, F, S, and R were estimated from a sample of adult anchovies collected by midwater trawl. For each parameter (here denoted y), a weighted mean, $\bar{y}$, and a weighted variance were estimated (Cochran 1963):

$$\bar{\bar{y}} = \sum_i [(m_i/\bar{m})\bar{y}_i]/n \qquad (6)$$

$$\mathrm{var}(\bar{\bar{y}}) = \sum_i [(m_i/\bar{m})^2(\bar{y}_i-\bar{\bar{y}})^2]/[n(n-1)] \qquad (7)$$

where m_i = the number of fish subsampled from the i^{th} trawl,
$\bar{m}$ = the average number of fish subsampled per trawl,
n = the number of positive trawls,
$\bar{y}_i$ = the average value for the i^{th} trawl = $\sum_j y_{ij}/m_i$, and
y_{ij} = the observed value for the j^{th} fish in the i^{th} trawl.

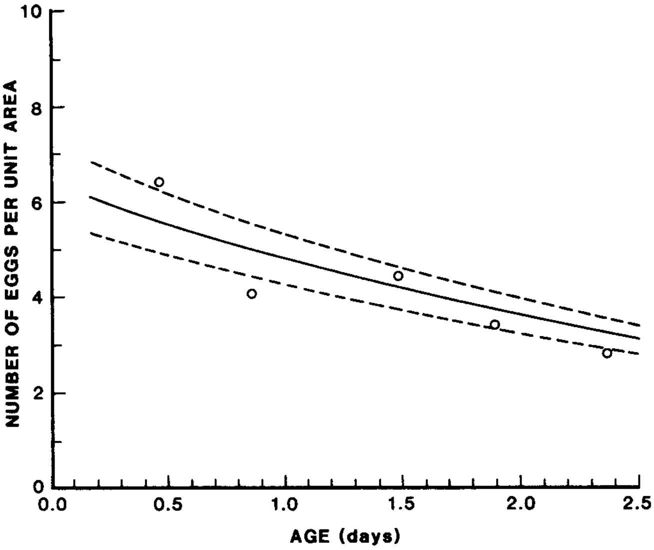

Figure 5. Egg mortality curve. The data are summarized as the mean abundance by half-day intervals, although the regression was fit to the individual data points. A 95% confidence region for the regression (*broken lines*) is indicated.

Average Female Weight

The average weight of an adult female, W, and its variance were estimated using equations 6 and 7, where $\bar{y}_i$ was the average female weight in the i^{th} trawl. I computed average female weight by selecting 25 mature females from each trawl; however, this was not always possible because some trawl samples were too small or were dominated by immature fish.

Just prior to spawning, the eggs in a mature female's ovaries become bloated with fluid (hydrated). I corrected for the extra weight of the hydrated eggs by regressing the weight of mature females without hydrated eggs against their ovary-free weight and then estimating the weight of the hydrated females as if they

TABLE 1
Parameters for Computing Daily Egg Production

	Stratum 0	Stratum 1	Total survey
P (eggs/day-0.05m^2)	0	6.41	4.77
var(P)	0	0.44	0.33
Z (day^{-1})	0	0.29	0.29
var(Z)	0	0.007	0.007
A (0.05m^2)	0.904×10^{12}	2.644×10^{12}	3.548×10^{12}
PA (eggs/day)			16.95×10^{12}
var(P)			4.11×10^{24}

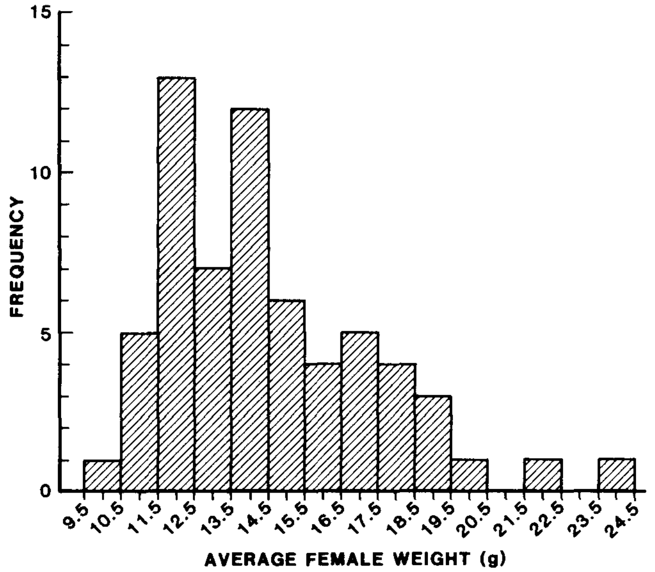

Figure 6. Frequency distribution of average mature female weight per trawl.

did not contain hydrated eggs. The following regression equation was found:

$$\hat{W} = -0.3030 + 1.09\,W^* \qquad (8)$$

where $\hat{W}$ = estimated weight in grams, and
W^* = ovary-free weight in grams.

The regression was highly significant, with a significance level much less than 0.001. The frequency distribution for average weight per trawl is described in Figure 6. The average weight of a female for the entire survey, W, and its variance are listed in Table 2.

Batch Fecundity

The batch fecundity, F, for each mature female is the average number of eggs spawned per female at each spawning event. The batch fecundity was estimated for each female fish by a two-step process. The first step was a regression of batch fecundity versus ovary-free weight from a sample of 85 hydrated females (Figure 7). The ovary-free weight distribution of these 85 fish was similar to the ovary-free weight distribution of all mature females (Figure 8). The estimated regression equation was:

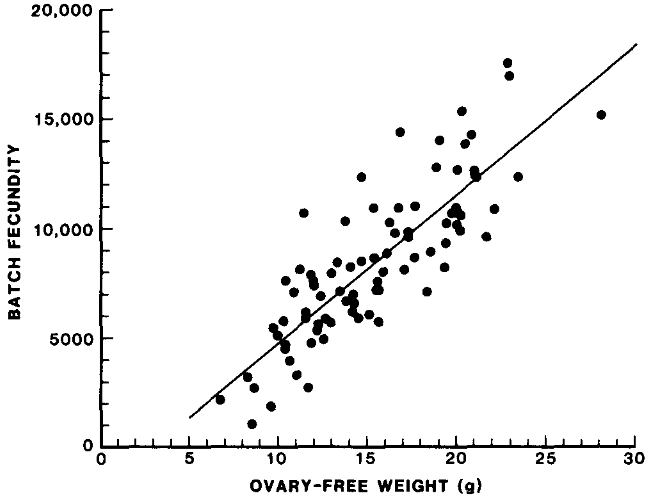

Figure 7. Linear regression of batch fecundity on ovary-free weight fit to 85 females with hydrated ovaries.

$$\hat{F} = -2035.6 + 682.1\,W^* \qquad (9)$$

where $\hat{F}$ = the estimated fecundity for a female with W^* ovary-free weight. The regression was highly significant, with a significance level less than 0.001. The second step was to estimate the batch fecundity for each mature female fish from its ovary-free weight and the above regression. I estimated the average batch fecundity for the entire survey area by using equation 6 where $y_{ij} = \hat{F}_{ij}$, the estimated batch fecundity; the de-

TABLE 2
Estimates of Egg Production Parameters, Variances, and Coefficients of Variation

Parameter		Value	Variance	Coefficient of variation
Daily egg production (eggs/day)	(*PA*)	16.95×10^{12}	4.11×10^{24}	15.6%
Average female weight (g)	(*W*)	14.494	0.105	2.2
Batch fecundity (eggs)	(*F*)	7,343.	1.145×10^{5}	4.6
Spawning fraction (day^{-1})	(*S*)	0.120	0.00024	12.9
Female fraction	(*R*)	0.610	0.00038	3.2
Daily specific fecundity (10^6 eggs/day -MT)		37.003		
Spawning biomass (MT) (not including San Francisco area)	(*B*)	458,024	7.374×10^{9}	18.7
Spawning biomass (MT) (including San Francisco area)	(*B*)	522,000		

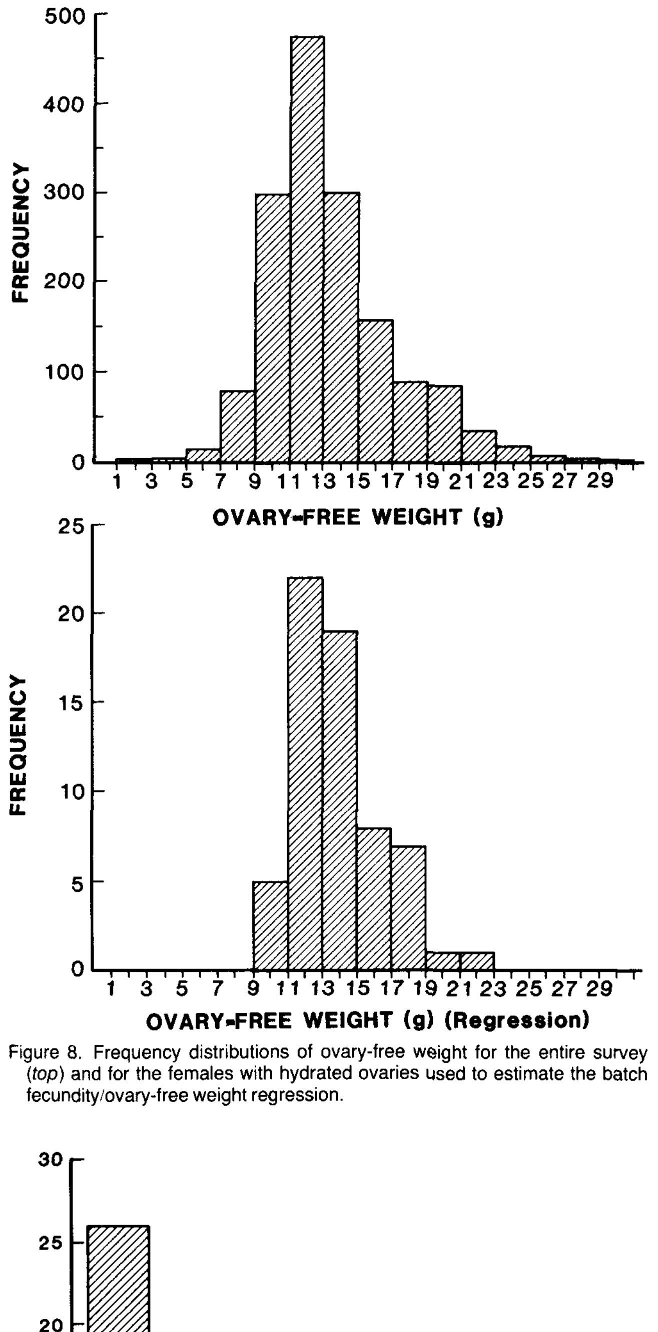

Figure 8. Frequency distributions of ovary-free weight for the entire survey (*top*) and for the females with hydrated ovaries used to estimate the batch fecundity/ovary-free weight regression.

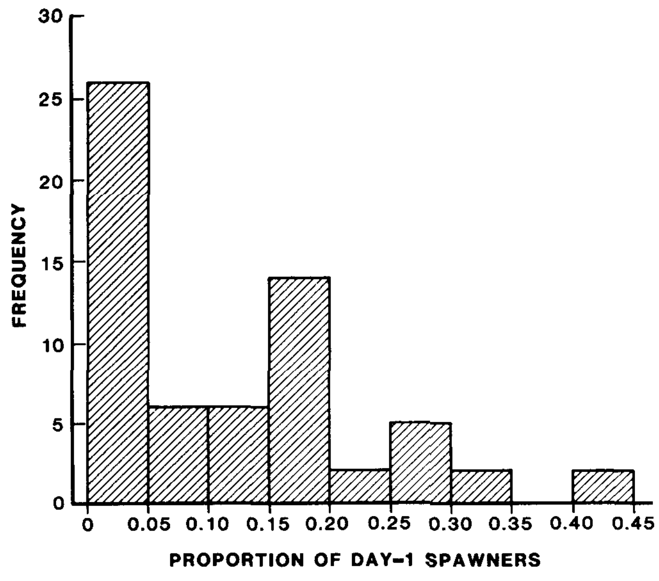

Figure 9. Frequency distribution of spawning fraction.

sired m_i was 25 females. The variance equation (7) was modified because of the extra source of variation from the fecundity/ovary-free weight regression (Draper and Smith 1966):

$$\mathrm{var}(\bar{\bar{F}}) = \sum_i (m_i/\bar{m})^2[(F_i\text{-}\bar{F})^2/(n\text{-}1) + S_h^2/85 + (\bar{W}_i^*\text{-}\bar{W}_h^*)^2\hat{\mathrm{var}}(b)]/n \qquad (10)$$

where S_h^2 = 3,748,191 is the variance about the regression,
$\bar{W}_i^*$ = average ovary-free weight for the i^{th} trawl,
$\bar{W}_h^*$ = 15.43 g, average ovary-free weight of the 85 hydrated females used in the regression,
$\hat{\mathrm{var}}(b)$ = 2,453, variance of the slope of the regression, and
n = 63, the number of positive trawls.

The average batch fecundity and its variance appear in Table 2.

Spawning Fraction

The spawning fraction is the proportion of mature females that spawned on the night prior to capture (day-1 spawners). The spawning fraction, S, and its variance were estimated using equations 6 and 7 where $\bar{y}_i = S_i$ was the spawning fraction found from the i^{th} trawl. The desired m_i—the sample size per trawl—was 25. Strong evidence indicates that females spawning on the night of capture (day-0 spawners) are oversampled by the trawl (Picquelle and Hewitt 1983). To account for this, I adjusted m_i by assuming that there was an equal incidence of day-0 and day-1 spawning fish and hence substituting the day-1 spawners for the day-0 spawners. The frequency distribution of the spawning fraction appears in Figure 9. The estimate of S and its variance are found in Table 2.

Female Fraction

The female fraction of the population by weight is the parameter R. Equations 6 and 7 were used where $\bar{y}_i = R_i$, the total weight of females in a subsample of approximately 50 fish divided by the total fish weight. For each trawl, average weights of male (n = 5) and female (n = 25) fish were measured, and the weights of hydrated females were adjusted using the regression given in equation 8. These average weights were used to estimate the total female weight and the total fish weight. The frequency distribution of R is given in Figure 10; the estimate and variance are shown in Table 2.

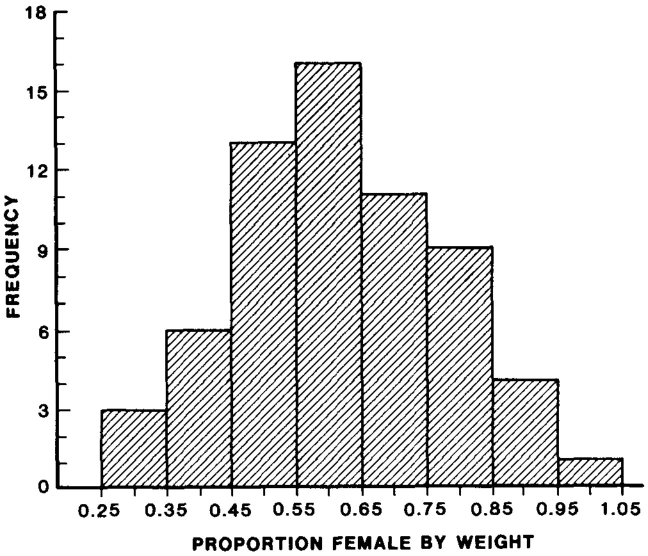

Figure 10. Frequency distribution of female fraction by weight.

BIOMASS ESTIMATE AND VARIANCE

Using equations 1 and 2, I estimated the spawning biomass for the portion of the population range covered by the survey to be 458,025 MT, with a standard error of 85,872 MT. This gives a coefficient of variation of 18.75% The values of the parameters that were used in the estimate, and their variances and covariances appear in Tables 2 and 3. The northern part of the population range was not covered by this survey.

The results of the *Mys Babushkina* cruise show that, as in past years, there is spawning off San Francisco. The Soviet cruise covered the area from Point Conception (CalCOFI line 80.0) north to line 70.7—the northern extent of our biomass survey (region 2)—as well as the region north of line 70.7 (region 1). The Soviets used a bongo net to collect anchovy eggs and larvae. Because larvae are less patchy than eggs, I used "scanned" larvae counts (Figure 3) as an indicator of relative spawning biomass in the two regions. Specific fecundity and subsequent mortality rates of eggs and larvae are assumed to be constant throughout the spawning area. The biomass of region 1 was calculated as:

$$B1 = B2 * \frac{\sum_i (L1_i * A_i)}{\sum_i (L2_i * A_i)} = 63{,}718 \text{ MT}$$

where $B1$ = estimated spawning biomass of region 1,

$B2$ = 29,090 MT is the spawning biomass of region 2 (biomass equation),

$L1_i$ = number of larvae caught at each station in region 1,

$L2_i$ = number of larvae caught at each station in region 2, and

A_i = area represented by station i.

The final biomass estimate for the survey area plus the northern area was 458,025 + 63,718 = 521,742 MT. The variance of this estimate was not computed. However, the coefficient of variation is certainly larger than the 19% associated with the entire region of the EPM survey (Table 2).

DISCUSSION

The 1985 egg production method estimate of the spawning biomass of the central subpopulation of the northern anchovy is up by 61% from its lowest point (since 1980) in 1984. Table 4 lists the historical time series of parameters. The change in spawning biomass is caused by a 31% increase in egg production and a 13% increase in the daily specific fecundity from 1984. The decrease in daily specific fecundity results from a drop in the spawning fraction to a level average for 1980-84 and an increase in batch fecundity. The larger batch fecundity is strongly related to a 21% increase in female weight, because the two are highly correlated (Table 3). The ratio of batch fecundity and mean weight (*F*/*W*) estimates the specific batch fecundity (Table 4). The increase in this ratio is less than the rise in batch fecundity, implying that much of the growth in batch fecundity is due to a larger average female weight. The egg mortality rate Z was higher this year than it has been since 1980. The very large 1980 rate, along with this year's high Z value, demonstrates the variability of Z. Female fraction remained very high compared to the years before 1984. The daily specific fecundity is lower than 1984 but is still above the average for 1980-83.

The EPM spawning biomass estimate can be compared to an annual acoustic survey, which provided a measure of total anchovy biomass. The California Department of Fish and Game conducted an acoustic and midwater trawl survey of the northern anchovy in February 1985 (Cruise Report 85-X-1, K.F. Mais, CDFG, Long Beach, California). The cruise was restricted to the area between Point Conception (CalCOFI line 80.0) and the U.S.-Mexican fishery boundary. In agreement with our results, Mais reports that the geographic distribution of anchovies was more offshore

TABLE 3
Covariances between Adult Parameters

	F	*S*	Female fraction (*R*)
Female weight (*W*)	66.25495	0.00076	0.00064759
Batch fecundity (*F*)		0.53235	0.44352668
Spawning fraction (*S*)			0.00005531

TABLE 4
Time Series of Egg Production Parameters (1980-85)

		1980	1981	1982	1983	1984	1985[a]
Daily egg production (10^{12} eggs/day)	(*PA*)	26.34	20.96	13.51	17.25	12.98	16.95
Egg mortality rate	(*Z*)	0.45	0.14	0.16	0.18	0.17	0.29
Average female weight (g)	(*W*)	17.44	13.37	18.83	11.20	12.02	14.50
Batch fecundity (eggs)	(*F*)	7,751	8,329	10,845	5,297	5,485	7,343
Spawning fraction	(*S*)	0.142	0.106	0.120	0.094	0.160	0.120
Female fraction	(*R*)	0.478	0.501	0.472	0.549	0.582	0.609
Daily specific fecundity (10^6 eggs/day/MT)		30.28	33.03	32.53	24.35	42.43	37.00
Specific batch fecundity (eggs/g)	(*F*/*W*)	444	623	576	473	456	506
Spawning biomass (10^3 MT)	(*B*)	870	635	415	652	309	522[b]
Coef. of variation for (*B*)		0.26	0.22	0.06	0.21	0.17	0.19[a]
Calif. Dept. Fish and Game acoustic biomass estimate (10^3 MT)		498 to 598	493 to 591	233 to 247	461 to 504	479 to 560	627 to 753[c]

[a] Does not include San Francisco area
[b] Includes San Francisco
[c] Does not include Mexican portion of anchovy population

and southward than in any other survey year. He also reported that the bulk of the population was "located in an arc of 80 miles west to south, and 30 miles east to south of San Clemente Island." This is where our survey found the greatest density of anchovy eggs (Figure 1). Mais calculated the total biomass of anchovies (not spawning biomass) to be 627,000-753,000 MT in U.S. waters off southern California. This is up 30.8%-34.5% from his results of 1984. He concludes that the 1985 estimate is the highest in five years and that it would have been higher if the proportion of the anchovy population located in Mexican waters been included.

In previous years the survey area was divided into regions in order to reduce the variance of the parameters and the variance of the biomass estimate (Picquelle and Hewitt 1983; Hewitt 1984). The regionalization was indicated because there were significant differences in one or more parameters between regions. There is no indication that regionalization would have reduced the variance of this year's estimates.

Anchovy eggs were found much farther offshore than in any year since the egg production method surveys began in 1980. A large number of eggs far offshore may have been missed by our survey. As mentioned earlier, if a significant number were missed, there would be a downward bias in our biomass estimate.

ACKNOWLEDGMENTS

A. MacCall of the Southwest Fisheries Center (SWFC) coordinated this year's biomass estimate. We would like to sincerely thank all those who took part in this year's project. J. Hunter, R. Lasker, G. Moser, and J. Thrailkill of SWFC, and L. Farrar of SWFC and the National Ocean Service directed the field collections, laboratory processing, and data analysis. The cruise was conducted by the crew of NOAA ship *David Starr Jordan* with its captain M. Roll. W. Flerx (SWFC) led the team of scientists participating on the cruise: they were, from SWFC, D. Abramenkoff, D. Ambrose, P. Arenas, J. Butler, and E. Lynn; and, from Mexico, A. Cota, F. Diaz, I. Vomend, and G. Vueltiflor. Laboratory processing of the samples was by L. Dunn, M. Farrell, J. Haddox, A. Lumpkins, and F. Pocinich of Scripps Institution of Oceanography (SIO), and by D. Ambrose, M. Busby, D. Gruber, E. Lynn, B. Macewicz, B. MacCall, P. Paloma, E. Sandknop, and E. Stevens of SWFC. N. Lo and P. Smith (SWFC) provided advice, and N. Lo's program was used to assign ages to the eggs. R. Ford (SWFC) entered the data, and R. Charter (SWFC) and Cindy Meyer (SWFC) produced the computer graphics. Roy Allen (SWFC) drafted the final figures. Julie Shoemaker (SWFC) provided clerical help.

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THE RELATIVE MAGNITUDE OF THE 1985 PACIFIC SARDINE SPAWNING BIOMASS OFF SOUTHERN CALIFORNIA

PATRICIA WOLF
California Department of Fish and Game
245 West Broadway
Long Beach, California 90802

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

ABSTRACT

The spawning biomass of the Pacific sardine off southern California during 1985 is considered to be at least 20,000 short tons[1]. This determination was made using an inverse egg production or "egg production area" method, which estimates the area over which a specified spawning biomass (20,000 tons) would be expected to occur. Our survey had a 95% probability of detecting the spawning area within the survey area if at least 20,000 tons of adults were present. This method was developed from the egg production method, which estimates adult biomass from measurements of egg production in the spawning area and from the egg production rate of the adult population. Using estimates of the components of egg production and specific fecundity for sardines from previous studies, we predicted that 20,000 tons of spawning biomass would cover a spawning area of about 500 n.mi^2.

A total of 86 sardine eggs was collected at 11 of 419 stations during the May 1985 survey, which ranged from San Diego to Point Conception and extended from within one mile of the coast to approximately 80 miles offshore. Spawning occurred mainly along the Santa Barbara/Ventura coast and covered an estimated 670 n.mi^2. A total of 1,170 anchovy eggs and 266 anchovy larvae were found at 114 and 69 of the stations, respectively.

As provided by state law when the sardine biomass reaches 20,000 tons, a 1,000-ton fishery for sardines was opened on January 1, 1986. This is the first directed fishery allowed for California sardines since a moratorium on sardine fishing was enacted in 1974. Adult reproductive parameters and egg survival must be determined for absolute biomass estimation.

RESUMEN

La biomasa de desove de la sardina del Pacifico frente al Sur de California fue estimada en por lo menos 20,000 toneladas cortas (1 tonelada corta = 0.907 toneladas métricas) en 1985. Esta determinación fue hecha por medio del método inverso de producción de huevos o "área de producción de huevos." Este método estima el área en la cual una biomasa de desove dada (20,000 toneladas) supuestamente tendrá lugar. Nuestro estudio permitiría localizar el área de desove dentro del área de estudio con un 95% de probabilidad si hubieran, al menos, 20,000 toneladas de adultos. Este método está basado en el método de producción de huevos el cual evalúa la biomasa de adultos a partir de medidas de la producción de huevos en el área de desove, y de la tasa de producción de huevos por la población de adultos. Sobre la base de estudios previos sobre la producción de huevos y la fecundidad específica de las sardinas, se pronostican 20,000 toneladas de biomasa de desove en un área de desove de alrededor de 500 mi.n^2.

Se colectaron 86 huevos de sardinas en 11 de 419 estaciones ubicadas entre San Diego y Point Conception, y que se extendían entre 1 y aproximadamente 80 millas mar afuera, durante mayo de 1985. El desove ocurrió a lo largo de la costa entre Santa Barbara y Ventura principalmente, cubriendo un área estimada en 670 mi.n^2. Se encontraron 1,170 huevos y 266 larvas de anchoveta en 114 y 69 de las estaciones, respectivamente.

De acuerdo con la legislación estatal, cuando la biomasa de sardina alcanzó 20,000 toneladas, se abrió una pesquería para 1,000 toneladas de este recurso el 1° de enero de 1986. Esta es la primera pesquería dirigida que se permite para las sardinas de California desde la implementación, en 1974, de una veda de esta pesquería. Para obtener una estimación absoluta de la biomasa, los parámetros reproductivos de los adultos y la sobrevivencia de los huevos deben ser determinados.

INTRODUCTION

This report assesses the 1985 spawning biomass of the Pacific sardine. Legislation closing the sardine fishery in 1974 requires the Department of Fish and Game to determine annually whether the spawning biomass is more than 20,000 tons. This legislation imposes a moratorium on fishing sardines while the biomass remains below 20,000 tons and allows a 1,000-

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[1] Commercial landings, tonnages specified in legislation, and tonnages in this paper are reported in short tons.

ton fishery when the biomass exceeds this level. Earlier assessments of the sardine spawning biomass were based on ichthyoplankton surveys, aerial observations, trawl surveys, and incidental landings in mackerel and live bait fisheries, and have shown signs of increase since 1980 (Wolf 1985; Klingbeil and Wolf 1984; Klingbeil 1981, 1982, 1983).

Because the sardine population appeared to increase, a quantitative method for detecting recovery and determining whether the biomass had exceeded 20,000 tons was required. Estimates of the sardine population biomass during the fishery were based on analysis of catch and age data (Murphy 1966; MacCall 1979). The egg production method (Parker 1980) is currently used to estimate spawning biomass of anchovies off California (Picquelle and Hewitt 1983) and anchovies and sardines off Peru (Santander et al. 1982). However, available methods of biomass estimation are not applicable at low biomass levels; the cost and effort necessary to achieve meaningful levels of precision are too high.

We developed the egg production area method to allow a cost-efficient, quantitative determination of the relative magnitude of spawning biomass while levels remain low. Details of the method and survey design are described by Wolf and Smith (1985). Here we apply the egg production area method to assess the relative magnitude of the sardine spawning biomass during 1985.

EGG PRODUCTION METHOD

The egg production method estimates spawning biomass as

$$B = P_o A \frac{kw}{RFS}$$

where B = spawning biomass (MT)
P_o = daily egg production, number of eggs produced per 0.05 m^2 of sea-surface area,
W = average weight of mature females (g),
R = sex ratio, fraction of population that is female, by weight (g),
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 m^2), and
k = conversion factor from grams to metric tons.

This method was derived by Parker (1980), and applied by Picquelle and Hewitt (1983, 1984) and Hewitt (1985) to estimate northern anchovy biomass.

EGG PRODUCTION AREA METHOD

In the egg production method, daily egg production and population fecundity parameters are measured during the survey. An exponential mortality model is fit to counts of aged eggs, and P_o is estimated by extrapolating back to the number of eggs at the time of spawning. Parameters W, F, S, and R are estimated from samples of adult fish collected during the survey.

In the egg production area method, the spawning biomass is specified and the equation solved for A_1:

$$A_1 = \frac{B_1 R F S m}{P_o k_1 W}$$

where A_1 = spawning area of biomass B_1 in nautical miles^2,
B_1 = spawning biomass, in short tons,
k_1 = conversion factor from grams to tons,
m = conversion factor from 0.05 m^2 to nautical miles^2.

The procedure for estimating sardine spawning area differs from that used for anchovy[2] in that occasional stations with no eggs are incorporated for anchovy: a slight increase in area is compensated by a slight decrease in mean abundance of eggs. For the sardine spawning area estimate, only stations with eggs are included. We assumed that an area represented by a single sample is not entirely covered, but that this is compensated by the fact that eggs might be present in another area represented by a sample containing no eggs.

We used information from previous studies to estimate the parameters, P_o, W, F, S, and R for sardines rather than collecting measurements during the survey. These values (Table 1) are not known or have not been measured recently for California sardines; we adapted existing information concerning sardines and related species (Wolf and Smith 1985).

Estimates of daily egg production for sardines and anchovies off Peru[3] indicate that egg production rates are lower for sardines than for anchovies by a factor of 1:2. We applied this relationship to annual estimates from 1980 through 1984 (Hewitt 1985) of daily egg production rates for anchovies (approximately 10 eggs/0.05 m^2) to obtain an estimate of sardine daily egg production of about 5 eggs/0.05 m^2. Historical CalCOFI egg surveys yielded an estimated California sardine daily egg production rate of approximately 1.5 eggs/0.05 m^2. This value is thought to be low, however, be-

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[2] Lasker, R. (ed.) MS. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*).

[3] Smith, P.E., H. Santander, and J. Alheit. MS. Comparison of the mortality and dispersal of sardine (*Sardinops sagax sagax*) and anchovy (*Engraulis ringens*) eggs off Peru.

TABLE 1
Parameters Used to Estimate Spawning Area, and Resulting Estimates

B_1	W	R	F	P_o	S	A_1
Spawning biomass (short tons)	Average female weight (g)	Sex ratio (females/total)	Batch fecundity (eggs/batch/ female)	Egg production (eggs/.05m^2-day)	Spawning fraction (spawning females/ total females)	Spawning area (nautical miles^2)
20,000	120	0.5	32,000	5.0	0.02	141
					0.05	353
					0.10	706
					0.15	1,058
				1.5	0.02	470
					0.05	1,176
					0.10	2,352
					0.15	3,528

cause the sampling technique (oblique tows instead of vertical tows) may have overestimated the surface area of water sampled. Both values of P_o were used (Table 1). Average weight of mature females, W, was estimated to be 120 grams, and batch fecundity, F, was estimated at 32,000 eggs (MacGregor 1957). The female fraction of the population by weight, R, was assumed to be half. Spawning fraction, S, for other pelagic species ranges from 0.02 females spawning per day (spawning once every 50 days) for Pacific sauries (Hatanaka 1956) to 0.14 females spawning per day (spawning once every 7 days) for anchovies (Hunter and Macewicz 1980). Spawning fraction for sardines off Peru (J. Alheit, Instituto del Mar del Perú, pers. comm.) and for sardines off the west coast of Baja California (J.R. Torres-Villegas, CICIMAR, unpublished data) has been estimated at about 0.06 females spawning per day. The range values of S was used (Table 1).

The calculated area, A_1, over which 20,000 tons of Pacific sardines could be expected to spawn ranges from 141 to 1,058 n.mi.^{2}, for an estimated daily egg production rate of 5 eggs/0.05 m^2 and an estimated range of values for spawning fraction, and from 470 to 3,525 n.mi.^{2} for a daily egg production rate of 1.5 eggs/ 0.05 m^2 and the same range of values for spawning fraction (Table 1). With available information, we consider the higher value of P_o—5.0 eggs/0.05 m^2—and a value of S ranging between 0.05 and 0.10 females spawning per day to be the best estimates of these parameters for sardines. Therefore, 500 n.mi.^{2} was selected as a useful estimate of A_1.

SURVEY DESIGN

The survey area and time of year over which sardine spawning would be likely to occur were determined from occurrences of sardine eggs and larvae in historical CalCOFI survey data (Wolf and Smith 1985). The critical spawning area, A_1, estimated at 500 n.mi.^{2}, was approximately 2% of the survey area, which included CalCOFI regions 7 and 8 and covered an estimated 32,000 n.mi.^{2} (Smith et al. 1976). Using a table for determining confidence limits of a proportion (Natrella 1963), we determined the number of stations (374) representing the minimum effort required to locate the spawning area within the survey area, with a high probability (95%) of detecting the spawning area if 20,000 tons of spawning adults were actually present. The stations were spaced 4 n.mi. apart offshore and 10 n.mi. apart alongshore according to standard anchovy egg production procedures. Because each station represents 40 n.mi.^{2}, the calculated spawning area that 20,000 tons of sardines would cover was expected to contain 12 or 13 positive stations.

SURVEY DESCRIPTION

The survey was conducted by NOAA ship *David Starr Jordan* from April 29 through May 19, 1985. Stations were occupied from south to north, beginning at San Diego and ending at Point Sal, and extending offshore an average distance of about 80 miles (Figure 1). Plankton samples were collected at 419 stations using a 25-cm-diameter CalVET (vertical egg tow) net of 150-micron mesh that was retrieved vertically from 70 m (when depth allowed) to the surface. Samples were collected at all hours. No stations were occupied in established shipping lanes.

Sardine and anchovy eggs and larvae were identified, sorted, and counted. A total of 86 sardine eggs occurred at 11 stations, with the number of eggs per station ranging from 1 to 42 (Figure 2). Most of the positive stations occurred along the coast near Santa Barbara, and in the eastern portion of the Santa Barbara Channel, from Port Hueneme to Anacapa and Santa Cruz islands. Two positive stations occurred off Newport Beach. Sardine larvae occurred at 10 stations, in approximately the same areas as eggs. Eggs and larvae in combination occurred at 16 stations.

Evidence of anchovy spawning (1,710 eggs and 266

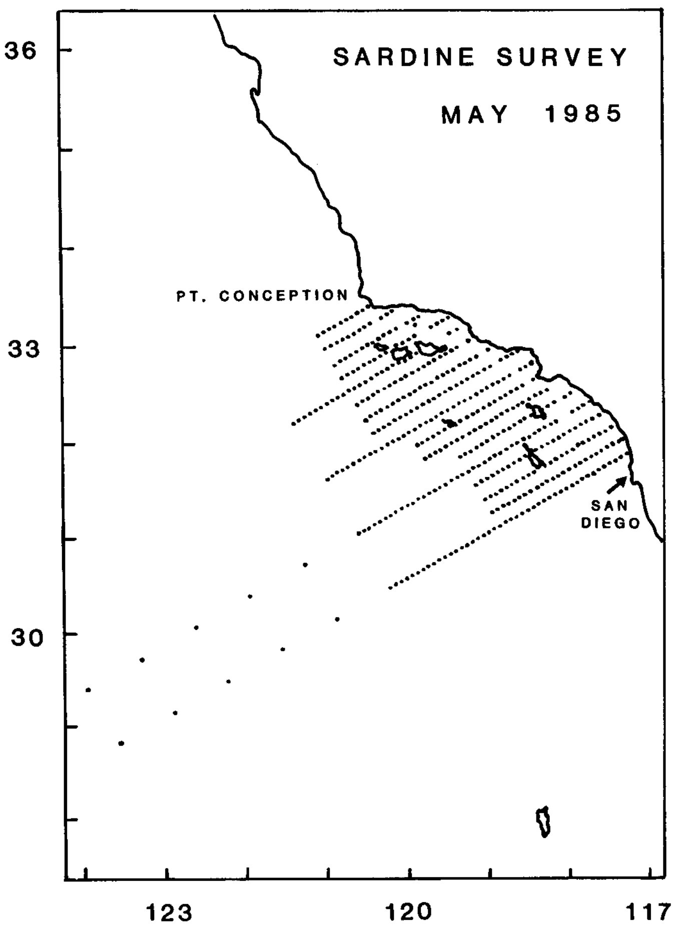

Figure 1. Stations occupied during sardine survey, May 1985.

larvae at 114 and 69 stations, respectively) was considerably more common but occurred in different areas than sardine spawning. Anchovy eggs and larvae were concentrated mostly in the southern portion of the survey near San Diego.

Two of the samples had to be discarded because of inadequate preservation. Neither were adjacent to or near stations at which sardine eggs occurred (Figure 2).

SPAWNING AREA

Spawning area was determined by multiplying the number of egg-positive stations by the area represented by each station (40 n.mi.^{2}). Some stations that were positive for sardine eggs were adjacent to areas that were not sampled, either because the area occurred in the shipping lanes or was close to shore and aligned in such a way that the station plan did not call for a sample. In order to consider these areas in the spawning area estimate, we adjusted the area of positive stations adjacent to an unsampled area to include half of the adjacent unsampled area, averaged along lines in order of station occupation and estimated by eye. The area of positive stations too near to shore to include an entire 40 n.mi.^{2} were also adjusted to reflect the portion of the 4 by 10 n.mi.^{2} actually sampled.

An unadjusted estimate of the spawning area equals 440 n. mi^2. An estimate of the spawning area adjusted as described above is 670 n.mi.^{2} (Figure 2). Both of these estimates are within the range of spawning area calculated for 20,000 tons of spawning biomass of sardines and are close to the selected estimate of A_1 (Table 1).

DISCUSSION

The egg production area method allows detection of the onset of sardine recovery and provides an objective, quantitative technique for determining the relative magnitude of spawning biomass. This is particularly useful when the management plan requires determining whether a specified spawning biomass level has been exceeded, but either the level to be ascertained remains low enough that developing a direct estimate with reasonable precision is cost- and effort-prohibitive, or information beyond the relative magnitude of biomass is unnecessary.

Because the spawning area observed during the survey was close to that predicted for 20,000 tons of adult sardines, the spawning biomass of sardines off California is considered to be at least 20,000 tons in 1985. As specified by state law, this determination allowed the initiation of a 1,000-ton fishery in January 1986. The provision for a fishery was included in the 1974 moratorium legislation because of concern that a total moratorium would preclude detecting the onset of recovery. Also, simulations of a 5% fishery at that biomass level projected no deleterious effects (W. Lenarz, NMFS, Tiburon, pers. comm.). MacCall's (1979) estimates of apparently lower recruitment rates at low biomass levels suggest that Lenarz's projections may be optimistic.

The large range of values calculated for A_1 resulted from using a range of values to estimate parameters P_o (daily egg production rate) and S (spawning fraction). These parameters are not known for Pacific sardines. Two other parameters—W (average female weight) and F (batch fecundity)—were estimated from sardines taken from the 1945-46 commercial catch. The average monthly mean weight of mature female sardines occurring incidentally with mackerel during 1985 was 142 grams. As discussed below, all of the components of egg production and specific fecundity are dynamic and have been shown to vary from year to year for northern anchovy (Hewitt 1985). Daily egg production rate and spawning fraction must be determined for Pacific sardines; the adult parameters should be obtained simultaneously. The egg production area method, however, uses historical information.

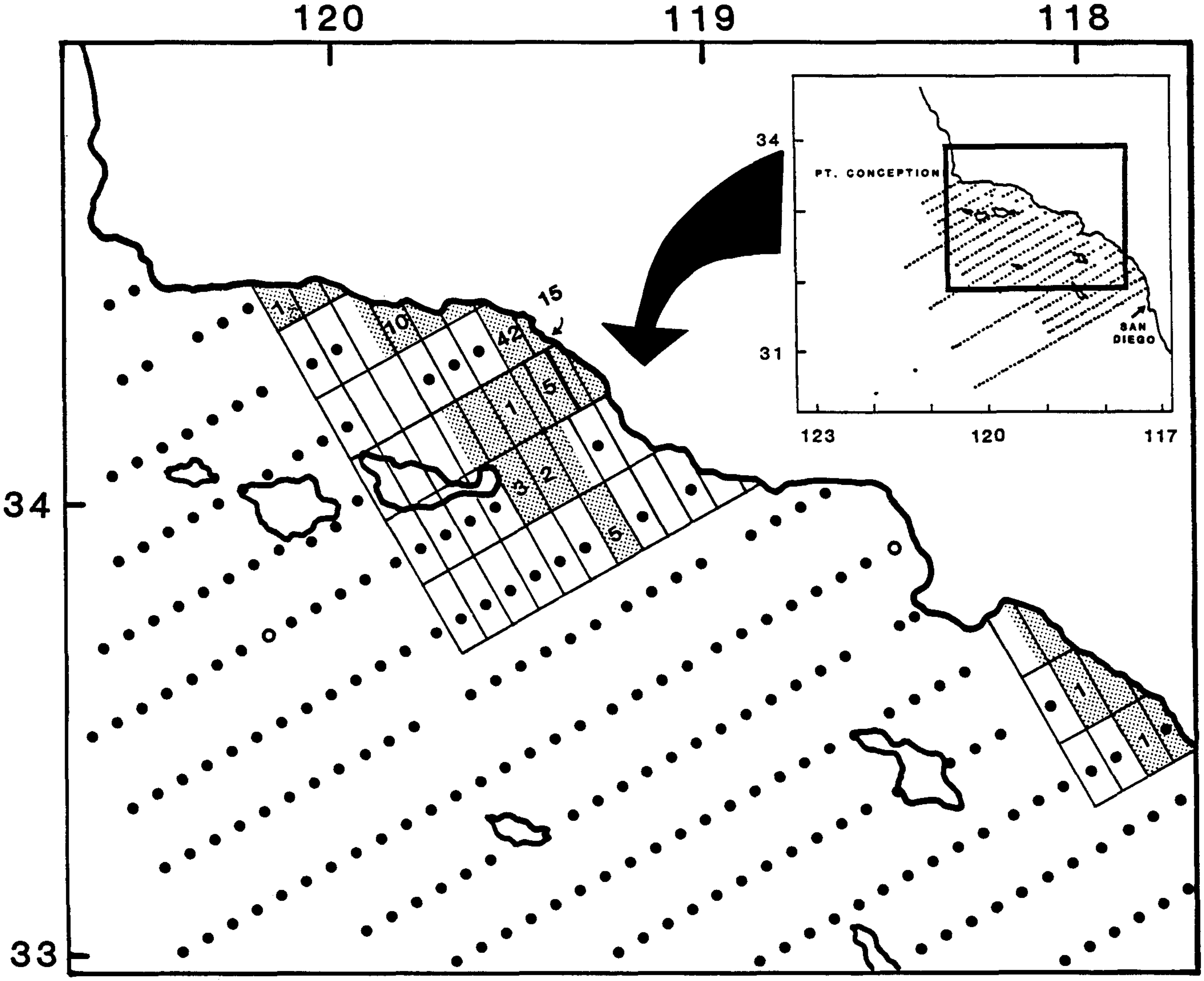

Figure 2. Number of eggs per station and location of stations that contained sardine eggs. Rectangles outline 4-by-10-n.mi.^{2} areas represented by each station to illustrate spawning area adjustment. Shaded area is adjusted sardine spawning area. Open circles are discarded samples.

Several other sources provide additional information concerning the status of the adult Pacific sardine population during 1985. Incidental landings of sardines with mackerel during 1985 totalled 652 tons, the largest annual take in 20 years ("Review of Some California Fisheries for 1985," this volume). Sardines have become increasingly more common in mackerel landings, occurring in 50% of observed landings in 1985 compared to 30% in 1984. Catch length frequencies of incidental sardines show a trend from 1983 through 1985 of a broader length distribution, indicating recruitment in 1985 (Figure 3). Sardines from the 1985 year class were detected in early 1966 in Monterey Bay, indicating that spawning occurred north of Point Conception and beyond the range of the survey. Sardines ranked first in biomass and third in abundance in purse seine hauls from Long Beach Harbor during 1983 and the first half of 1984 (C. Mitchell, MBC Applied Environmental Sciences, pers. comm.). No detectable trend, however, was observed in the mean number of sardines captured by purse seine off San Onofre from 1983 through 1985 (E. DeMartini, UCSB Fish Program, pers. comm.).

The abundance of sardine eggs and larvae in four nearshore ichthyoplankton transects in the Southern California Bight increased two to three orders of magnitude from 1978-79 through 1982-84, and sardines ranked third in overall abundance during that period (R.J. Lavenberg, Los Angeles County Natural History Museum, pers. comm.). From 1978 through 1984, monthly mean numbers of sardine larvae in coastal waters near San Onofre increased steadily (W. Watson, Marine Ecological Consultants of Southern California, pers. comm.). Both of these studies indicate that a sub-

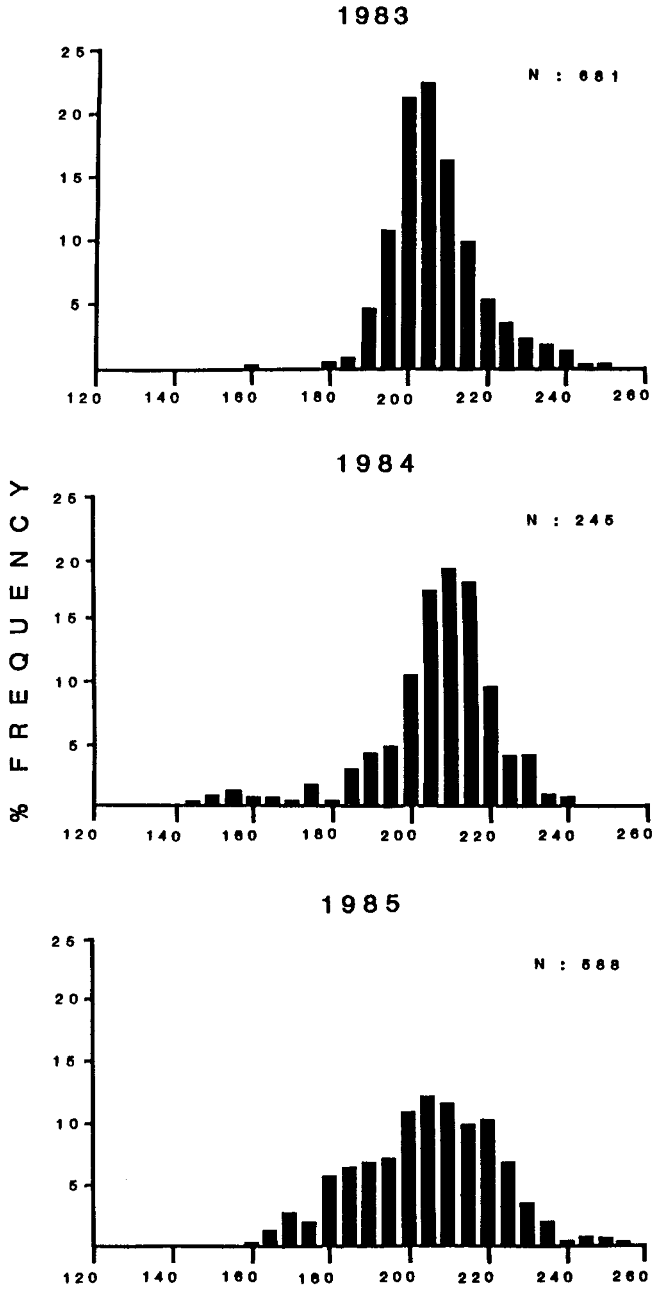

Figure 3. Catch length frequencies of sardines landed incidentally with mackerel in 1983, 1984, and 1985. Mean weights of modal length classes for each year are: 1983, 130 g, 205-209 mm SL; 1984, 147 g, 210-214 mm SL; 1985, 143 g, 205-209 mm SL.

stantial portion of sardine spawning in recent years has occurred relatively near to shore (within the 75-m contour) and during summer and fall.

Although the limited interpretation of the 1985 survey is conclusive in the original objectives relative to 20,000-ton spawning biomass, we resist broadening these few results for a biomass estimate or fishery quota. The spawning area of 670 n.mi.^{2} is nearly identical to the 500 n.mi.^{2} criterion adopted for this technique. This means that any deviation from the assumed adult parameters could change the evaluation. Another critical feature is that we can estimate only the standing crop of eggs from this small set, not the egg production. The two unevaluated factors are mortality rate of the eggs and the precision of the intercept estimate. Future surveys must quantify the mortality rate and the frequency distribution of eggs.

The estimated mean of positive samples in the 1985 survey is high relative to samples of the 1930s to 1950s (Table 2). It appears that the high value is due to the chance encounter of more observations with high values. We believe the cause of this difference is technical rather than biological, although this cannot be determined from these few samples. It is important to note that all the other distributions result from oblique or horizontal tows and that the new results are from a vertical tow. The scale of the integration is 25 cm for the CalVET net and on the order of meters for all but one of the other nets, and kilometers for the high-speed net used in 1950. The smaller CalVET net will have a greater probability of sampling zero eggs. Also, the sampling threshold of the CalVET net (1 egg in a CalVET is equivalent to 50 eggs in a 1-m oblique tow) might cause the lower end of the frequency distribution of egg densities to be undersampled. Both of these characteristics would cause the mean observed density of positive samples to be inflated. This would imply that the entire area of sardine spawning was not detected and that 20,000 tons is a conservative estimate.

The high mean value could also result from a lower than normal mortality or higher than normal per capita egg production rate, which would imply a lower spawning biomass. These biological factors will all have to be separately assessed for the absolute biomass to be estimated from egg production rates.

Analogous data from the anchovy egg production procedure indicate the great importance of the adult sampling effort for biomass estimation. If the interval between batches of eggs is long, for example 20 days, the ratio of gonads with evidence of spawning in the previous day is only 5%. This ratio would require many independent samples to precisely determine the spawning fraction. Individual samples of anchovy females range from 0% spawning to over 40% when the mean is 15%. Thus the overall precision of spawning biomass estimates may be determined by the ability to obtain a sufficient number of independent samples of adult females.

In summary, at least one more year of field and laboratory work on additional egg samples and adult collections will be required before the procedure for an absolute biomass estimate can be designed.

TABLE 2

Pacific Sardine Egg Sample Frequency Distributions at Different Levels of Spawning Biomass[a]

#/10 m²		Net types and years					
		CalVET	CF&G 2-m	1-m	0.5-m	Hi-speed	1-m
x	ln (x)	1985	1931-32	1941	1941	1950	1959
.125	−2.08	—[b]	2	—	—	—	—
.5	−0.69	—	4	—	—	—	—
2	0.69	—	6	21	—	—	28
8	2.08	—	7	22	8	—	28
32	3.47	—	14	16	15	—	30
128	4.85	4	12	31	29	77	23
512	6.24	4	13	27	14	20	12
2,048	7.62	2	5	17	10	7	5
8,192	9.01	1	2	3	2	1	4
Estimated mean		1,564	544	569	619	406	410
Biomass (MT)[c]		0.02	3.9	2.7	2.7	1.0	0.2

[a](Smith and Richardson 1977)
[b]Value below sampler threshold
[c](Murphy 1966)

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

IDYLLWILD, CALIFORNIA

OCTOBER 22, 1985

SOUTHERN CALIFORNIA NEARSHORE WATERS: SELECTED PATTERNS AND PROCESSES

PHYSICAL-CHEMICAL CHARACTERISTICS AND ZOOPLANKTON BIOMASS ON THE CONTINENTAL SHELF OFF SOUTHERN CALIFORNIA

JAMES H. PETERSEN, ANDREW E. JAHN,
ROBERT J. LAVENBERG, GERALD E. McGOWEN
Los Angeles County Natural History Museum
Section of Fishes
900 Exposition Boulevard
Los Angeles, California 90007

ROBERT S. GROVE
Southern California Edison Company
System Planning and Research
P.O. Box 800
Rosemead, California 91770

ABSTRACT

Between June 1978 and December 1984, temperature, salinity, and nutrient profiles, and data on total zooplankton biomass were collected monthly or bimonthly at nearshore stations (8-m to 75-m isobaths) throughout the Southern California Bight. Primary transects were located off Ormond Beach, Playa del Rey, Seal Beach, and San Onofre. Seasonal warming and cooling of nearshore water were generally coherent throughout the bight except near headlands where local upwelling plumes slowed spring warming by 1-2 months. Nitrate and nitrite were low throughout the water column from late summer through winter, except when strong downcoast winds caused coastal upwelling and strong cross-shelf gradients. During spring and early summer, mesoscale upwelling or longshore advection increased nutrient levels; summer thermoclines were underlain by cool, nitrate-rich waters that may be an important source of nutrients for the nearshore biological community. During spring and early summer, zooplankton biomass usually had a cross-shelf maximum at the 15-m to 36-m isobaths. Unusually warm water, as part of the 1982-83 El Niño phenomenon, was observed throughout the bight, with maximum anomalies occurring in fall 1983. Anomalously warm water persisted through most of 1984. Zooplankton biomass declined during 1983 and 1984, presumably in direct response to El Niño conditions or from reduced primary productivity. Our results and studies by others suggest that tidal mixing, internal waves, and local upwelling are important processes that distinguish the inner continental shelf of the Southern California Bight from waters farther offshore.

RESUMEN

Los parámetros hidrográficos temperatura, salinidad, y nutrientes, y la biomasa total de zooplancton fueron muestrados mensual o bimestralmente entre junio de 1978 y diciembre de 1984 en varias estaciones costeras (8-75 m de profundidad) en la Bahía del Sur de California. Las estaciones principales están ubicadas frente a Ormond Beach, Playa del Rey, Seal Beach, y San Onofre. El calentamiento y enfriamiento estacional de las aguas costeras fue observado en toda la bahía excepto en aquellas áreas donde, a causa del relieve costero, eventos locales de surgencia retrasan en 1-2 meses el calentamiento primaveral.

Las concentraciones de nitratos y nitritos en la columna de agua fueron bajas en el período correspondiente a fines del verano y el invierno, excepto cuando los vientos fuertes, paralelos a la costa, indujeron afloramientos costeros y fuertes gradientes de concentración ubicados en forma perpendicular a la costa. Durante la primavera y comienzos del verano, los procesos de afloramiento costero o advección aumentaron las concentraciones de nutrientes. Debajo de la termoclina estival, se extendían aguas frías, ricas en nutrientes las cuales pueden ser una importante fuente de nutrientes para la comunidad biológica costera. Durante este mismo período, la biomasa de zooplancton presentó un máximo entre 15 y 36 m de profundidad.

Aguas anómalamente calientes fueron observadas en la bahía durante el fenómeno de El Niño de 1982-83, y las anomalías máximas fueron detectadas en el otoño de 1983. Estas aguas anómalas estuvieron presentes en la bahía durante la mayor parte de 1984. La biomasa de zooplancton disminuyó durante 1983 y 1984, probablemente como una respuesta directa a las condiciones vinculadas con El Niño o debido a una producción primaria reducida. La mezcla por la acción de las mareas, las ondas internas, y los afloramientos costeros parecen ser los procesos que diferencian las aguas de la plataforma continental de la Bahía del Sur de California de las aguas ubicadas mar afuera.

INTRODUCTION

Nearshore current patterns, upwelling, and mixing processes make the zone within approximately 20 km of the coast of southern California a different marine environment from waters farther offshore. The California Current brings cool, low-salinity water south past Point Conception into the Southern California Bight (Jones 1971; Tsuchiya 1980). During April and May, this current extends farthest inshore, and flow throughout the bight is to the south (Jones 1971). During other months, a large counterclockwise gyre exists in the bight, with the southward-flowing California Current offshore and the northward-flowing

Southern California Countercurrent (SCC) inshore of the Channel Islands. However, a narrow nearshore current often exists within 10-20 km of the mainland California coast, distinct from the SCC (Tsuchiya 1980). Long-term surface flow of this nearshore current, ranging to 10 cm/s, is to the south, although near-bottom water flows northward during spring and summer (Winant and Bratkovich 1981).

Upwelling along the southern California coast has been recognized as an important process that transports deep, nutrient-rich water to the surface and thus increases local and regional productivity (e.g., Yoshida 1955; Jones 1971; Kamykowski 1974; Tont 1976; Eppley et al. 1979a; Dorman and Palmer 1981; Huyer 1983; Dykstra et al. 1984). Mesoscale upwelling, on a scale of hundreds of kilometers, is strongest from April to June (Jones 1971; Huyer 1983), when seasonal winds blow from the northwest, causing mass offshore transport of surface water through Ekman veering and replacement of nearshore surface water with deep water. Upwelling on this scale affects water conditions throughout the Southern California Bight; its influence on temperature and productivity are readily seen in satellite images (Lasker et al. 1981; Fiedler 1983, 1984). The region south of Point Conception is an area of especially intense upwelling on this scale (Fiedler 1983). Local coastal upwelling, which occurs within approximately 20 km of the shore, appears to be a major factor influencing water conditions on the inner part of the continental shelf. Dorman and Palmer (1981) summarized much of the information on coastal upwelling off southern California and described the frequency and geographic extent of summer upwellings. They found that strong coastal upwelling events, with temperature drops over 5°C, tend to occur twice each summer and are forced by local wind blowing downcoast. Stations from Balboa to San Diego experienced coastal upwelling simultaneously; areas farther north also had summer upwelling, but these events did not necessarily coincide with strong upwelling in the southern part of the bight. Upwelling events were highly correlated with strong downcoast winds (Dorman and Palmer 1981), which did not have the same intensity or direction at Los Angeles and San Diego. Downwelling events, associated with northward-moving tropical storms, tend to occur once or twice each summer (Winant 1980).

Increased tidal action on continental shelves (Riley 1967) and frequent internal waves off southern California (Armstrong and LaFond 1966; Cairns 1967; Zimmerman and Kremer 1984) also seem to be important mechanisms causing vertical and horizontal mixing, particularly within 40-50 km of the coast (Yoshida 1955). Nutrient transfer into the euphotic zone is probably the most important consequence of these mixing processes. Zimmerman and Kremer (1984) found seasonal and twice-daily components of nutrient availability near Santa Catalina Island. Frequent upward excursions of cold, nutrient-rich water were of short duration but may be important to some shallow-water species such as kelp, particularly during periods of very low nutrient concentrations (Zimmerman and Robertson 1985).

Freshwater flow from rivers and streams into the Southern California Bight is small, and rainfall is only 25-40 cm/yr; thus terrigenous nutrient input is generally low except during occasional winter storms. Large sewage outfalls are located at Santa Monica Bay, Palos Verdes Peninsula, Huntington Beach, and Point Loma, with total flows of 0.5×10^6 to 1.4×10^6 m^3/day (Meistrell and Montagne 1983). Other potential sources of nutrient input include tidal and subtidal flux of groundwater (Johannes 1980), refinery outfalls, and significant *in situ* regeneration (Harrison 1978; Eppley and Peterson 1979; Eppley et al. 1979b; Barnett and Jahn, in press). Nutrient input from these sources may be significant at specific sites or times.

Few long-term studies of physical and biological oceanography have been conducted in the nearshore habitat off southern California. Some exceptions are studies of temperature and currents near the shore (e.g., List and Koh 1976; Tsuchiya 1980; Winant and Bratkovich 1981), as well as work by Eppley and coworkers, who have examined nutrients and primary productivity in the Los Angeles to San Diego region. Most data collected within 20 km of the coast have been from shore monitoring stations (e.g., National Ocean Survey, Scripps Pier) or through short-term projects that address specific biological or physical questions (e.g., Cairns and Nelson 1970; Kamykowski 1974; Eppley et al. 1978; Fiedler 1983; Dykstra et al. 1984). In contrast, the CalCOFI program has been collecting physical, chemical, and biological data since 1949 in a grid off California and Baja California, Mexico (approximately 20-400 km from shore). The extensive CalCOFI data base has been used in studies of zooplankton (e.g., Fleminger 1964; Colebrook 1977), physical and biological interactions in the California Current (Bernal and McGowan 1981; Chelton et al. 1982), larval fish populations (e.g., Ahlstrom 1969; Smith and Lasker 1978; Loeb et al. 1983) and many other topics. Long-term data series, similar to the CalCOFI data set, should be valuable in understanding the coupling of biological and physical processes in the shallow nearshore zone (see Denman and Powell 1984).

This report presents physical, nutrient, and zooplankton biomass data collected in the nearshore zone of the Southern California Bight. Longshore and cross-shelf patterns will be described, and physical processes that may have caused observed patterns will also be considered. Interaction of local and oceanic processes in the Southern California Bight in determining nearshore conditions will also be discussed. "Nearshore" refers to the narrow coastal band between the 8-m and 75-m isobaths—roughly 1-20 km from the shore. "Offshore" means the region of ocean between 20 and 400 km off southern California—the area regularly sampled by CalCOFI. Some general descriptions of currents, temperature variation, and coastal upwelling in offshore waters of the Southern California Bight may be found in Sverdrup and Fleming (1941), Jones (1971), Hickey (1979), Tsuchiya (1980), and Dorman and Palmer (1981).

METHODS

Physical-chemical and zooplankton data were collected in conjunction with a program to monitor nearshore ichthyoplankton distributions in southern California waters (Lavenberg et al. 1986). Ten transects, from Point Conception to the U.S.-Mexican border, were sampled monthly from June 1978 to July 1979 (Brewer et al. 1981). Between August 1979 and July 1980, 20 transects, including the 10 of the previous year, were also sampled monthly (Figure 1). Coordinates and descriptions of these early transects can be found in Brewer and Smith (1982). Sampling was sporadic from August 1980 until February 1982, when bimonthly sampling on four transects began (Figure 1; Table 1). Most data presented in this report were collected during 1982-84, although some temperature and salinity measurements from 1978 to 1980 are included.

During the first 26 months of the program (1978-80), two to four stations per transect were occupied (8-, 15-, 22-, and 36-m isobaths). Beginning in 1982, a fifth station at the 75-m isobath was added on each transect. Coordinates for the twenty stations occupied during 1982-84 are listed in Table 1. Temperature, salinity, oxygen, pH, nitrate, nitrite, ammonium, phosphate, and silicate data were collected from surface and depths of 2, 4, 6, 8, 10, 15, 22, 30, 36, 50, 70, and 75 m.

Temperature was measured with a Martek water quality analyzer (Mark IV) or reversing thermometers attached to Niskin bottles, which collected water samples from discrete depths. Water samples from depth were analyzed on board for salinity (Beckman induction salinometer model RS7-C), dissolved oxygen (Yellow Springs Instruments model 51A), and pH (Orion Research ion analyzer model 407A). Nutrient samples were frozen at sea and later processed by the University of Southern California Ecosystems Group using a Technicon autoanalyzer (model II).

TABLE 1
Coordinates of Stations Occupied, 1982-1984

Transect (CalCOFI line)	Station (m)	N. latitude	W. longitude
Ormond Beach (84.7)	8	34°07.5′	119°16.6′
	15	34°07.0′	119°11.0′
	22	34°06.6′	119°11.7′
	36	34°06.0′	119°12.8′
	75	34°04.5′	119°11.9′
Playa del Rey (86.8)	8	33°57.0′	118°27.1′
	15	33°57.0′	118°27.9′
	22	33°56.9′	118°28.6′
	36	33°57.0′	118°30.1′
	75	33°57.2′	118°34.0′
Seal Beach (88.4)	8	33°42.4′	118°04.3′
	15	33°41.2′	118°04.8′
	22	33°39.6′	118°05.1′
	36	33°37.3′	118°05.7′
	75	33°34.8′	118°08.9′
San Onofre (90.9)	8	33°21.7′	117°33.8′
	15	33°20.9′	117°34.1′
	22	33°20.4′	117°34.7′
	36	33°19.9′	117°35.0′
	75	33°18.5′	117°35.6′

Specific density (sigma-t) was calculated from temperature and salinity data using formulae given in Millero and Poisson (1981, 1982). Surface temperature "anomalies" (STA) were calculated as the difference between average cross-shelf temperature (8-m to 75-m isobaths) and the long-term (20-24 years) surface temperature for the day of the year at a nearby shore station. Long-term daily temperatures were computed from monthly means (Tekmarine 1983) by linear interpolation.

Wind-driven coastal upwelling was estimated by using an index of mass transport, $M(x)$ (Bakun 1975; Bowden 1983), computed from average daily wind speed. Wind data were from Los Angeles International Airport (NOAA 1984) near the Playa del Rey transect. Alongshore wind vectors were computed for the Southern California Bight assuming a shoreline angle of 129° from true north (Bakun 1975), and upwelling indices were computed from these vectors. Shore angle at the four major transects varies between 120° at Ormond Beach and 135° at Seal Beach, so Bakun's shoreline angle was a reasonable approximation.

Zooplankton displacement volumes were estimated from samples collected with 70-cm-diameter bongo nets (333-micrometer Nitex mesh) that were towed obliquely from the bottom to the surface (Brewer and Smith 1982). Adult and large juvenile fishes, squid,

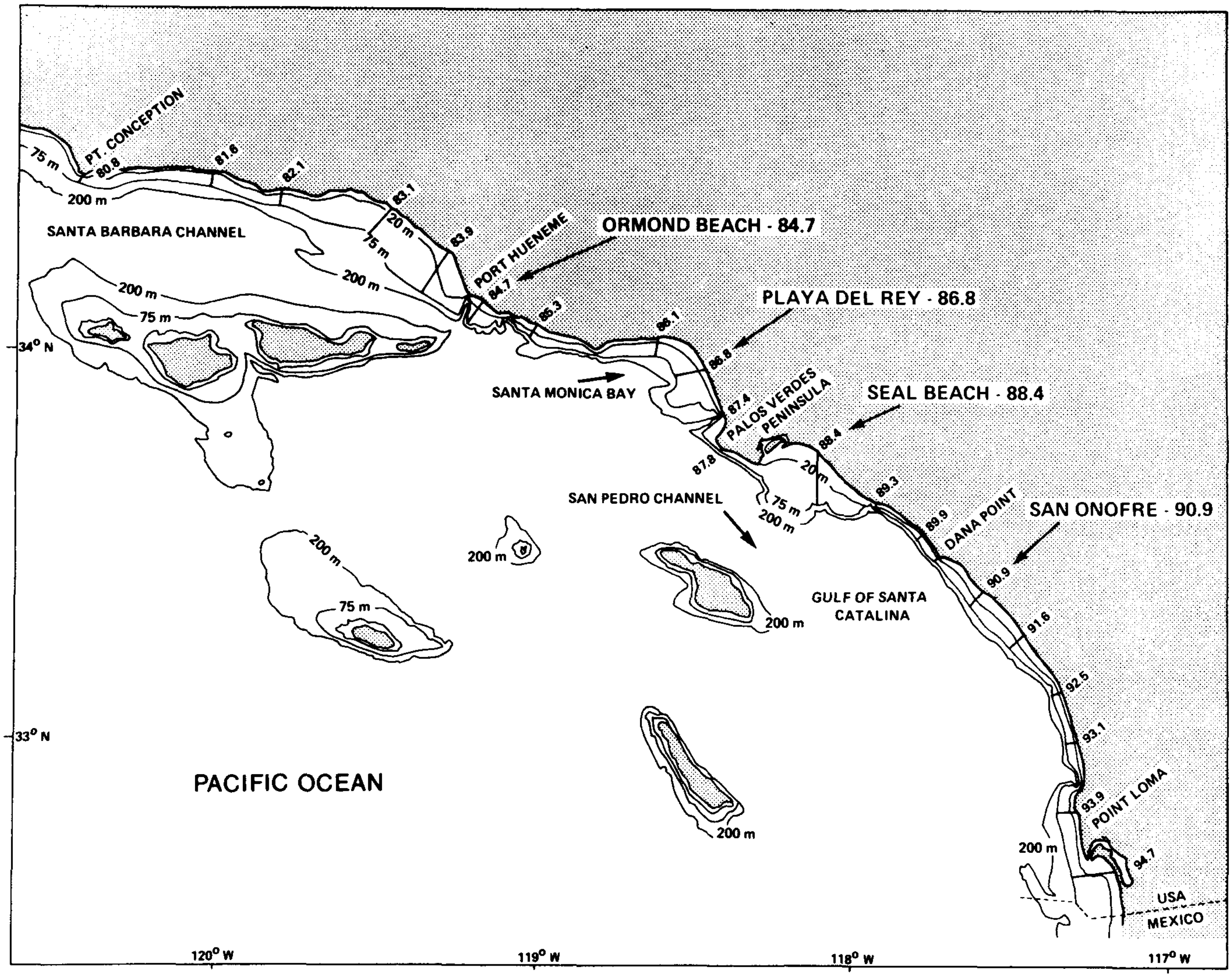

Figure 1. Location and CalCOFI numbers for all transects sampled between 1978 and 1984 in the Southern California Bight.

octopuses, and large algae were removed from fixed (buffered 5% Formalin) samples and were not considered in the volume estimates. Sample volume was adjusted to a standard level, and zooplankton was removed by draining the sample through 333-micrometer Nitex mesh. Using a buret, we added enough Formalin to the Formalin filtrate to reach the standard volume. The volume of Formalin added from the buret equaled net zooplankton displacement volume.

RESULTS

Temperature and Salinity

Seasonal warming of surface waters during spring and early summer was not synchronous throughout the bight. At Ormond Beach, seasonal warming began about 1-2 months later than at Playa del Rey, Seal Beach, and San Onofre, whose cycles coincided closely (Figure 2). Surface temperature in the nearshore zone was highest in August for all years studied, except 1983, when maximum temperatures were recorded during the October cruises (Figure 2). Annual low temperatures generally occurred during January or February, although unseasonably cold water, corresponding to intense upwelling periods, was occasionally encountered during spring or summer. Seasonal minimum water temperatures occurred at about the same time throughout the bight during any given year (Figure 2).

A spring-summer thermocline has been described for shallow water off southern California (Cairns and Nelson 1970). Surface temperatures increased by about 1°-3°C at almost all stations between April and June (Figure 2), probably as the result of solar warming and reduced mixing. Temperature near the bottom of the water column generally declined by a few degrees as surface temperatures rose (see also Winant and Bratkovich 1981). During fall and winter, nearshore water

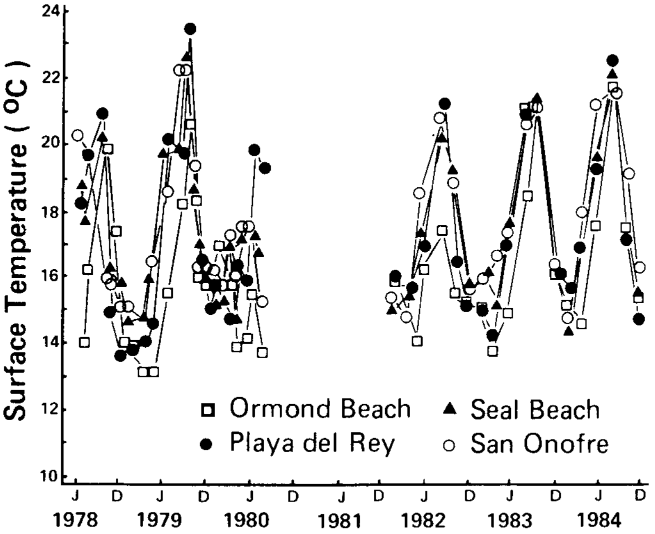

Figure 2. Average cross-shelf surface temperature at major transects. Some data points are hidden.

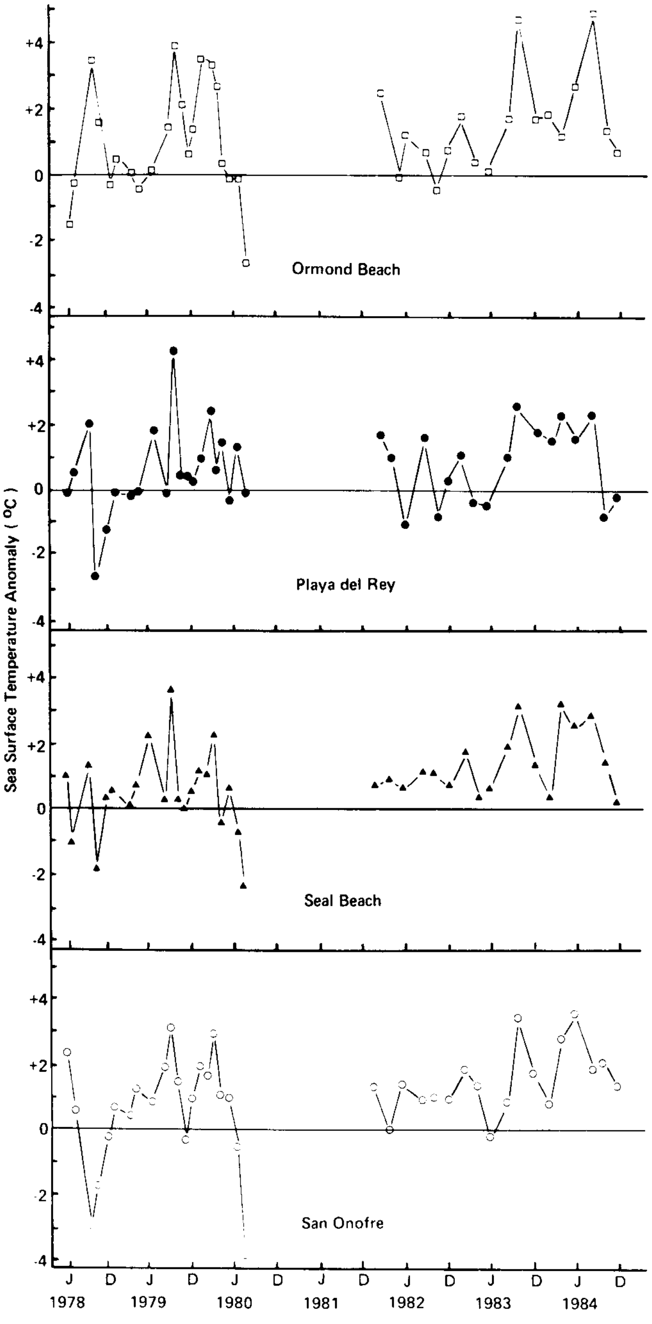

Figure 3. Sea-surface temperature anomalies at major transects.

was well mixed, and temperature and salinity were similar from the surface to the bottom.

Several anomalous (nonseasonal) warm and cool periods can be identified in transect temperature records collected between 1978 and 1984 (Figure 3). During September 1979, surface temperature anomaly (STA) was +3° to +4°C at all transects. During July 1980, temperatures were particularly low, being 2°-4°C below average, except at Playa del Rey, where temperatures were near the long-term average. Nearshore temperatures were only slightly above normal in the fall of 1982, and STAs during February 1983 ranged from +1.1° to +1.8°C. Unusually warm water was found during fall 1983 and again during spring and summer 1984; surface temperature was near normal during other periods. Of course, resolution of the start and end of these phenomena is fairly coarse, being limited by the sampling frequency of 30-60 days.

Temperature-salinity (T/S) relationships were examined to determine water mass origins, particularly during the 1982-83 El Niño. We selected October for comparison because the largest positive STA occurred in October 1983 (Figure 3), indicating strong El Niño conditions. We used long-term averages of temperature and salinity from a shallow CalCOFI station (approximately 200 m deep; number 90028 off Dana Point) to construct a reference T/S curve (Figure 4). During October 1979 and October 1984, temperature (surface to 75 m) ranged from about 12°-20°C, and salinity averaged around 33.8‰. In October 1982, temperature was similar to 1979 and 1984, but salinity had declined to about 33.4‰. This reduced salinity may have been caused by (1) diluted surface water from a rainstorm that immediately preceded sampling of the Playa del Rey and Ormond Beach transects, or (2) movement of a low-salinity water mass into the area, possibly from the north. During October 1983, when surface temperature anomalies were greatest (Figure 3), the overall temperature range had increased about 2°C over 1979, 1982, and 1984. Salinity was as low as 33.0‰ in some samples collected in October 1983 (Figure 4), suggesting a different water mass during this period. Mean salinities in the upper 50 m from June-December 1984 cruises, and preliminary data from 1985, were similar to "usual" (non-El Niño period) salinities, ranging from 33.53-33.78‰

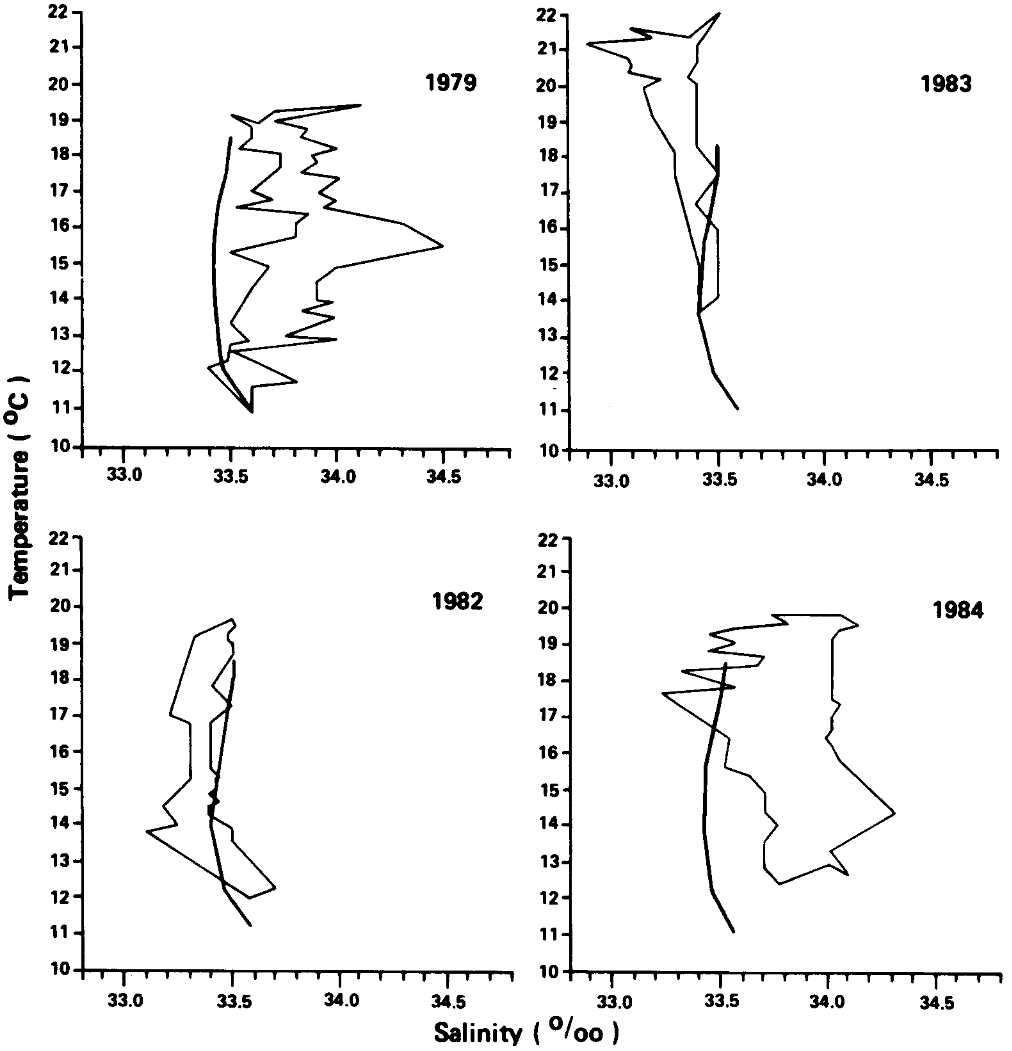

Figure 4. Temperature-salinity envelopes for October of 1979, 1982, 1983, and 1984, using data from all four major transects. The heavy line is the long-term T/S curve for CalCOFI station 90028 (data from Lynn et al. 1982).

Nutrients

Because nitrogen is the principal limiting nutrient of primary production in coastal waters, ammonium and nitrate distribution patterns will be emphasized. Enrichment experiments have shown that nitrogen increases algal growth and reproduction in the ocean, with very dramatic increases on the continental shelf (e.g., Ryther and Dunstan 1971; Eppley et al. 1979a; Laws and Redalje 1979). Eppley et al. (1979a), working from 0.9-107 km off the coast of southern California, demonstrated that nitrate is a major factor regulating the standing stock and production of phytoplankton in the euphotic zone. Also, concentrations of major nutrients (nitrate, phosphate, silicate, carbonate carbon) and several trace metals are linearly related to each other (e.g., Redfield et al. 1963). "Nitrate" values reported here are nitrate plus nitrite; nitrite concentrations were generally much less than nitrate concentrations, usually 5%-20% of the total nitrate-plus-nitrite value.

We calculated average ammonium and nitrate in the upper 15 m of the water column to examine longshore and temporal patterns. We selected the upper 15 m to allow computations at four cross-shelf stations (15, 22, 36, and 75 m) and so all samples would be within the euphotic zone (Jackson 1983). Station depth was not a significant factor affecting these 15-m-deep averages for nitrate (3-way ANOVA, depth not significant at $P = .05$), so we averaged means from across the shelf. Ammonium concentrations were significantly higher (3-way ANOVA, $P < .05$ for station effect) at the 15-m isobath (0.45 μg-atoms·l^{-1}) than at deeper stations (0.37-0.38 μg-atoms·l^{-1}). This cross-shelf difference was probably caused by inclusion of a "bottom" datum in 15-m means at the 15-m station, since ammonium concentrations have been shown to be higher near the bottom (Eppley et al. 1979b; Barnett and Jahn, in press). Since the cross-shelf ammonium differences were relatively small compared to the expected precision of measurements in this range (approx. 0.1 μg-atoms·l^{-1}; Eppley et al. 1979b), we also averaged 15-m deep ammonium means across the shelf.

Ammonium is an important source of nitrogen for plant growth in the Southern California Bight, representing about 40% of the sum of ammonium, nitrate, and urea-N assimilation by phytoplankton (McCarthy 1972; Eppley et al. 1979b). Ammonium concentration is often low relative to other nitrogenous forms because of its rapid recycling by phytoplankton. Ammonium concentrations and patterns that we observed were similar to results of other studies in the nearshore zone of southern California (Eppley et al. 1979b; Barnett and Jahn, in press). Mean concentration of ammonium between mid-1982 and December 1984 was 0.39 μg-atoms·l^{-1}, and there was no obvious seasonal pattern (Figure 5). Highest concentrations (2-3 μg-atoms·l^{-1}) were observed within Santa Monica Bay in December 1982 and February 1983, although concentrations up to 5-20 μg-atoms·l^{-1} were observed by Eppley et al. (1979b) in this area in 1974-77. These differences were probably the result of station location within Santa Monica Bay and local current patterns, since sewage and refinery wastes were suggested sources of high ammonium concentrations in 1974-77 (Eppley et al. 1979b). Lowest ammonium levels were observed at three of the four transects in October 1983, during a period of unseasonably warm water (Figures 2 and 3).

Nitrate concentrations were often less than 1.0 μg-atoms·l^{-1} at the surface (Figure 6), except during periods of strong upwelling. Such low concentrations in surface waters have been noted previously (e.g., Eppley et al. 1979a; Zimmerman and Kremer 1984) and may be a result of phytoplankton's rapid use of nitrate within the euphotic zone. Macroalgae, such as the giant kelp (*Macrocystis pyrifera*), are also a large sink for nutrients in the littoral zone (Jackson 1977). Profiles of nitrate at Seal Beach (Figure 6) were typical of profiles at the other three transects and will therefore be used to describe the general onshore-offshore and seasonal trends. Between August 1982 and February 1983, nitrate profiles along the Seal Beach transect were similar, with low concentrations throughout the water column at the inshore stations (8-36 m). Profiles at 75 m had low levels down to about 40 m and a significant nitrate pool (bottom cencentrations to 15.5 μg-atoms·l^{-1}) below 40 m (Figure 6). During the April and June 1983 cruises, the nitracline became shallower, and high nitrate concentrations were thus observed near the bottom at the 75-, 36-, and 22-m isobaths.

Nitrate levels were low from the surface down to at least 75 m during late summer to early winter of 1983. The nitracline observed during August to December 1983 was deeper, and therefore the nutrient pool was farther offshore than during the same period of 1982. Sampling at Seal Beach during February 1984 followed a strong wind event that produced intense nearshore upwelling of cold water. Finally, nitrate profiles taken in April 1984 were fairly similar to those of the previous year, with high concentrations near the bottom at 75-m and 36-m stations and moderately low levels at shallower stations. We discarded nutrient data from June to December 1984 because of equipment malfunction.

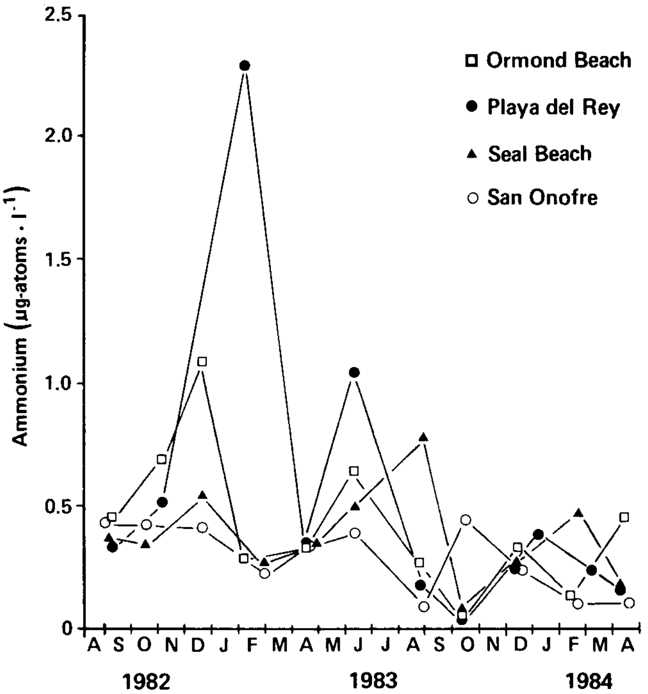

Figure 5. Average ammonium in the upper 15 m at major transects. Each point is a cross-shelf average of 15-m, 22-m, 36-m, and 75-m stations.

The temporal pattern of average nitrate suggests two major periods or events of increased nitrate concentration (Figure 7). First, three of the four transects showed increased nitrate levels during the early summer of 1983. At the Playa del Rey transect, nitrate levels increased steadily from August 1982 to a high of over 3.0 μg-atoms·l^{-1} in early June 1983, whereas nitrate at Ormond Beach and San Onofre showed significant increases between April and June 1983. Nitrate at Seal Beach was relatively constant during spring-summer of 1983. Closer examination of the data indicates that increased nitrate levels at Ormond Beach, Playa del Rey, and San Onofre between April and June 1983 primarily resulted from increased concentrations in the lower part of the 15-m water column. Nitrate increased near the bottom at almost all stations of these three transects, while near-surface (surface-to-6-m) levels remained low and similar from April to June.

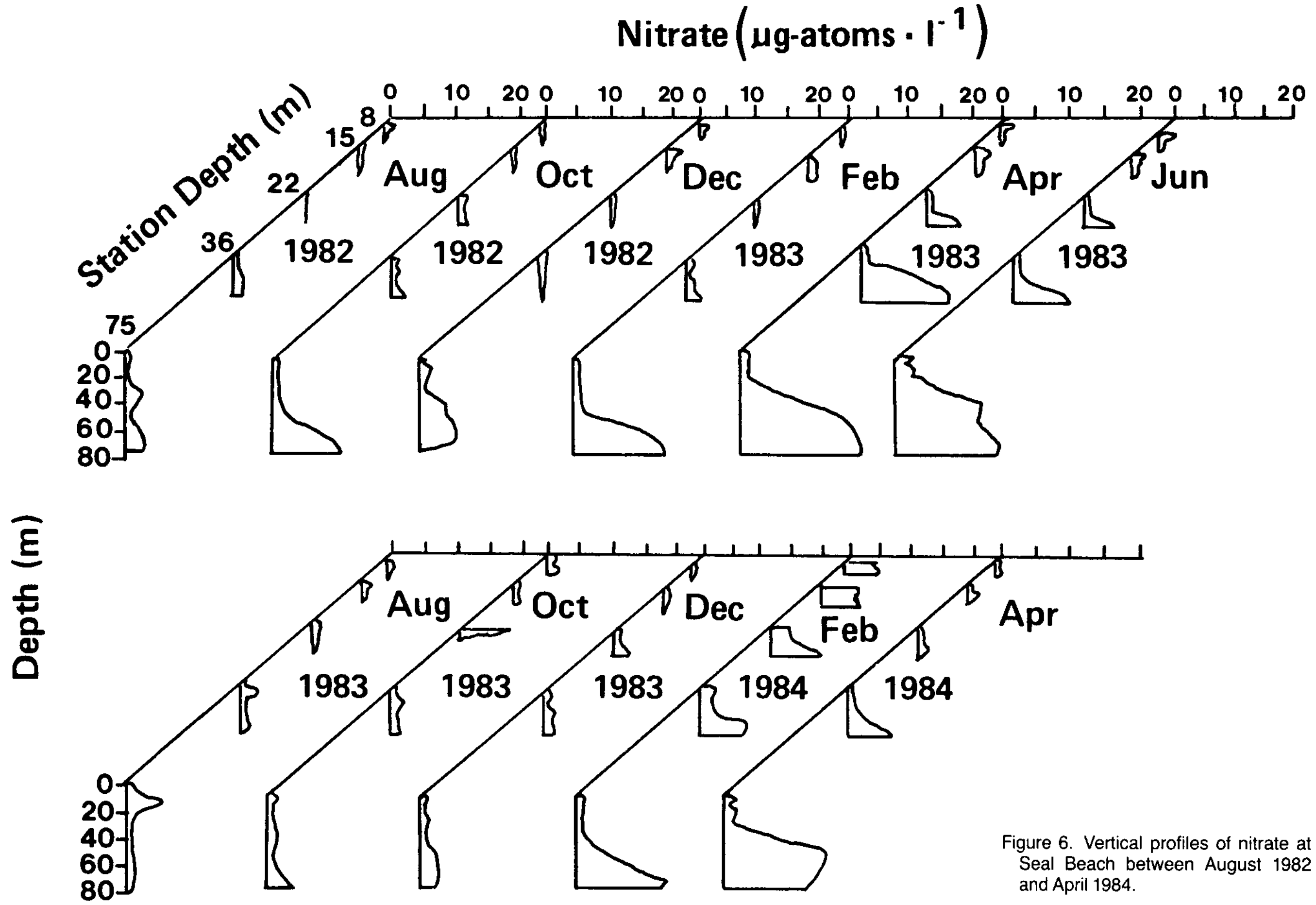

Figure 6. Vertical profiles of nitrate at Seal Beach between August 1982 and April 1984.

The second period of increased nitrate levels occurred during February 1984 (Figure 7). Nitrate increased slightly at Ormond Beach and San Onofre between December 1983 and February 1984 but showed a dramatic rise at Seal Beach—from 0.3 µg-atoms·l^{-1} to 5.5 µg-atoms·l^{-1} at the 15-m isobath. Bightwide sampling during February 1984 was interrupted by a strong, brief windstorm that caused nearshore upwelling and significant cross-shelf gradients in temperature, salinity, and nutrients. Normal sampling protocol called for the ship to begin on the northernmost transect (Ormond Beach) and proceed south to successive transects over a period not to exceed 10 days. Ormond Beach was sampled on February 15, 1984, but strong winds and heavy seas forced the ship off the scheduled Playa del Rey transect, which was finally sampled on March 7. Average daily wind speed at Los Angeles International Airport (LAX) increased from 2.8 m/sec on February 15, 1984, to 7.9 m/sec on February 16 (NOAA 1984). Winds remained strong on February 17, averaging 6.8 m/sec. During the storm, the wind blew steadily from the northwest. Winds from this direction were parallel to the shoreline of the Southern California Bight and produced strong offshore transport of nearshore surface waters, as suggested by the upwelling index calculated for this period (Figure 8). Seal Beach and San Onofre transects were sampled soon after the wind event, on February 20 and 22, respectively.

Specific density (sigma-t) and nitrate profiles at Seal Beach (Figure 9) for the February 1984 cruise indicate intense movement of surface water away from the shore and replacement of this water from depth. Water from the 8-m station was significantly more dense than

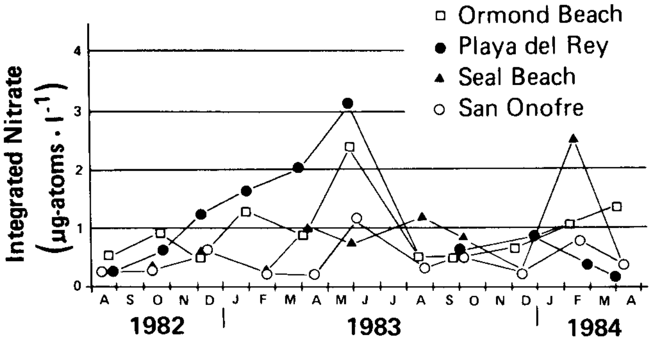

Figure 7. Average nitrate in the upper 15 m at major transects. Each point is a cross-shelf average of 15-m, 22-m, 36-m, and 75-m stations.

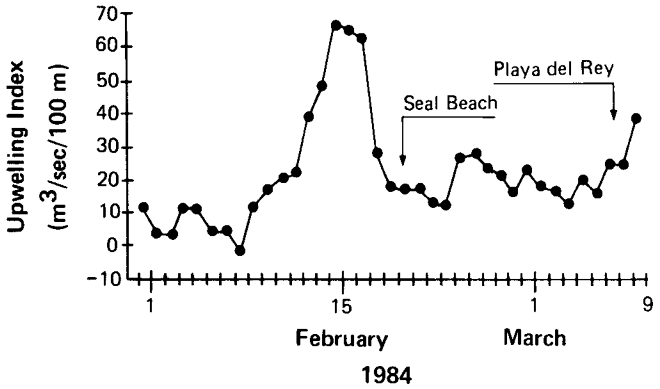

Figure 8. Upwelling index, *M*(*x*), during cruise 47. Each point is a 3-day running average. Dates when the Seal Beach and Playa del Rey transects were sampled are indicated. *M*(*x*) was computed from daily wind data at Los Angeles International Airport and has units of cubic meters per second per 100 m of coastline.

water from similar depths farther offshore, and isopycnal lines showed strong inshore sloping. Nitrate in near-surface water reached very high levels (5.1 μg-atoms·l^{-1}) at 8 m, while comparable surface water over the 75-m contour had only 0.7 μg-atoms·l^{-1}, a more typical concentration for the coastal zone during winter (Kamykowski 1974; Eppley et al. 1978; unpublished data; see Figure 7).

To assess the persistence of local upwelling caused by the storm of February 15-17, we compared the vertical structure of the water column at the Playa del Rey transect with Seal Beach profiles. The continental shelf is similar at these transects (Figures 1, 9, and 10), although Seal Beach is located just south of a large headland, the Palos Verdes Peninsula, in a semi-permanent upwelling area (Dorman and Palmer 1981; Dykstra et al. 1984). Winds at Seal Beach and Playa del Rey during and after this wind event were compared using the alongshore component of daily winds (NOAA 1984) measured at LAX and Long Beach Airport, near Seal Beach. The alongshore wind components, which may cause upwelling or downwelling, were significantly correlated ($r = 0.73$; $P < .001$) between LAX and Long Beach Airport for February and early March 1984, implying that wind speeds and directions in the nearshore zone were similar during this period. Profiles of sigma-t and nitrate from the Playa del Rey transect, measured 17 days after the storm and following a relatively calm period (Figure 8), indicate that the effects of the windstorm were short-lived, since near-coast water conditions were stable and there were no indications of upwelling (Figure 10).

Infrared satellite images showing relative sea-surface temperature suggest that nearshore upwelling was widespread in the Southern California Bight during the mid-February 1984 windstorm (Figure 11). Just

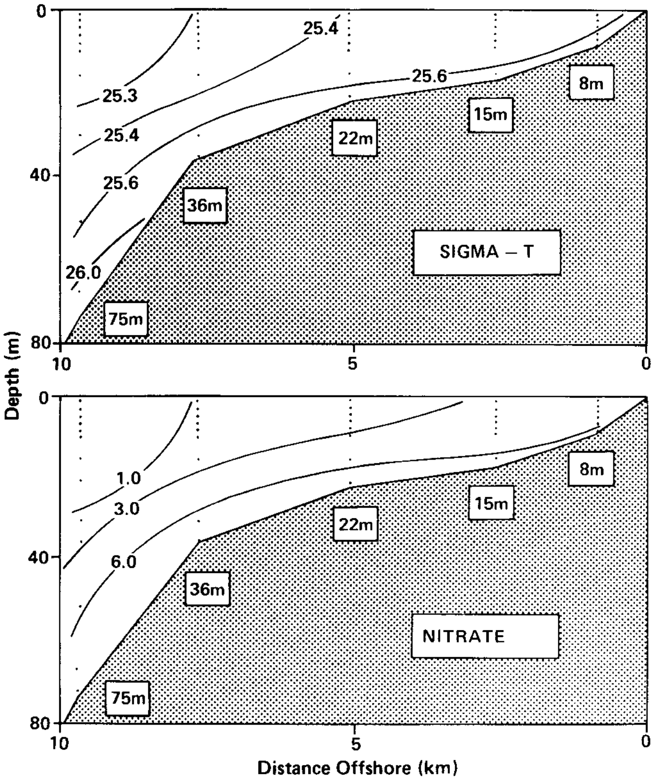

Figure 9. Cross-shelf distribution of sigma-t and nitrate (μg-atoms·l^{-1}) at Seal Beach on February 20, 1984.

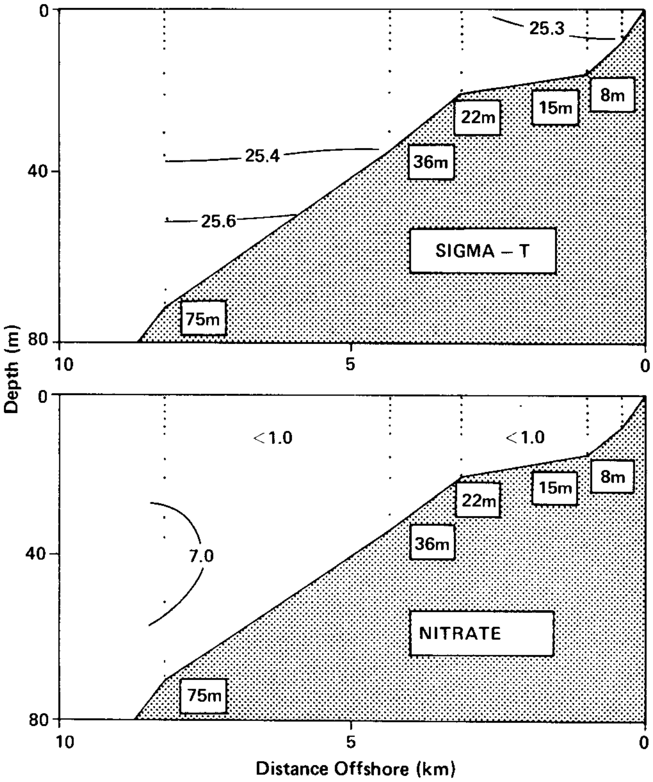

Figure 10. Cross-shelf distribution of sigma-t and nitrate (μg-atoms·l^{-1}) at Playa del Rey on March 7, 1984.

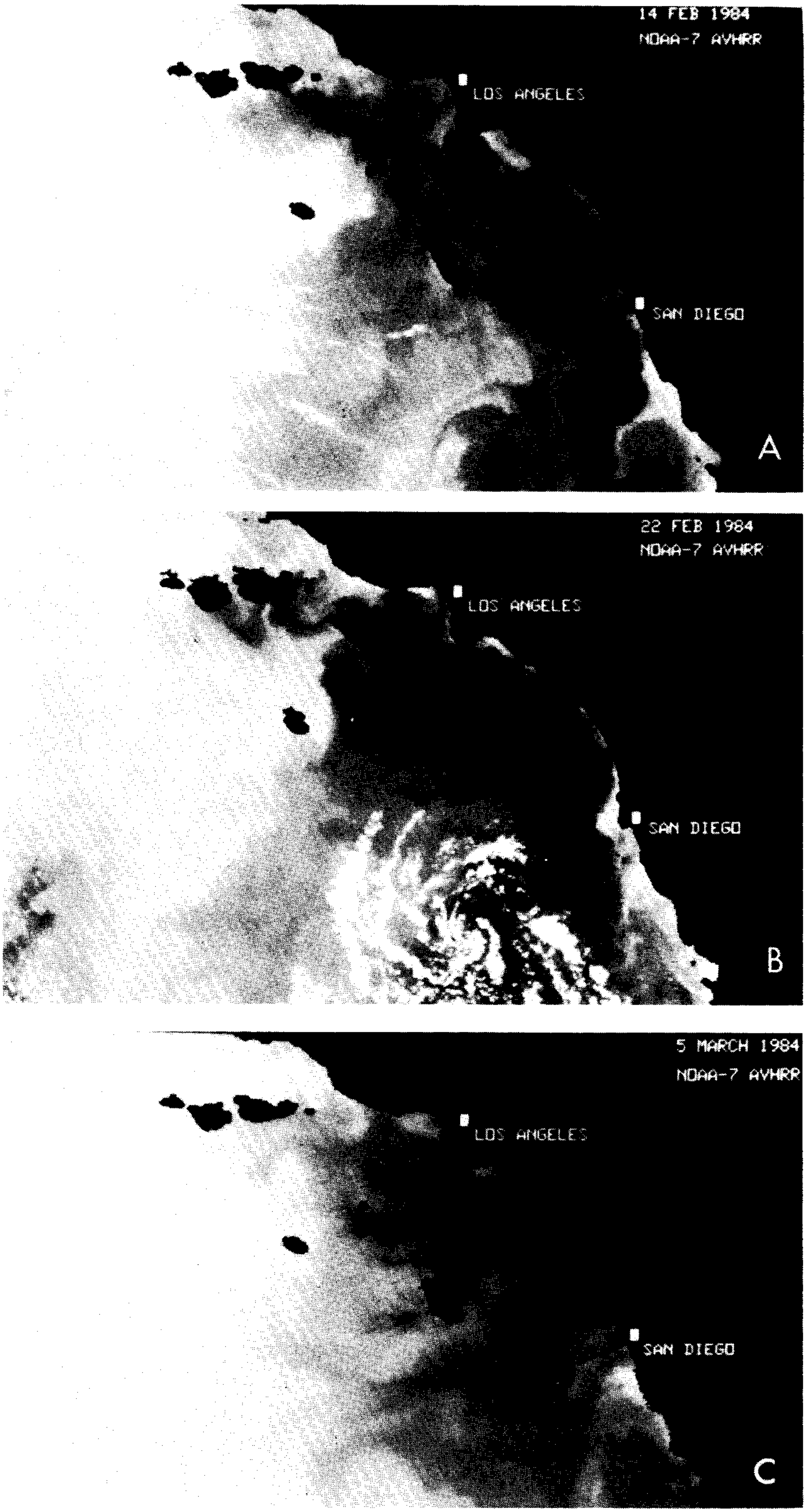

Figure 11. Infrared satellite imagery of relative sea-surface temperature before and after the windstorm of February 15-17, 1984. White areas show relatively cold water; gray-to-black areas are warmer water.

prior to the storm, a long plume of cold water stretched southeast of the Palos Verdes Peninsula, but other nearshore areas of the bight had surface temperatures similar to areas farther offshore, or only slightly cooler (Figure 11a). Five days after the storm, strands of cold surface water were observed off Point Dume, in the northern part of Santa Monica Bay, south of Palos Verdes Peninsula, and in the Point Loma area (Figure 11b). Upwelling occurred along much of the coast from Point Dume to San Diego during the windstorm. In agreement with transect data, no well-defined patches of cold water were present along the coast on March 5, indicating that upwelling had relaxed and surface waters had warmed by solar heating or horizontal advection (Figure 11c). Satellite images from other days during this period could not be used because of cloud cover.

Zooplankton Biomass

Zooplankton volumes were first averaged over each transect to examine seasonal, annual, and geographic variability (Figure 12). Nearshore zooplankton biomass showed strong seasonality, with highest volumes during April-June and minima during December-February. Analyses of the variation of zooplankton volumes for each month (Feb, Apr, June, Aug, Oct, Dec) indicated a significant transect-by-year interaction for all months except February (Table 2), suggesting that zooplankton communities at different transects responded asynchronously during 1982-84. The seasonal pattern of biomass observed at Seal Beach seems to have differed from the other three transects during this 3-year period (Figure 12). Ormond Beach, Playa del Rey, and San Onofre zooplankton volumes followed similar patterns through the 36 months of sampling, having been somewhat lower during 1983 and 1984 than during 1982. Biomass levels appeared to be about the same during 1983 and 1984 at these three transects. In contrast, Seal Beach zooplankton volumes were similar during 1982 and 1983 but dropped sharply during the spring and summer of 1984. June 1984 zooplankton volume at Seal Beach was lowest of the four transects, whereas estimates were generally higher at Seal Beach than the other three transects during 1982 and 1983.

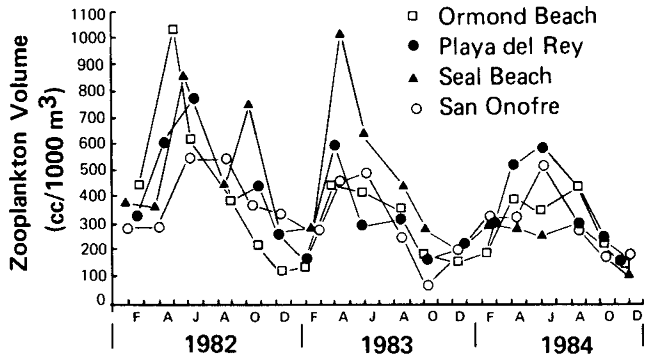

Figure 12. Average zooplankton displacement volume along the major transects.

Cross-shelf zooplankton biomass averages for all nearshore transects were higher very near the coast than at the 75-m depth contour, particularly from August through December (Figure 13; Table 2). Zooplankton biomass at the 75-m stations was always lower than at stations closer to the shore, being only 38.5% of the nearshore maximum in October. From February to August, peak zooplankton biomass was found at stations from the 15-36-m depth contours, although the trend for February, April, and June was not statistically significant (Table 2). During the period of increasing zooplankton abundance—February through June—the mode of maximum zooplankton biomass shifted progressively from inshore (15-m isobath) to mid-transect (36-m isobath), suggesting that the zone of highest zooplankton production and/or survivorship near the coast gradually shifts farther offshore as the season develops (Figure 13). This seasonal movement of the zooplankton biomass mode was observed during 1982 and 1983, but zooplankton volumes, within a sample period, were similar from the 8-m depth to the 36-m station in 1984. Between June and August, zooplankton volumes declined at each depth across the shelf. Minimum zooplankton biomass was observed in December.

The source of nutrients, particularly nitrate, that

TABLE 2

Monthly Means and Effects of Transect, Year, and Station Depth for Zooplankton Displacement Volume (1982-1984)

Month	Mean (S.D.) (cc/1000m^3)	3-way ANOVA results					
		Transect (T)	Year (Y)	Station (S)	T × Y	T × S	Y × S
February	278.8 (140.1)	NS	**	NS	NS	NS	NS
April	518.7 (319.5)	—	—	NS	***	NS	NS
June	520.4 (273.0)	—	—	NS	*	NS	NS
August	370.8 (147.5)	—	—	***	**	NS	NS
October	264.5 (234.1)	—	—	**	**	NS	NS
December	189.1 (95.4)	—	—	**	*	NS	NS

NS = not significant; *$P < .05$; **$P < .01$; ***$P < .001$

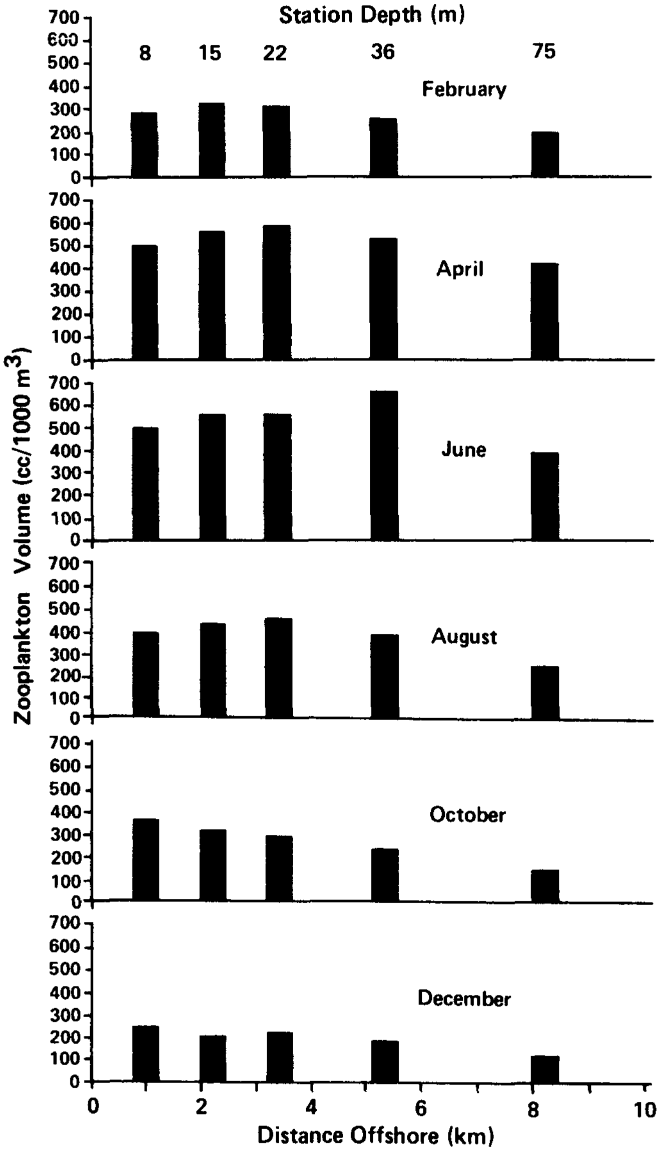

Figure 13. Average monthly zooplankton displacement volume for all four major transects during 1982-84.

could stimulate increased primary production and, ultimately, increased secondary production (zooplankton biomass) on the inner continental shelf appears to be moderately deep water (Figure 14). Mean zooplankton volumes across the shelf were significantly correlated with nitrate levels at the 75-m station and the 36-m station ($r^2 = 0.25$) but not at shallower stations ($P > .10$; $r^2 < 0.07$). Although we do not have data to relate increased primary production with increased nutrients in the nearshore, other studies have shown this relationship (e.g., Ryther and Dunstan 1971; Eppley et al. 1979a). Processes that mix outer-shelf water into the shallow nearshore zone should be important mechanisms for explaining primary and secondary production in shallow coastal waters off southern California.

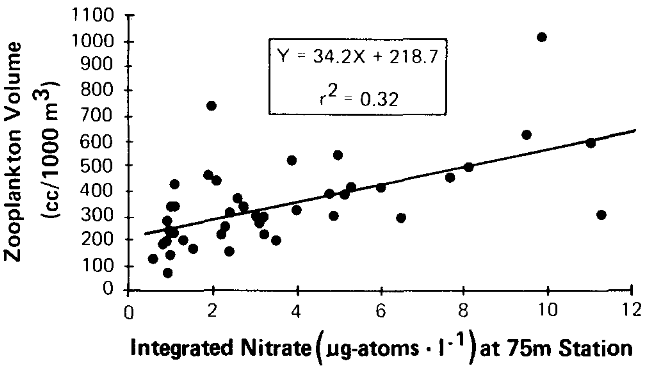

Figure 14. Effect of offshore nitrate (75-m station) on cross-shelf zooplankton volume. The regression equation is significant at $P < .001$.

DISCUSSION

Seasonal Patterns

Two important seasonal processes related to nutrient mixing off southern California are temperature stratification and upwelling. Seasonal development of the thermocline in nearshore water begins in April or May and persists through September (Cairns and Nelson 1970; Winant and Bratkovich 1981). Several physical and chemical changes accompany this process. Surface water becomes warmer during these months, but near-bottom temperatures usually decline. Mean vertical temperature or heat content changes little during the year in shallow water, but the vertical structure of the current field shifts dramatically (Winant and Bratkovich 1981). During fall and winter, the water column is well mixed, and water flow is toward the south. In spring and summer, surface water continues flowing southward, but water below the thermocline usually moves in the opposite direction.

The cool, offshore water mass observed beneath the summer thermocline is almost certainly the major source of nutrients for primary production in nearshore waters. Internal waves that propagate onto the continental shelf are thought to be a major contributor to mixing in the upper part of the water column (Gregg and Briscoe 1979). Recent studies on other continental shelves have shown how large-amplitude internal waves may "pump" deep-water nutrients across the shelf edge and into shallow water on the inner continental shelf (Sandstrom and Elliott 1984; Holloway et al. 1985). Large temperature fluctuations, representing surges of cold water moving onshore, occur at approximately tidal frequencies in shallow waters off southern California (Cairns 1967; Winant 1974; Zimmerman and Kremer 1984). Isotherms on the leading edge of cold surges are often vertical, or even pass vertical and become inclined toward the shore, with cold water overlaying warmer water in an unstable configuration (Cairns 1967; Winant 1974). Such instabilities probably cause vertical mixing by shear or convective (overturning) processes.

Barnett and Jahn (in press), working between 8 and 100 m near San Onofre, also observed a spring-summer encroachment of nutrient-rich water onto the shallower parts of the shelf, and mixed, nutrient-poor water in the upper part of the water column during fall and winter. A deep pool of nitrate-rich water was also common, but not always present. Eddy diffusion of nitrogen from depth and regeneration of nutrients were offered as likely explanations of nearshore enrichment, although Barnett and Jahn also considered longshore transport of water from semipermanent upwelling centers (e.g., Palos Verdes Peninsula, Dana Point, and San Mateo Point) as a possible mechanism supplying nutrients.

Nearshore upwelling off southern California occurs during several months of the year and may affect primary production by transporting nutrient-rich water into the euphotic zone (Kamykowski 1974; Dorman and Palmer 1981). In all cases, local winds have been the putative cause of nearshore upwelling off southern California (Kamykowski 1974; Dorman and Palmer 1981; Dorman 1982), although other mechanisms are possible, such as continental shelf waves or internal Kelvin waves (Bowden 1983).

Nearshore winds off San Diego have a strong diurnal component, blowing offshore from late night to early morning and onshore at other hours (Dorman 1982). Mean seasonal winds at San Diego are generally toward the east and southeast (Dorman 1982). Tropical storms, which occur once or twice from mid to late summer, move north along the coast of Baja California causing strong northward winds and downwelling near the shore (Winant 1980). Other summer wind events cause strong southeastward wind flow and significant upwelling (Dorman and Palmer 1981). Relatively weak coastal winds (e.g., 7 m/sec) over a narrow continental shelf result in nearshore upwelling that is 30 times as intense as the typical open-ocean upwelling observed off San Diego (Dorman 1982). Wind stress increases with distance from shore, often by a factor of three or four (Dorman 1982). Therefore large-scale analysis of wind data collected at offshore (beyond about 20 km) ship stations (e.g., Bakun 1975) is not representative of nearshore winds and wind-forced processes.

Storm-driven upwelling events have been observed in the nearshore zone during several months of the year (Kamykowski 1974; Dorman and Palmer 1981; this study, and unpublished data). Kamykowski (1974) described a nearshore upwelling event off La Jolla, California, during February 1971. Winds of 5.5 m/sec, with gusts up to 9.7 m/sec, produced upwelling at a station 1 km offshore. Increased nutrients from upwelled water caused increased primary production and a phytoplankton succession that was followed for three weeks. An average of two upwelling events occur during summer months in the southern part of the bight (Dorman and Palmer 1981). Nearshore upwelling events produce strong cross-shelf gradients in nutrients, temperature, and, probably, zooplankton distribution patterns. These gradients are within approximately 10 km of the shore and are created by conditions that do not cause strong offshore mesoscale upwelling.

El Niño Conditions in the Nearshore Zone

The most significant long-term phenomenon observed during sampling was the El Niño event that began in the tropical Pacific in 1982 (Philander 1983). This was an exceptionally strong meteorological and oceanographic event that produced very warm surface waters throughout the Central and Eastern Tropical Pacific Ocean. Anomalous, large-scale atmospheric circulation presumably caused warm ocean conditions off the coast of California and Mexico during the 1982-83 El Niño (Lynn 1983; Simpson 1983, 1984a, 1984b). Unusually warm temperatures were first observed at offshore stations in the California Current during the fall of 1982, with full development of large-scale warming by January 1983 (Auer 1982-83; Simpson 1983) and persistence of the phenomenon to at least January 1984 (McGowan 1984; Simpson 1984a). Monthly mean sea level, an indicator of an El Niño event, was about 0.2 m above the long-term mean at Scripps Pier during the fall of 1982 (Dykstra and Sonu 1985), signifying the beginning of this El Niño event.

Nearshore processes that mix cool, deep water with surface water presumably created a complex temperature signal close to the shore during the 1982-83 El Niño (Figure 3). During the first few months of the El Niño event (fall 1982), surface temperatures measured at Scripps Pier and on our nearshore transects were near normal or slightly above normal (North 1985). Surface temperatures were 1°-2°C above normal in the first few months of 1983 (Dayton and Tegner 1984). During spring and summer of 1983, nearshore surface temperatures were again near normal. The strongest nearshore development of El Niño conditions was observed during fall 1983 and again during spring and summer 1984; surface temperature was a little warmer than average during the winter of 1983-84, with some significant events of below-normal cold water (North 1985). Thus periods of near-normal hydrographic conditions (surface temperature and presumably other variables) were imposed upon the strong El Niño nearshore, and the near-normal temperatures during part of 1983 were probably the result of intense nearshore mixing and upwelling processes that advected cool, high-salinity, deep water to the surface. Warm "El Niño-like" conditions persisted in the Southern California Bight through most of 1984, suggesting that a considerable time lag is necessary for regional temperatures to return to normal following a global El Niño event (J. Simpson, MS).

Simpson (1984a) showed that water properties within the inner part of the Southern California Bight were probably caused by onshore movement of Pacific subarctic water from the offshore part of the California Current. Subarctic water is distinguishable by low temperature, high nutrient concentrations, and low salinity (Reid et al. 1958). After subarctic water enters the California Current around 48°N, it warms as it moves south, but remains recognizable by its relatively low salinity as far south as 25°N (Reid et al. 1958; Simpson 1984a). Conditions in the fall of 1983 suggest the presence of this subarctic water mass in the nearshore zone. No long-term averages of nitrate were available for comparison with nitrate concentrations measured during 1983 and 1984, but nutrient levels may have been lower, since a strong inverse relationship exists between temperature and nutrients (Zimmerman and Kremer 1984; Barnett and Jahn, in press).

The lower zooplankton biomasses at most transects during 1983 and 1984 were most likely caused by the 1982-83 El Niño. Fiedler (1984) has shown that reduced phytoplankton production off the coast of southern California during El Niño was associated with weakened mesoscale upwelling. Reduced nutrients over the continental shelf may have caused slower phytoplankton growth following the onset of El Niño conditions in late 1982, and therefore less input to the zooplankton food chain. Zooplankton biomass was lower at all transects in June 1983 than in June 1982 (Figure 12), although unusually warm water was not observed until September and October of 1983. Temperature, per se, was probably not regulating zooplankton abundance, and other factors such as nutrient limitation or increased offshore transport were probably responsible for low zooplankton biomass. Continued anomalous conditions in the nearshore zone through most of 1984, although the tropical El Niño phenomenon ended in 1983 (Cane 1983), may have caused primary productivity and zooplankton biomass to remain low during 1984.

Cross-Shelf Patterns

Cross-shelf gradients were particularly obvious for zooplankton biomass. Zooplankton studies off southern California generally emphasize biological interactions (grazing, predator-prey relationships) or species-distribution patterns (vertical, horizontal, patchiness). However, zooplankton biomass estimates made in the California Current have also been used to study interannual variability and the effects of large-scale physical processes on the planktonic community (Bernal and McGowan 1981; Chelton et al. 1982). Biomass estimates of many broad taxonomic categories (total copepods, chaetognaths, decapods, euphasiids, etc.) are highly correlated throughout the region (Colebrook 1977), and biomass fluctuations have been common during the last 200 years (Soutar and Isaacs 1969, 1974). High correlations among taxa on a regional scale suggest that zooplankton biomass may be used as a measure of community response to large or mesoscale physical or chemical phenomena (Bernal and McGowan 1981). Biological interactions undoubtedly cause fluctuations of populations of some zooplankton species, but time series of zooplankton biomass, interpreted in light of major physical processes, should give a reasonable picture of community "condition," particularly when most major taxa respond simultaneously throughout the ecosystem.

Zooplankton biomass shows an offshore peak in abundance at about 100-200 km off the coast of central and southern California (Smith 1971; Bernal and McGowan 1981). Chelton (1982) has shown that the offshore zooplankton peaks are associated with offshore upwelling driven by the wind stress curl. Bernal and McGowan (1981) described the onshore-offshore distribution of zooplankton biomass in the California Current and discussed the possible existence of an additional nearshore maximum within approximately 50 km of the shore. Using data from special CalCOFI stations within 50 km of the coast (also, see maps in Smith 1971), they observed no nearshore peak in zooplankton. Our nearshore data are not directly comparable to the CalCOFI data, since different mesh sizes were used (333 μ vs 505 μ), and offshore (CalCOFI) tows sampled below the euphotic zone, whereas our nearshore tows did not. We can, however, examine our data for cross-shelf pattern and compare these results to those of Bernal and McGowan (1981) in a qualitative manner.

We observed zooplankton biomass peaks, for most months of the year, that were inside the 75-m isobath. The low zooplankton volumes found at 75-m depths may be the result of a real nearshore maximum or, possibly, sampling bias caused by sampling through water columns of different depth. The lower portion of the 75-m sample was probably below the 1% surface light level, thus some of the water strained on these tows was relatively unproductive and not strictly comparable to shallower stations. However, other workers' results suggest that dynamics are different nearshore and that zooplankton is denser very near the coast. Beers and Stewart (1967) found a decline in the density of microplanktonic metazoans between 25 and 200 m in the upper part of the water column. Barnett and Jahn (in press) distinguished nearshore and offshore assemblages of zooplankton, with the change occurring at about the 30-m isobath. Nearshore taxa shifted slightly seaward in spring and summer at the San Onofre transect (Barnett and Jahn, in press), a phenomenon that may be related to the shift of biomass peaks noted above. Other studies of mysids, copepods, ctenophores, and fish larvae have also found large abundance peaks within 10 km of the coastline (e.g., Clutter 1967; Barnett 1974; Hirota 1974; Barnett et al. 1984).

Failure of Bernal and McGowan (1981) to see a nearshore zooplankton maximum was probably caused by the close proximity of the abundance peak to the shore and the offshore location of "nearshore" CalCOFI stations. CalCOFI stations nearest the shore (in Smith 1971), used by Bernal and McGowan (1981) as a test of an inshore zooplankton peak, appear to be in 200 m of water, well offshore of waters shown here and elsewhere to be strongly influenced by shelf processes.

The nearshore zooplankton biomass peak that we observed, and other nearshore distribution patterns cited above are probably the combined result of recycling and vertical mixing in shallow water that keeps nutrients available in the euphotic zone and increases phytoplankton growth, relative to that of deeper waters. Mesoscale hydrographic processes in offshore waters, such as seasonal upwelling and storm-induced mixing, transport nutrients from deep water into the euphotic zone throughout the bight, and local upwelling increases nutrients on the shelf at times when offshore waters may remain stratified. Once nutrients have been mixed or advected onto the shelf, turbulent mixing and recycling probably maintain higher nutrient concentrations in the shallow waters, increasing the standing stock of plankton (Walsh 1981).

Bightwide Coherence of Processes

Results from our nearshore cruises, and long-term (20-63 years) temperature records from shore stations between Gaviota and San Diego (Jones 1971; Tekmarine 1983; E. Stewart, pers. comm.) indicate that nearshore continental shelf waters usually show coherent patterns throughout the Southern California Bight, except near headlands. Delayed warming occurs at major headlands throughout the bight, particularly at Point Conception, Port Hueneme-Point Dume, and Palos Verdes Peninsula (Tekmarine 1983; this study). Local upwelling near headlands, which is particularly active during spring and summer (Roden 1972; Dorman and Palmer 1981; Huyer 1983), brings cool water to the surface in these areas and may produce slower warming of the surface layer. List and Koh (1976) analyzed shore temperatures collected between Neah Bay, Washington, and La Jolla, California, with most stations being in the Southern California Bight. Data were separated into three frequency components identified as low (seasonal; several months), intermediate (two weeks to one season), and high (less than two weeks). Seasonal and intermediate time-scale temperature events were highly correlated in southern California, with many temperature phenomena occurring almost simultaneously at stations throughout the bight. List and Koh (1976) did not observe slower spring warming at headlands because none of their stations were near major promontories. Occasional events within the intermediate temporal component had a smaller spatial scale on the order of 200 km. High-frequency phenomena tended to be local and were most likely associated with internal waves (Winant 1974) or wind (Cairns and La Fond 1966).

CONCLUSION

Oceanic, mesoscale, and local processes combine within the Southern California Bight to produce the physical and nutrient conditions observed in the nearshore zone. Basin-wide phenomena like the 1982-83 El Niño affect waters throughout the bight, although local processes such as coastal upwelling occasionally seem to dominate in the nearshore zone, resulting in "normal" hydrographic conditions at certain locations during a large-scale anomalous period. Mesoscale upwelling forced by strong offshore winds brings nutrient-rich water to the surface over large areas of the bight, including the nearshore waters. Such upwelling is a seasonal phenomenon, being most intense in spring and early summer. Local upwelling, often observed near headlands, has been observed at other times of the year, however, and greatly changes nearshore conditions and gradients. Nearshore mixing of waters from depth by tidal action and internal waves also brings important nutrients into the euphotic zone and increases production compared to waters farther from the coastline. Longshore advection may also enhance phytoplankton populations through higher nutrient levels and may cause increased nearshore productivity compared to productivity on the outer continental shelf and areas farther offshore. These observations and other studies from the nearshore zone suggest that physical processes often distinguish "nearshore" waters from "offshore" waters.

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ABUNDANCE OF SOUTHERN CALIFORNIA NEARSHORE ICHTHYOPLANKTON: 1978-1984

ROBERT J. LAVENBERG, GERALD E. McGOWEN,
ANDREW E. JAHN, JAMES H. PETERSEN
Los Angeles County Natural History Museum
Section of Fishes
900 Exposition Boulevard
Los Angeles, California 90007

TERRY C. SCIARROTTA
Southern California Edison
System Planning and Research
P.O. Box 800
Rosemead, California 91770

ABSTRACT

More than 150 ichthyoplankton taxa were collected in the nearshore zone of the Southern California Bight between 1978 and 1984. Aspects of the abundance patterns of six taxa of sport and commercial value in the nearshore zone are presented: northern anchovy (*Engraulis mordax*), which constituted 67% of total larvae; white croaker (*Genyonemus lineatus*), 6.6%; Pacific sardine (*Sardinops sagax*), 5.9%; queenfish (*Seriphus politus*), 2.1%; California halibut (*Paralichthys californicus*), 1.0%; and sea basses (*Paralabrax* spp.), 0.6%.

Greatest abundances of northern anchovy larvae occurred along the 75-m isobath, whereas larvae of the other fishes occurred chiefly from 36-m shoreward. Northern anchovy, white croaker, and California halibut spawned all year, but most intensely in late winter and spring. Queenfish spawned mainly in spring and summer, Pacific sardine chiefly in late summer and fall, and sea basses of the genus *Paralabrax* only in summer. Abundance of sardine eggs and larvae increased by 2-3 orders of magnitude between 1980 and 1982.

RESUMEN

Más de 150 taxa de ictioplancton fueron colectados en la zona costera de la Bahía del Sur de California entre 1978 y 1984. Se presentan los patrones de abundancia de seis taxa de importancia recreativa y comercial: *Engraulis mordax* (anchoveta del Norte) constituyó el 67% de las larvas presente; *Genyonemus lineatus*, 6.6%; *Sardinops sagax* (sardina), 5.9%; *Seriphus politus*, 2.1%; *Paralichthys californicus* (lenguado), 1.0%; y *Paralabrax* spp., 0.6%.

Las mayores abundancias de larvas de la anchoveta del Norte fueron encontradas a 75 m de profundidad y las otras larvas a 36 m de profundidad. La anchoveta del Norte, *Genyonemus lineatus*, y *Paralichthys californicus* desovaron durante todo el año y más intensamente a fines de invierno y en primavera. *Seriphus politus* desovó principalmente en primavera y verano, la sardina a fines de verano y en otoño, y el género *Paralabrax* sólo en verano. La abundancia de huevos y larvas de sardina aumentó 2 a 3 órdenes de magnitud entre 1980 y 1982.

INTRODUCTION

Systematic sampling for fish eggs and larvae in the waters off California has been conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) for more than three decades. One of the primary purposes for conducting these surveys is to draw conclusions about the abundance of adult fish populations and their distribution at the time of spawning, which can be determined from the distribution and abundance of the larval stages. Larval rather than adult stages are used because they can be sampled with less cost and fewer biases (Ahlstrom 1965, 1967).

CalCOFI surveys in the Southern California Bight have principally been conducted in offshore waters, and have emphasized distributions and abundances of offshore, commercially important fishes, e.g., northern anchovy (*Engraulis mordax*), hake (*Merluccius productus*), and jack mackerel (*Scomber japonicus*) (Ahlstrom 1965; Loeb et al. 1983). A two-year study by Gruber et al. (1982) entailed quarterly sampling of three transects from the inner shelf (<50 m) out to deep water (>1,000 m), providing a preliminary look at the abundance and seasonality of shelf species. Our surveys, begun in 1978 (Brewer et al. 1981), are coastal and bightwide in scope (Brewer and Smith 1982), and like that of Barnett et al. (1984) provide data to assess medium-to-long-term temporal and spatial patterns of fishes on the continental shelf. Some species—e.g., white croaker (*Genyonemus lineatus*) and queenfish (*Seriphus politus*)—absolutely depend on nearshore waters. Other fishes occur in both offshore and nearshore regions (e.g., northern anchovy and Pacific sardine [*Sardinops sagax*]); knowledge of the distribution, abundance, and interannual variation of their larvae in coastal waters will allow evaluation of the nearshore region as a potential area for spawning and larval survival.

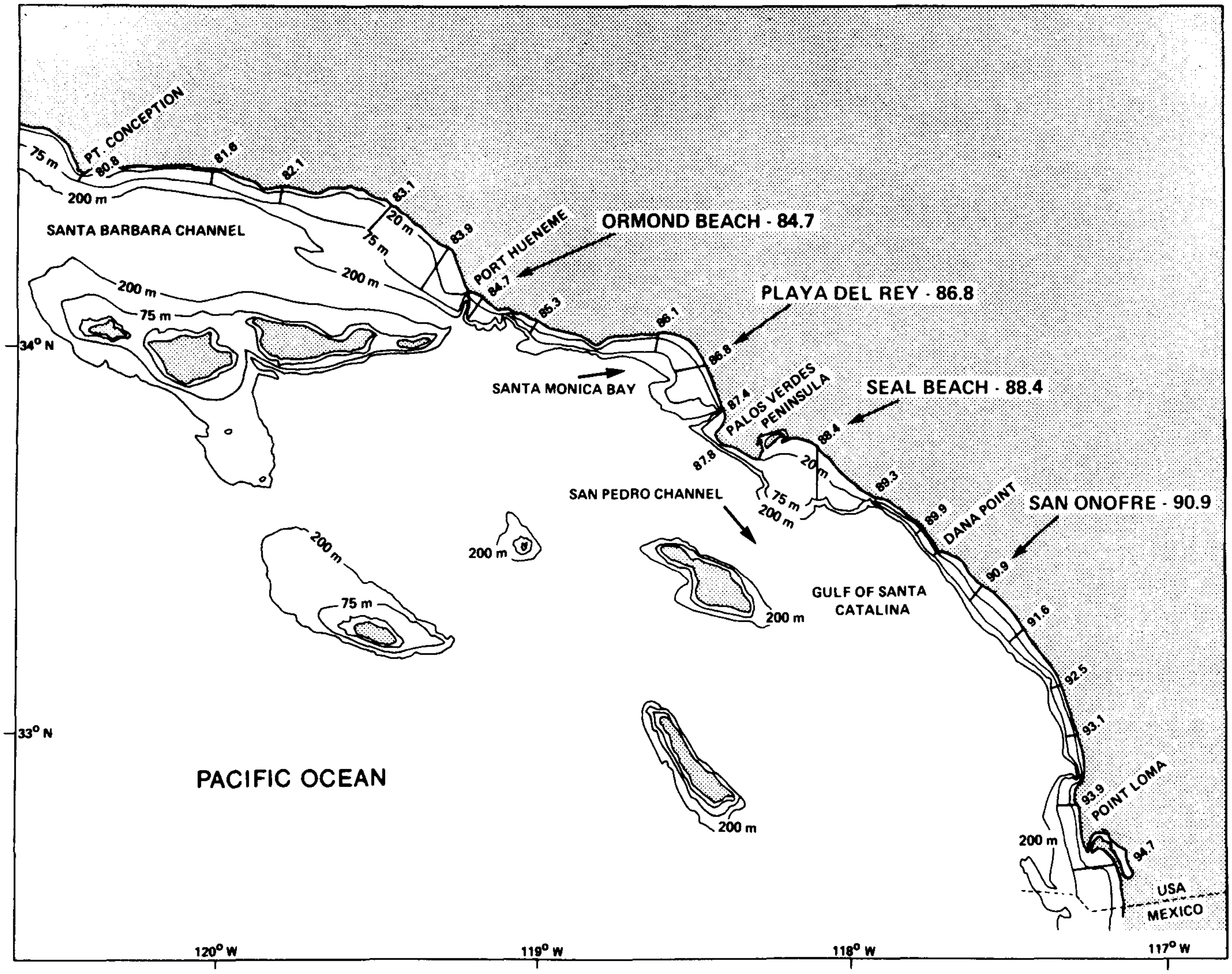

Figure 1. Location and CalCOFI line-number designations for all transects sampled between 1978 and 1984 in the Southern California Bight.

This report presents bightwide estimates of egg and larval abundance for the dominant nearshore species, northern anchovy and Pacific sardine; and larval abundance only for white croaker, queenfish, California halibut (*Paralichthys californicus*), and sea basses —which include kelp bass (*Paralabrax clathratus*), barred sand bass (*Paralabrax nebulifer*), and spotted sand bass (*Paralabrax maculatofasciatus*). Longshore and cross-shelf patterns of distribution, interannual variation, and seasonality of abundance are described. Concurrent with the egg and larval surveys, physical, nutrient, and zooplankton biomass data were collected and analyzed (Petersen et al. 1986).

METHODS

Field techniques and laboratory procedures for samples taken between June 1978 and July 1980 (cruises 1 to 26) are described by Brewer and Smith (1982). Ichthyoplankton studies in the coastal zone resumed in 1981 after a 7-month hiatus. The 1981 collections have not been worked up. Many aspects of the earlier program (1978-80) have remained unchanged, although cruises were taken every two months in 1982-84 (cruises 34 to 52), replacing the monthly sampling of 1979-80. Sampling dates and locations are presented in Figure 1 and Tables 1 and 2.

For compatibility, transect designations previously identified by numbers and letters were changed to CalCOFI line numbers, a change made retroactive to 1978 in this report. Sampling protocols are as described by Brewer and Smith (1982), except that when the *Vantuna* began collecting in 1982 the use of the instrumented trawl block and depth transducer was discontinued. All data treated here are from oblique tows of a 70-cm bongo sampler (333-μ mesh) fitted with wheels so that tows started right at the bottom (gauged by vibrations transmitted through the towing wire), a known layer of concentration of certain taxa

TABLE 1
Coordinates of Stations Occupied During 1982-1984

Transect (CalCOFI line)	Station (m)	N. Latitude	W. Longitude
Ormond Beach	8	34°07.5′	119°16.6′
(84.7)	15	34°07.0′	119°11.0′
	22	34°06.6′	119°11.7′
	36	34°06.0′	119°12.8′
	75	34°04.5′	119°11.9′
Playa del Rey	8	33°57.0′	118°27.1′
(86.8)	15	33°57.0′	118°27.9′
	22	33°56.9′	118°28.6′
	36	33°57.0′	118°30.1′
	75	33°57.2′	118°34.0′
Seal Beach	8	33°42.4′	118°04.3′
(88.4)	15	33°41.2′	118°04.8′
	22	33°39.6′	118°05.1′
	36	33°37.3′	118°05.7′
	75	33°34.8′	118°08.9′
San Onofre	8	33°21.7′	117°33.8′
(90.9)	15	33°20.9′	117°34.1′
	22	33°20.4′	117°34.7′
	36	33°19.9′	117°35.0′
	75	33°18.5′	117°35.6′

TABLE 2
Dates of Collection, Cruises 1-52

Cruise no.	Month and year	Cruise no.	Month and year
Monthly programs (10 transects)			(20 transects)
1	June 1978	15	August 1979
2	July 1978	16	September 1979
3*	August 1978	17	October 1979
4	September 1978	18	November 1979
5	October 1978	19	December 1979
6*	November 1978	20	January 1980
7	December 1978	21	February 1980
8	January 1979	22	March 1980
9*	February 1979	23	April 1980
10	March 1979	24	May 1980
11	April 1979	25	June 1980
12*	May 1979	26	July 1980
13*	June 1979		
14*	July 1979		
Bimonthly program (4 transects)			
34	February 1982 (January 30)		
35	March-May 1982 (31-11)		
36	June 1982		
37	August 1982		
38	October 1982		
39	December 1982		
40	February 1983		
41**	March 1983		
42	April 1983		
43	June 1983		
44	August 1983		
45	October 1983		
46	December 1983		
47	February 1984		
48	April 1984		
49	June 1984		
50	August 1984		
51	October 1984		
52	December 1984		

*Collections not worked up
**Nonstandard cruise

(Schlotterbeck and Connally 1982; Barnett et al. 1984). Net retrieval rates were about twice those employed from August 1979 to July 1980 (Phase II sampling as described by Brewer and Smith 1982), but replicates were not combined, i.e., the nets filtered about 6-8 m^3 of water per meter of depth. Procedures and assumptions for processing fish eggs and larvae were the same as those described by Brewer and Smith (1982), except that no aliquots were taken. Samples were 100% sorted from either the port or starboard side of the bongo plankton sampler.

Species of the genus *Paralabrax* are not separable at all stages (Butler et al. 1982) and have therefore been treated together as a single taxon. However, progress has been made in the identification of *Paralichthys californicus* larvae[1], and the abundance of this species as reported here is for the first time uncontaminated with that of the similar *Xystreurys liolepis*.

Areal Estimates

The transects sampled during this project are assumed to be representative of the coastal zone shoreward of 75 m in the Southern California Bight. Thus an estimate of the magnitude of ichthyoplankton populations in the narrow band of nearshore waters along the coast can be based on data from these transects.

The Apple Graphics Tablet was used to determine the areas bounded by depth contours on National Ocean Survey bathymetric maps (nos. 1306N-15, -16, -19, and -20). The maps were juxtaposed, and a composite made that had 10-m intervals out to 100 m. The 75-m contour was drawn in (Figure 1). We drew the 20 sampling transects approximately perpendicular to the 75-m contour, then drew lines perpendicular from the midpoints between the intersections. The latter set of lines defined 20 blocks, centered on the transects, on which all areal determinations were based. Block 1 (CalCOFI line 80.8 off Cojo Bay) was bounded on the northwest by a line extending from Point Conception perpendicular to the 75-m contour, and block 20 (CalCOFI line 94.7 off Imperial Beach)

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[1] Carlson-Oda, D. Description of the early life history of the California halibut, *Paralichthys californicus*, with comparisons to other members of the family Bothidae. Abstract presented at CalCOFI annual conference, 1985.

TABLE 3
Bightwide Estimates of Area in Square Kilometers

	Depth contours (in meters)							
Transects	0-10	10-20	20-30	30-40	40-50	50-60	60-75	Totals
80.8	11	19	11	11	10	13	15	90
81.6	14	18	11	13	13	26	52	147
82.1	20	16	11	11	14	33	46	150
83.1	27	30	40	73	59	42	58	329
83.9	14	69	94	34	11	9	15	246
84.7	11	25	19	16	10	8	8	97
85.3	13	18	10	12	7	13	18	91
86.1	18	26	18	21	16	21	16	136
86.8	11	16	16	15	20	37	33	148
87.4	11	13	9	8	5	6	12	64
87.8	26	22	18	12	12	5	9	104
88.4	35	75	114	54	39	28	16	361
89.3	11	17	7	5	6	7	3	56
89.9	12	10	6	9	6	10	7	60
90.9	29	37	18	12	11	15	20	142
91.6	20	31	14	12	7	9	12	105
92.5	11	14	3	7	5	6	9	55
93.1	12	12	11	6	10	7	9	67
93.9	12	17	17	3	9	16	28	102
94.7	30	65	38	38	29	22	24	246
Totals	348	550	485	371	299	333	410	2796

TABLE 4
Bightwide Estimates of Area (in km^2) for Sampling Depth Strata*

	Depth contours (in meters)					
Block number	0-8	8-15	15-22	22-36	36-75	Totals
1	88	120	137	258	549	1152
2	31	35	36	60	185	347
3	67	79	91	163	180	580
4	91	111	108	129	278	717
Totals	277	345	372	610	1192	2796

Block 1 comprises CalCOFI lines 80.8 (Cojo, 80); 81.6 (DR); 82.1 (Goleta, 81.5); 83.1 (RN); 83.9 (Ventura, 83); 84.7 (OB); 85.3 (Trancas, 85).
Block 2 comprises CalCOFI lines 86.1 (Malibu); 86.8 (PR, 87); 87.4 (RB).
Block 3 comprises CalCOFI lines 87.8 (PV); 88.4 (SB, 88); 89.3 (Balboa); 89.9 (Laguna, 90).
Block 4 comprises CalCOFI lines 90.9 (SO); 91.6 (Pendleton, 91); 92.5 (Carlsbad); 93.1 (Del Mar, 93); 93.9 (MB); 94.7 (San Diego, 95).
*based upon data from Table 3.

was bounded on the south by the Mexican border. The 20 blocks were combined into 4 bigger blocks representative of the four transects sampled in recent years. Areal determinations for sampling depth strata were determined by linear interpolation of the raw data (Tables 3 and 4).

The 1982-84 nearshore sampling zone is considered to extend from near Point Conception to the Mexican border and seaward from shore to the 75-m contour, an area of 2,796 km^2. Although the coastal part of the Southern California Bight includes almost all of the coastal portion of CalCOFI region 7, it constitutes about 4% of its total area. The 1978-80 area, which extends seaward only to the 36-m contour, has an area of 1,604 km^2. Brewer and Smith's (1982) estimate of 2,652 km^2 for the area to the 43-m isobath was obtained by extrapolating the average seaward distance of the stations along the 8-, 15-, 22-, and 36-m isobaths. We estimate the same area to be 1,834 km^2 based upon linear interpolation of actual measurements from charts of areas to the 40- and 50-m contours.

For analysis, all species data were scaled to numbers of individuals under 10 m^2 of sea surface (Smith and Richardson 1977). Confidence intervals on mean abundance for each cruise were determined by a nonparametric method known as the bootstrap (Efron 1982), which has been shown to be a reasonable approach for these data (Jahn MS). Temporal trends of abundance are presented graphically as extrapolated "bightwide" abundances, calculated as the mean of all stations to the 36-m contour multiplied by the 0-36-m area (1,604 km^2). For the years 1982-84 the mean 75-m abundance was multiplied by the area between 36 and 75 m (1,192 km^2) to estimate a bightwide abundance for this outer-shelf band.

The presentation of alongshore pattern is incomplete in that not all data sets were statistically analyzed. Plots showing the three-dimensional (alongshore, cross-shelf, time) disposition of all species and life stages were visually examined for obvious trends. Only when these plots showed obvious differences among transects were the data subjected to further analysis. In such cases, the effects of station depth, transect, and year were tested with 3-way ANOVA using log-transformed ($\ln\{x + 1\}$) scaled (no. per 10 m^2) abundance. Only the 1982-84 data were so treated, because earlier sampling designs were nonuniform. Seasonal effects were not tested, since these were readily apparent in all graphs. The ANOVA results are supported by the original three-dimensional plots as well as by graphs of mean annual transect abundance, expressed as number per m^2.

RESULTS

Over the seven-year period more than 1,400 zooplankton collections were sorted for fish eggs and larvae. Among these we identified 152 fish taxa (80 to species; 40 to genus, family, or order; 32 to an unknown fish type), which approaches 70% of the inshore fish fauna of the Southern California Bight. One

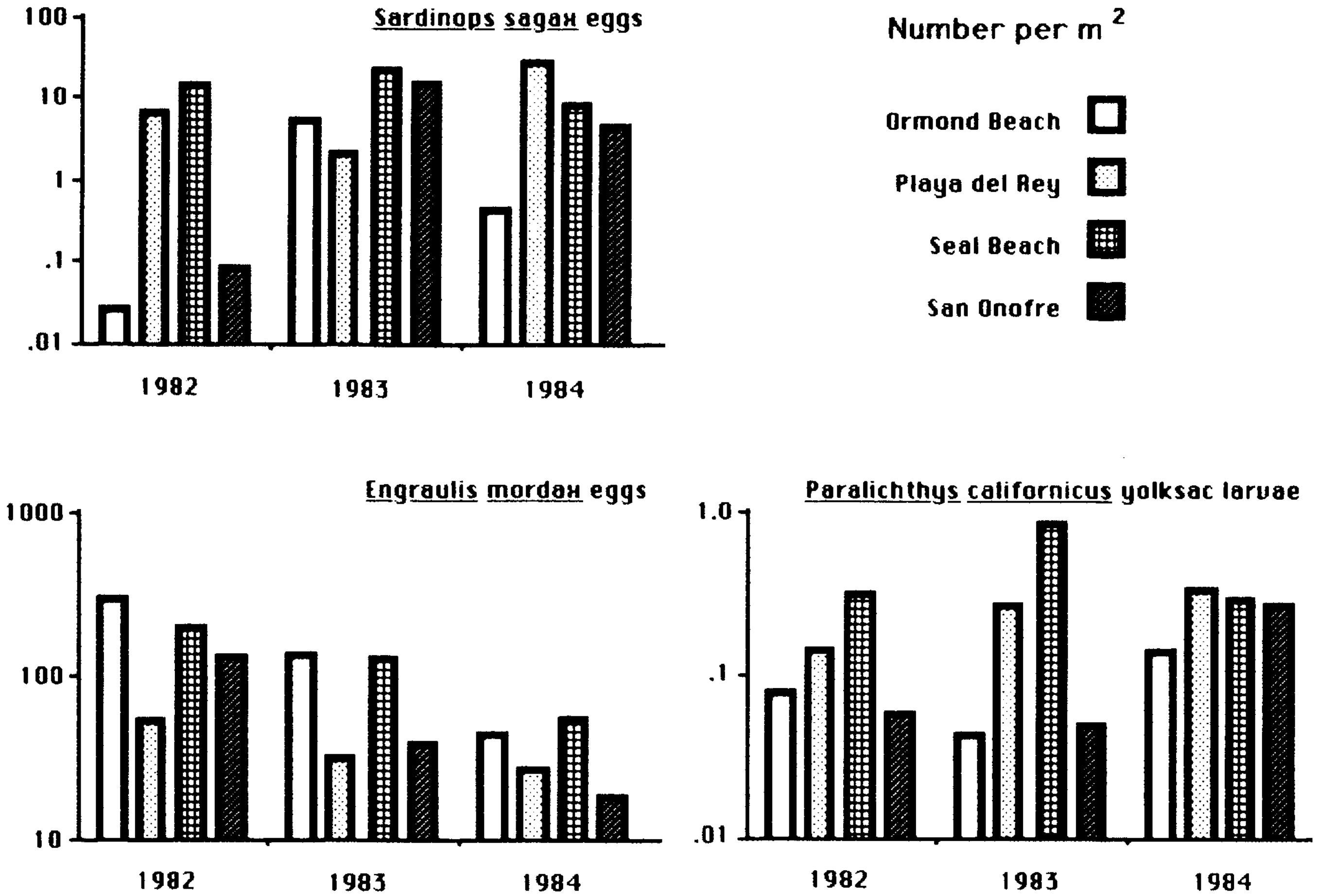

Figure 2. Mean annual transect abundance for eggs of *Sardinops sagax* and *Engraulis mordax*, and yolk-sac larvae of *Paralichthys californicus*, 1982-84.

planktivorous species that had not previously been sampled in our nearshore survey region, round herring (*Etrumeus acuminatus*), suddenly appeared in the samples in August 1983. Round herring larvae occurred in Santa Monica Bay and off Seal Beach in densities approaching 10 per m^2. There was also an unusually high number of unidentified larval types collected in 1983. Although the number of unidentified types subsided in 1984, *Etrumeus* larvae were noted again from June through October at the same locations and in about the same abundance as in 1983.

Northern anchovy always ranked first in abundance, and—except for 1984—white croaker was second. In 1978-79 sardine was not among the 15 most abundant taxa, but increased to third in 1982. Sardine remained third in 1983 before becoming the second most abundant taxon in 1984, replacing white croaker. Queenfish was steadily surpassed by other species, dropping from third most abundant in 1978-79 to fifth in 1984. Halibut consistently had a rank between fifth and seventh, while sea bass ranked between eighth and eleventh. In the following sections these six important species are discussed in some detail.

As stated above, we visually inspected abundance plots of all species and life stages for indications of differences among transects. In most cases, there were no apparently nonrandom differences in abundance among transects. Exceptions were early stages of three species—eggs of sardine, eggs and yolk-sac larvae of anchovy, and yolk-sac larvae of halibut. Eggs of sardine and anchovy, and yolk-sac larvae of halibut were therefore tested and found to show statistically significant depth (station location) and transect or years × transect "effects" (Table 5). These are discussed below in the species accounts. Mean yearly transect abundance (Figure 2) supports our initial impression that spawning of these three species tends to be above average at Seal Beach, and spawning of anchovy is above average at Ormond Beach.

In the species accounts, the mean abundance of larvae for each cruise is scaled up to the area of nearshore habitat with the implicit assumption that the mean abundance at the sampled locations is representative of the Southern California Bight's entire nearshore zone. The validity of this assumption is presently under scrutiny, and no defense for it is offered here.

TABLE 5
Results of Three-Way ANOVAs

	Factor						
	Depth (D)	Year (Y)	Transect (T)	D × Y	D × T	Y × T	D × Y × T
Sardine eggs	***	—	—	NS	NS	*	NS
Anchovy eggs	*	—	—	NS	NS	*	NS
Halibut yolk-sac larvae	***	NS	***	NS	NS	NS	NS

NS Not significant at $P = .05$; * $P < .05$; *** $P < .001$; -*f*-ratio not tested because of significant first-order interaction effect involving this factor.

However, given that the 20 to 46 collections from each cruise can serve as a random sample to estimate the bightwide population mean, the precision of such estimates can be easily addressed. The bootstrapped confidence intervals (Table 6) suggest that the estimated populations could be low by a factor of 1/2 or high by a factor of generally 2 to 5, depending on abundance.

Sardinops sagax

Pacific sardine (*Sardinops sagax*) dramatically increased in numbers in the bight between 1980 and 1982 (Figure 3). The expansion of the sardine population may have begun in 1981, but no data are available from that year. The order-of-magnitude increases of sardine larvae in the spring and fall of 1982 compared to 1979-80 signal the presence of many spawning adults. Between 1982 and 1984 sardine were seasonal spawners in the bight, eggs and larvae being most abundant in summer-fall. After the 1982 expansion, annual abundance of larval sardine remained relatively constant (Figure 3).

Abundances and average densities of sardine eggs were low off Ormond Beach in the north and San Onofre in the south, particularly in 1982 (Figures 2 and 4). High numbers of eggs were consistently recorded off Seal Beach, where they were taken in all of our samples, except for February 1984. In 1982 and 1983 sardine spawning appears to have been concentrated at the Seal Beach transect (Figure 2), and closer inshore than offshore (Figure 4). The significant year-by-transect interaction (Table 5) for sardine egg densities

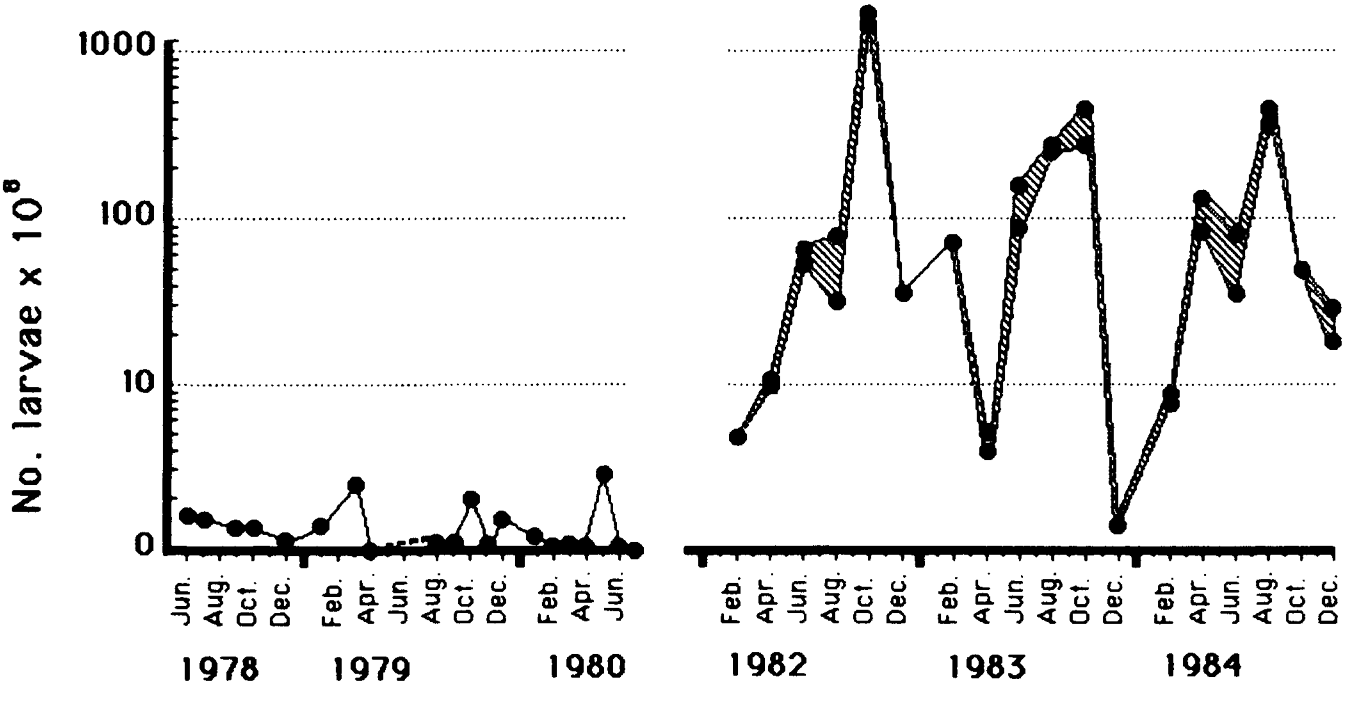

Figure 3. Estimated abundance of Pacific sardine (*Sardinops sagax*) larvae in the Southern California Bight between the shore and the 36-m contour (1978-80 data, and lower line of 1982-84 data). Hatched area represents abundance between the 36- and 75-m contour (1982-84 only). There are no data for 1981.

TABLE 6
Means with Confidence Limits of 2.5 and 97.5 Percentage Points of Bootstrapped Means, no./10m^2, Based on 1,000 Runs

	Sardinops sagax		*Engraulis mordax*		*Paralabrax* spp.		*Genyonemus lineatus*		*Seriphus politus*		*Paralichthys californicus*	
Cruise	Mean	2.5-97.5%	Mean	2.5-97.5%	Mean	2.5-97.5%	Mean	2.5-97.5%	Mean	2.5-97.5%	Mean	2.5-97.5%
1 1978	1.0	.2-2.1	246	143-381	.7	.01-1.5	.1	.01-.2	34	16-58	(Cruises 1-33: data not available)	
2	.6	.01-1.7	92	52-143	2.6	.4-5.6	.1	.01-.3	89	45-143		
4	.4	.1-.9	123	71-188	22	12-34	23	7-43	41	20-70		
5	.4	.1-.9	164	73-303	.6	.18-1.0	44	12-89	2.2	.7-4.1		
7	.1	.01-.4	310	185-465	.1	.01-.2	75	46-109	0	-		
8 1979	.4	.1-.9	254	176-336	0	-	165	69-280	0	-		
10	1.6	.3-3.4	663	406-987	0	-	358	190-555	2.7	1.2-4.7		
11	0	-	832	375-1438	0	-	27	15-43	22	5-50		
15	1.7	.4-3.9	137	90-193	29	16-45	.1	-	27	18-39		
16	2.8	1.4-4.7	134	77-213	2.4	1.1-4.2	4.4	1.7-7.9	29	17-44		
17	14	5-28	29	19-43	0	-	9.7	5.7-14.2	.6	.3-1.3		
18	1.8	.7-3.0	14	5-25	0	-	17	7-29	0	-		
19	4.0	1.3-7.2	63	35-97	0	-	156	76-267	0	-		
20 1980	2.4	1.1-4.2	511	274-784	0	-	324	178-490	0	-		
21	.3	.1-.6	722	460-1029	0	-	182	110-273	.3	.1-.6		
22	1.0	.4-1.8	1378	1013-1778	0	-	991	603-1431	70	38-108		
23	1.1	.2-2.4	368	271-481	0	-	290	171-443	43	27-61		
24	16	1-46	172	100-264	.2	.01-.5	46.6	10-103	30	19-46		
25	.4	.1-.9	62	36-96	0	-	3.2	.9-6.3	19	9-31		
26	0	-	16	10-23	0	-	.3	.1-.7	25	14-37		
34 1982	2.4	.1-5.8	2900	1870-4100	0	-	269	159-396	.4	.01-1.1	12	7-18.1
35	4.0	1.6-7.0	2065	1490-2730	1.2	.1-3.2	211	84-361	229	42-477	30.0	12-54
36	28	7-60	668	307-1131	27	16-40	5.2	2.1-8.9	58	22-106	8.7	1.4-18.5
37	24	9-45	322	202-459	23	4-51	1.5	.2-3.1	8.2	3.7-14.7	3.5	1.3-6.5
38	381	115-725	307	195-439	0	-	43	22-66	.8	.2-1.9	15	6-28
39	19	3-45	50	24-81	0	-	136	17-293	0	-	5.9	2.1-11.2
40 1983	36	2-83	1754	670-2920	0	-	346	143-633	23	4-48	54	24-95
42	3.5	1.0-7.1	2242	1280-3360	.2	.01-.5	58	24-102	4.6	1.6-8.0	4.8	1.8-8.6
43	54	11-113	130	82-193	28	13-45	4.8	.3-11.7	40	14-73	2.2	.6-4.1
44	125	65-201	55	23-102	9.7	3.2-16.9	.1	.01-.4	1.9	.4-3.7	3.7	1.7-6.0
45	168	67-300	127	57-207	0	-	.1	.01-.5	2.6	.8-5.2	3.2	.3-7.4
46	.7	.01-1.5	301	182-437	0	-	29	9-54	0	-	3.8	.4-9.0
47 1984	4.0	1.2-7.2	1514	580-2830	0	-	71	42-106	.9	.01-2.1	17	11-25
48	52	17-97	1625	870-2510	.3	.01-.9	47	28-71	32	18-50	26	10-49
49	30	9-58	130	73-190	6.0	2.3-10	.2	.01-.7	31	16-52	2.6	1.0-4.5
50	211	78-383	114	66-173	39	22-56	1.9	.1-4.8	30	9-58	4.6	1.7-8.2
51	26	6-59	58	26-96	.7	.01-.9	4.6	.4-9.1	.7	.01-1.6	2.1	.1-5.6
52	8.2	2.8-14.7	185	45-404	0	-	142	71-224	0	-	2.6	.3-6.0

can be seen in Figure 2. Spawning was greatest in Santa Monica Bay during 1984 but reached maxima at Seal Beach and San Onofre in 1983.

Sardine larvae occurred in nearshore rather than offshore waters (Figure 3). Sardine appeared to spawn onshore, for their eggs were found inside of 75 m. There was a significant effect of station depth upon egg density during 1982-84 (Table 5). During this 3-year period, average density of eggs at the 75-m station was 12.7 eggs per m^2, but it increased to 195.3 per m^2 at the 8-m isobath.

Engraulis mordax

Northern anchovy (*Engraulis mordax*) larvae were present year-round in the bight, and showed a consistent winter-spring pattern of high abundance (Figure 5). The significant year-by-transect interaction (Table 5) is probably due to the unusually intense spawning off San Onofre in April 1982 (Figure 6). Of the four transects, San Onofre in the south had the lowest mean annual abundances through time, followed closely by Playa del Rey (Figures 2 and 6). Anchovy yolk-sac larvae showed a bightwide pattern similar to that described for the eggs: high at Ormond Beach and low at Playa del Rey and San Onofre. There was no indication of longshore pattern after yolk-sac absorption.

Abundances of larval northern anchovy increased with depth. Brewer and Smith (1982) demonstrated that the number of northern anchovy larvae increased linearly with increasing depth to 36 m. Our data show a substantial contribution to the total larvae seaward of the 36-m contour (Figure 5), in keeping with earlier observations.

Although mean annual anchovy egg abundance at the four transects declined steadily from 1982 to 1984 (Figure 2), the peak annual abundance of larvae in the nearshore waters of the bight has been relatively constant from 1978 through 1984 (Figure 5).

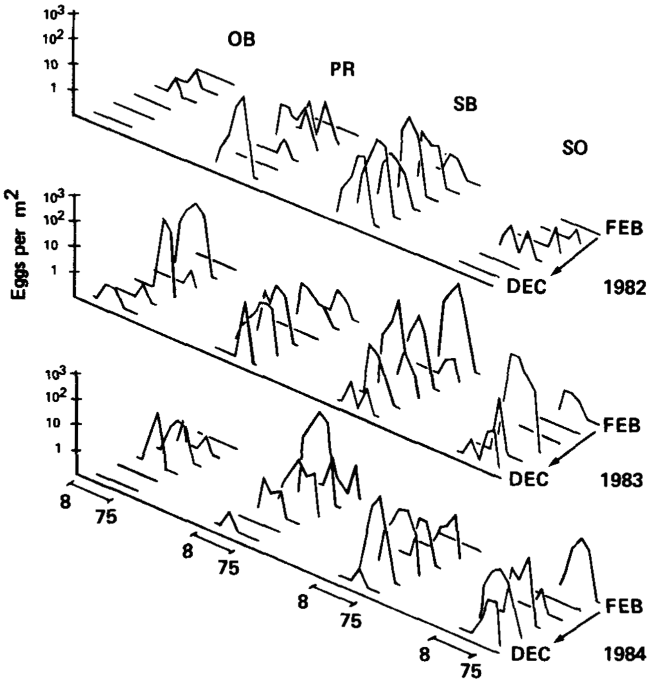

Figure 4. Density of Pacific sardine eggs at Ormond Beach (OB: transect 84.7), Playa del Rey (PR: transect 86.8), Seal Beach (SB: transect 88.4), and San Onofre (SO: transect 90.9), 1982-84. Each graph shows a year of bimonthly sampling at all four transects, with density at 8, 15, 22, 36, and 75 m plotted left to right. For continuity, each individual plot begins and ends on the baseline, but zero density at 8 and 75 m is always represented by a short segment parallel to the baseline; e.g., February through August 1984 75-m densities at San Onofre were zero, but the October and December values were not *(lower right)*.

Paralabrax *spp.*

Larvae of sea basses (*Paralabrax* spp.) were the most seasonal among the six taxa discussed here. The major spawning effort of sea bass began in early summer and peaked in August (Figure 7). During the period of peak abundance, larval *Paralabrax* were found throughout the bight. Smith and Young (1966) found that *P. clathratus* began to mature in April and had ripe eggs and sperm from June through September. Little or no spawning was detected in June and July 1980, when exceptionally cool temperatures prevailed (Petersen et al. 1986). *Paralabrax* spawns mostly inside the 36-m contour (Figure 7).

Genyonemus lineatus

White croaker (*Genyonemus lineatus*) larvae, like northern anchovy, were present year-round but most abundant in winter-spring (Figure 8). Spawning centered on March agrees with data on gonad maturation (Love et al. 1984). Love et al. (unpublished) show a strong correlation between the numbers of larvae and the numbers of trawl-caught adults in this species. The small contribution of the 75-m stations to total larvae is consistent with the general pattern of nearshore spawning in white croaker (Barnett et al. 1984; Love et al. 1984).

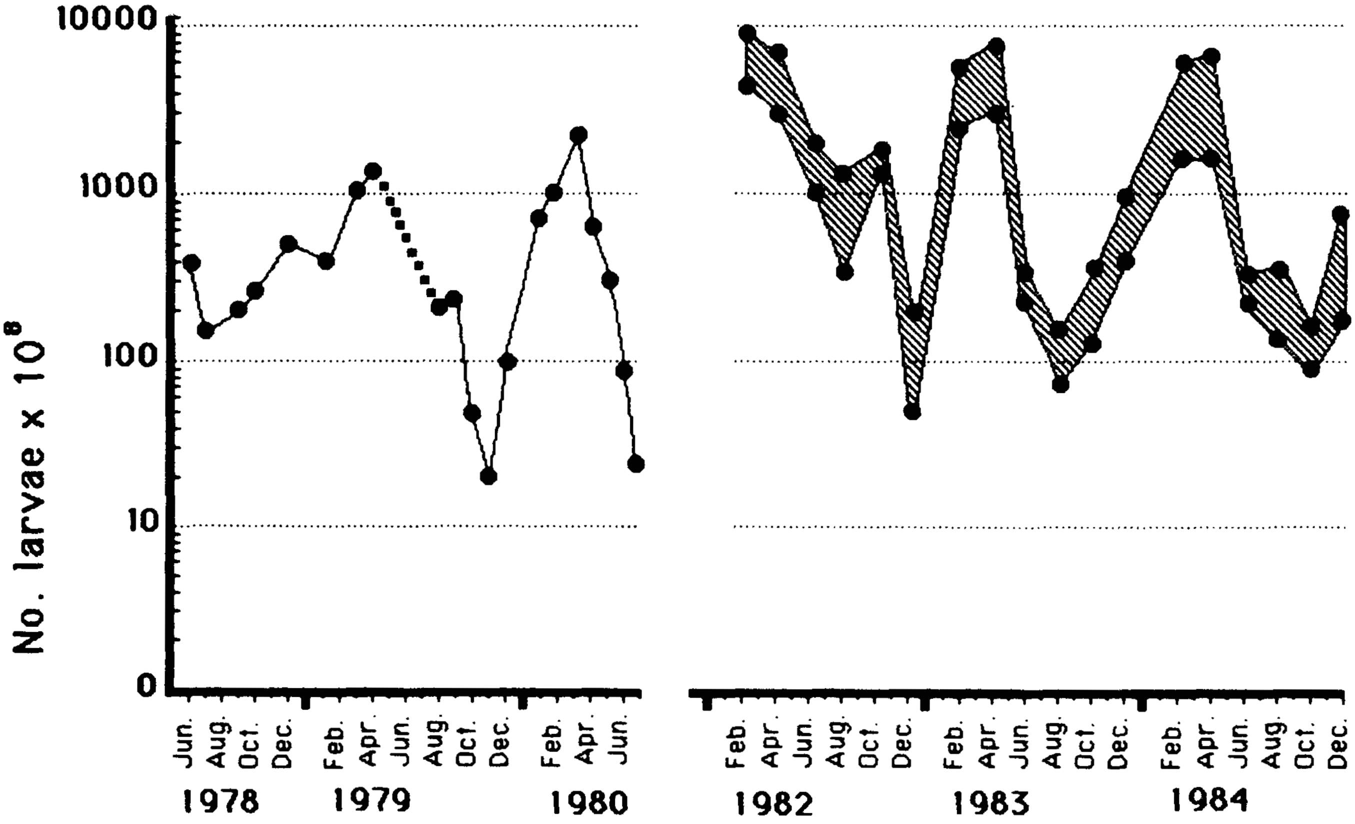

Figure 5. Estimated abundance of northern anchovy (*Engraulis mordax*) larvae, 1978-84. See legend of Figure 3.

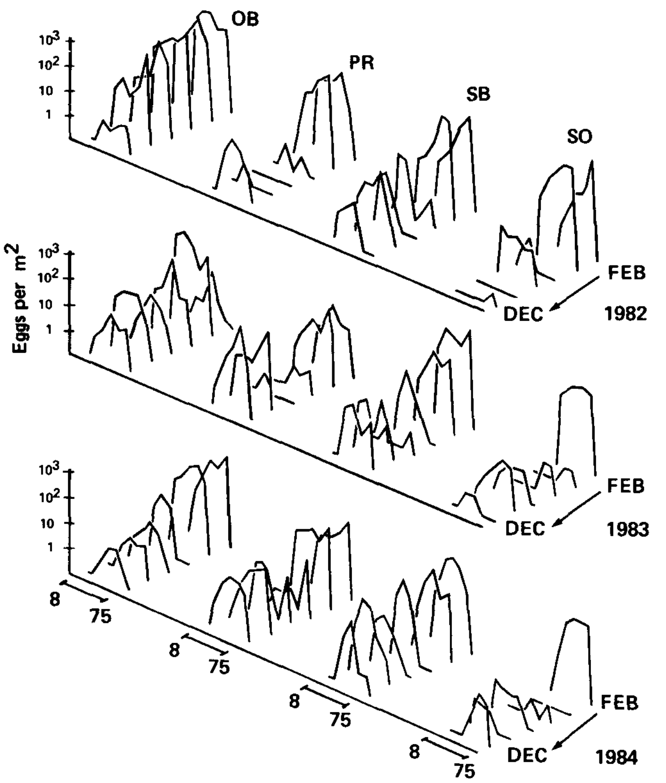

Figure 6. Density of northern anchovy (*Engraulis mordax*) eggs, 1982-84. See legend of Figure 4.

Seriphus politus

Queenfish (*Seriphus politus*) larvae were abundant mainly in spring-summer (Figure 9). Annual abundance was quite similar in all six spawning seasons represented here, the peak in April 1982 being mostly due to high abundance at a single transect (Ormond Beach). Although queenfish spawn during nocturnal seaward migrations (DeMartini et al. 1985), their larvae were distributed about as near shore as any (Figure 9; see also Barnett et al. 1984).

Paralichthys californicus

California halibut (*Paralichthys californicus*) larvae were found year-round in the bight, showing a consistent winter-spring pattern of high abundance (Figure 10). Halibut spawning appeared to be concentrated in the central bight at Seal Beach, especially in 1983 when larval abundance at the other transects was particularly low (Figures 2 and 11). The summer minimum of spawning effort was apparent throughout the bight. *P. californicus* spawns mainly inshore of the 75-m contour, as evidenced by the highly significant (Table 5) station-depth effect on distribution of yolk-sac larvae (Figure 11) and the low contribution of larval abundance at 75-m to the total (Figure 10).

DISCUSSION

Five taxa (*Sardinops*, *Paralabrax*, *Genyonemus*, *Seriphus*, *Paralichthys*) predominantly occurred inside 36 m, and only one offshore beyond 36 m (*Engraulis*). Though longshore pattern was not a strong feature of these data, there were indications that Seal Beach was a somewhat special place. The 1982 resurgence of sardine was centered at the Seal Beach transect; anchovy spawning was consistently intense there; and the contracted spawning of halibut in 1983

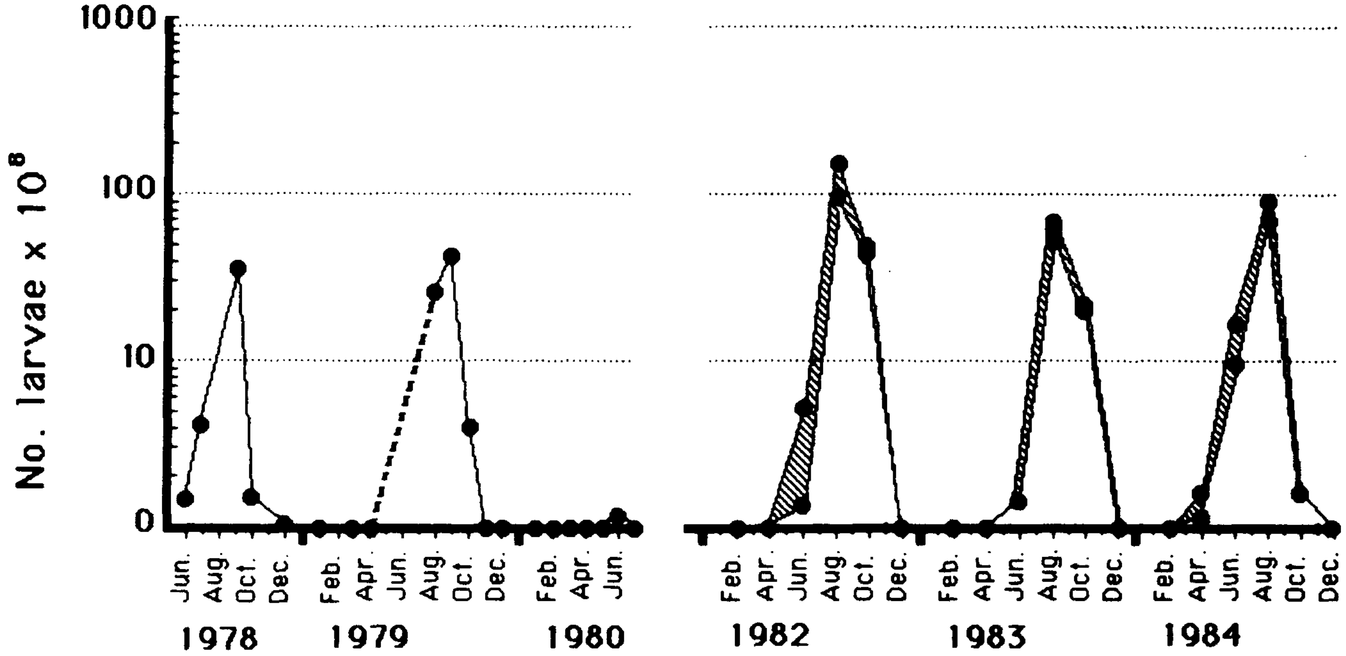

Figure 7. Estimated abundance of sea basses (*Paralabrax* spp.) larvae, 1978-84. See legend of Figure 3.

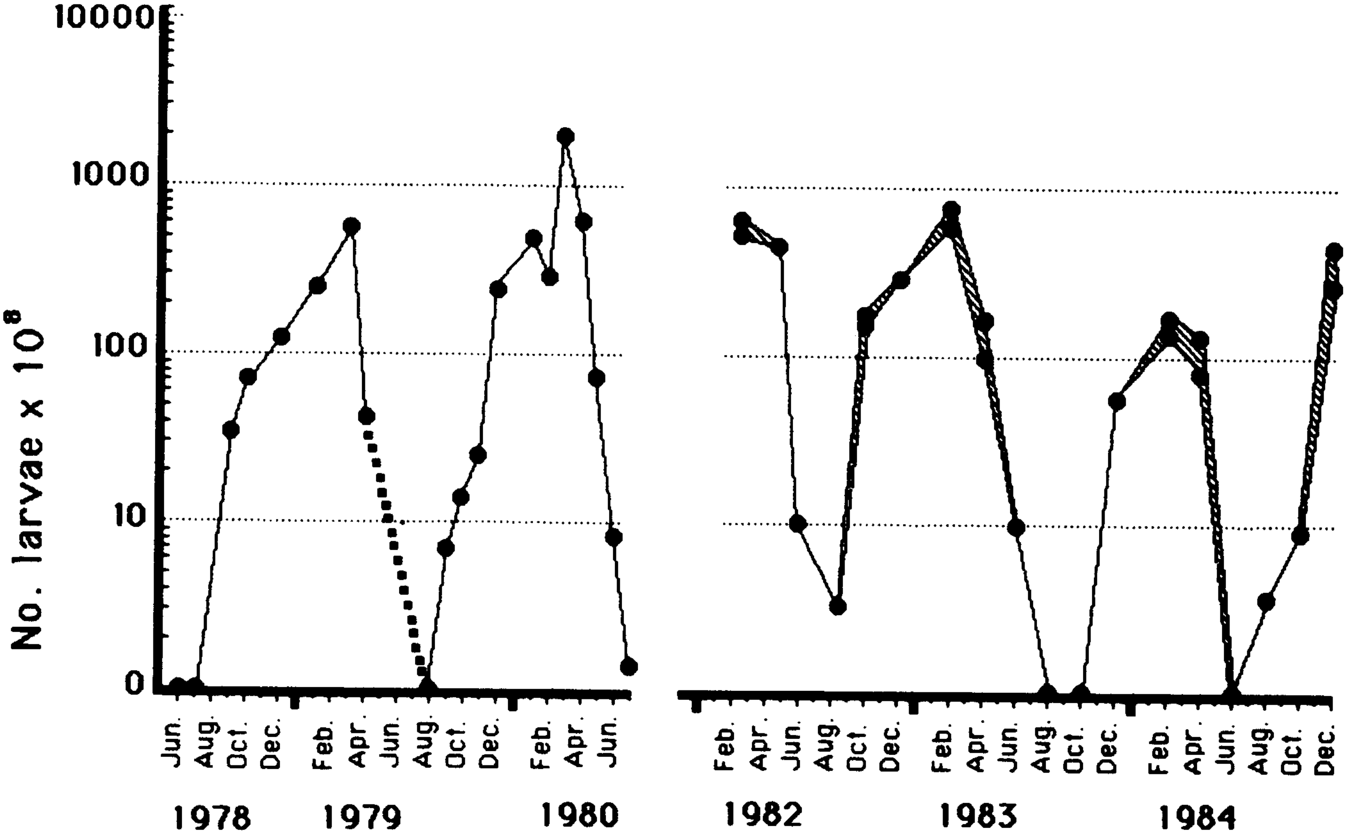

Figure 8. Estimated abundance of white croaker (*Genyonemus lineatus*) larvae, 1978-84. See legend of Figure 3.

was concentrated in this area, in the lee of the Palos Verdes Peninsula. Although northern anchovy is a wide-ranging, common, planktivorous fish that spawns extensively in the bight, its effort in the south off San Onofre is poor. Barnett et al. (1984) remarked on the low abundances of *E. mordax* eggs off San Onofre, concluding that the large number of excess larvae must come from outside the sampling area. Our

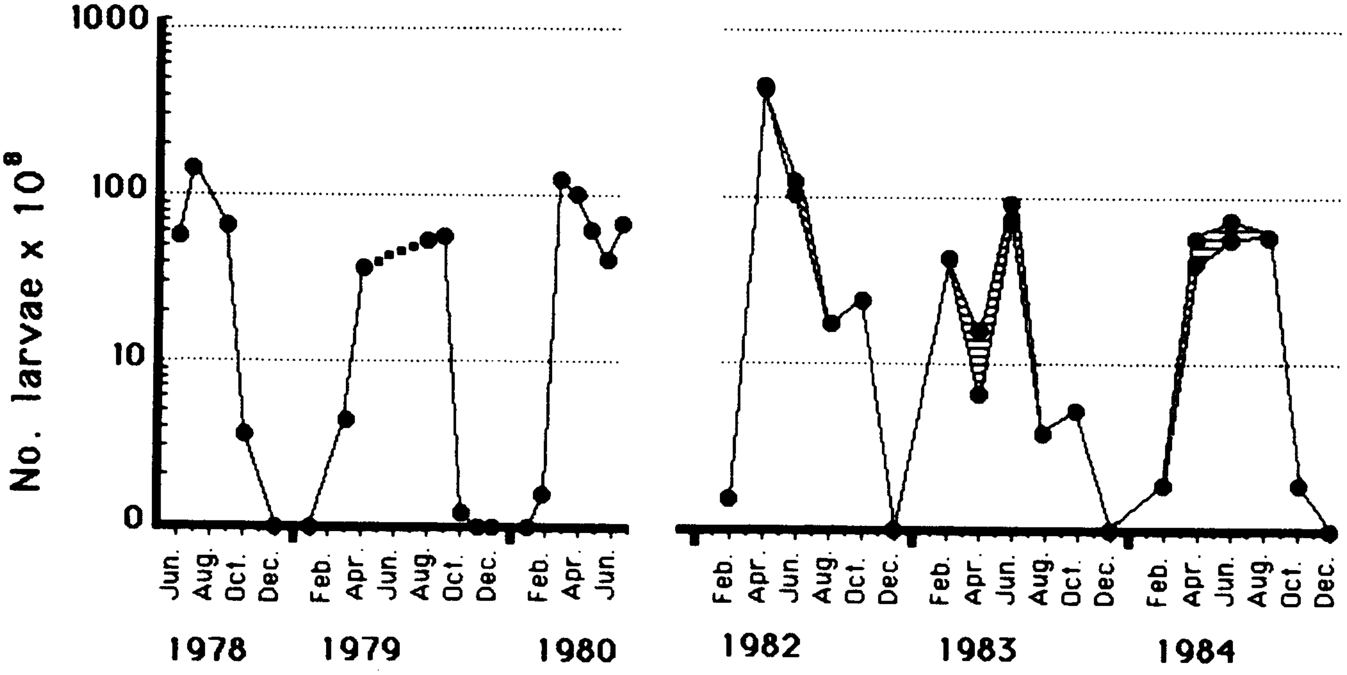

Figure 9. Estimated abundance of queenfish (*Seriphus politus*) larvae, 1978-84. See legend of Figure 3.

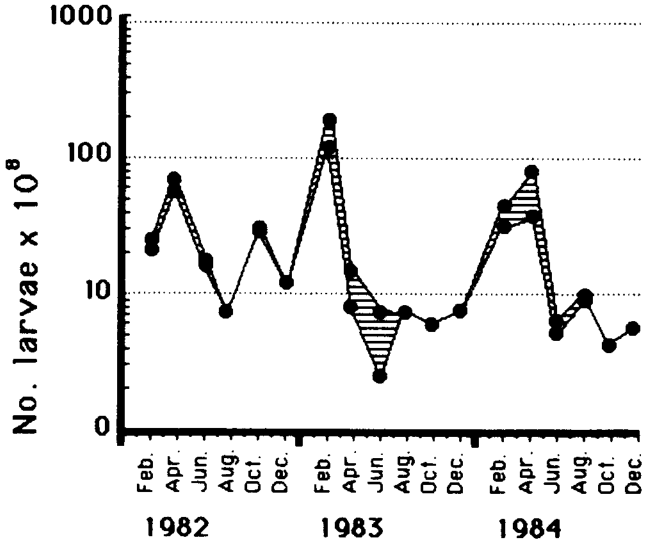

Figure 10. Estimated abundance of California halibut (*Paralichthys californicus*) larvae, 1982-84. At the time of this writing, earlier counts (1978-80) of this species were contaminated with those of fantail sole, *Xystreurys liolepis*. The hatched area represents abundance between the 36- and 75-m contours.

data of northern anchovy egg distributions support their conclusion.

McCall (1983) predicted that as the spawning biomass of a planktivorous fish stock shrinks, the spawning should tend to contract into a few favorable nearshore locations. Pacific sardine, which once was an important commercial fish in offshore waters, is such a depleted stock, its spawning biomass having reached particularly reduced values between 1974 and 1978 (Wolf 1985). Sardine larvae were first encountered in nearshore waters in the central portion of the bight at Seal Beach, and as the intensity of their spawning increased they spread into surrounding coastal waters. Our data suggest that MacCall's model for a recovering fish stock may apply to this species.

Ahlstrom (1967) reported spring and fall spawning of Pacific sardine, the spawning during the second half of the year being confined to a southern subpopulation in waters adjacent to central Baja California. Because the spawning effort of the recovering sardine stock has primarily been in late summer and fall, the springtime egg production noted by Wolf and Smith (1985) probably underestimates the adult stock off southern California. It is not known whether the large increases of sardine eggs and larvae in the bight in the fall of 1982 were due to a shift in seasonality of a recovering northern stock, or whether a fall-spawning southern stock moved northward, or both.

There were apparent manifestations of the California El Niño in these ichthyoplankton data. In the fall of 1983 round herring suddenly appeared in the bight. This fish had not previously been identified from our samples, and normally occurs in waters well to the south of the bight. Pacific sardine spawning intensified, and was sustained over a long season (June-October). The number of larval taxa increased in 1983. There was also a reduced level of spawning of California halibut, which was contracted into the area off Seal Beach, as mentioned above. The 1982 recovery of sardine corresponded with the onset of El Niño conditions in the tropics, but preceded by a year the full development of anomalous hydrographic conditions in the Southern California Bight (McGowan 1984; Petersen et al. 1986). One of us (G.E.M.) is currently investigating the relationship between spawning intensity and aspects of the ocean environment.

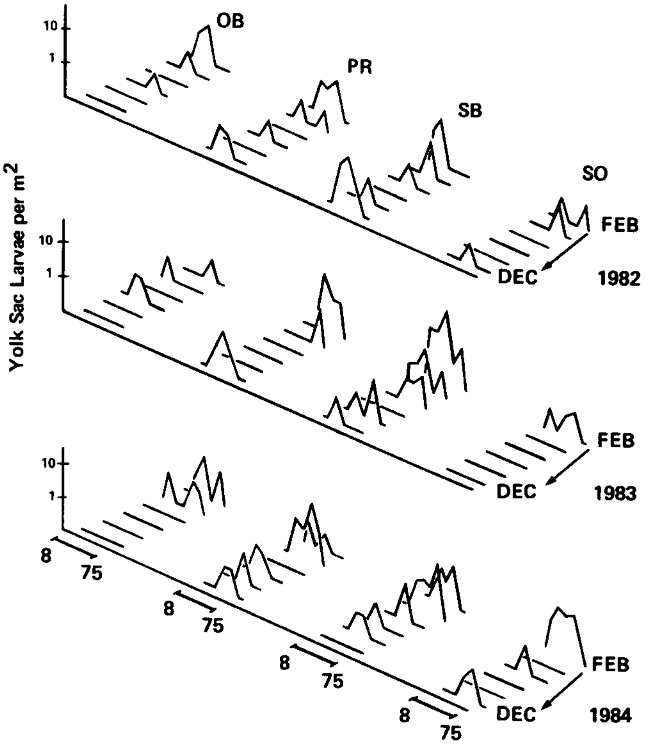

Figure 11. Density of California halibut yolk-sac larvae, 1982-84. See legend of Figure 4.

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CAN WE RELATE LARVAL FISH ABUNDANCE TO RECRUITMENT OR POPULATION STABILITY? A PRELIMINARY ANALYSIS OF RECRUITMENT TO A TEMPERATE ROCKY REEF

JOHN S. STEPHENS, JR., GARY A. JORDAN,
PAMELA A. MORRIS, MICHAEL M. SINGER
Vantuna Research Group
Occidental College
Los Angeles, California 90041

GERALD E. McGOWEN
Los Angeles County Natural History Museum
Section of Fishes
900 Exposition Boulevard
Los Angeles, California 90007

ABSTRACT

The fish assemblage at King Harbor, California, has been studied since 1974 by means of diver transect and ichthyoplankton collection. This preliminary report is an attempt to relate abundance data sets (larvae, juveniles, subadults, and adults, by species) to fluctuations in the fish assemblage. The significant changes that have occurred are probably associated with the El Niño events of 1978-79 and 1982-84. These warming trends have reduced the abundance of cool-temperate species while increasing the proportion of warm-temperate ones. These changes could result from adult emigration or reproductive and recruitment failure. The decrease in viviparous embiotocids seems to correlate with fewer juveniles since 1976. For oviparous species, changes in adult abundance may be reflected in larval abundance, but in most cases recruitment and larval abundance do not appear closely correlated. This situation may result from a sampling bias toward early (post-yolk-sac, preflexion) larval stages. The relationship between larval abundance and recruitment has been experimentally examined on a predator-cleared reef. Assuming that a gauntlet of resident predators is responsible for removing a large percentage of settling recruits, we have removed all fish monthly from an isolated reef and compared rates of settling to observed planktonic abundances. Two species, *Lythrypnus dalli* and *Artedius creaseri*, have shown correspondence between larval abundance and recruitment, and this method appears to provide a way of relating the two data sets. Future expanded recruitment sampling and increased knowledge of larval longevity should increase the utility of these data.

RESUMEN

Los peces de King Harbor, California, han sido estudiados por medio de buzos y de colecta de ictioplancton. Este estudio preliminar intenta relacionar datos de abundancia (larvas, juveniles, subadultos y adultos, por especie) con fluctuaciones en el conjunto de peces. Los cambios significativos que han ocurrido están probablemente relacionados con los eventos El Niño de 1978-79 y 1982-84. Estos calentamientos han reducido la abundancia de las especies frío-temperadas y aumentado la proporción de aquellas cálido-temperadas. Estos cambios pueden ser el resultado de una emigración de adultos, o un fracaso en la reproducción y en el reclutamiento. Desde 1976, la disminución de embiotócidos vivíparos parece estar relacionada con una escasez de juveniles. Los cambios en la abundancia de adultos de especies ovíparas pueden estar reflejados en la abundancia larval; sin embargo, en la mayoría de los casos, el reclutamiento y la abundancia larval no parecen estar relacionados. Esta situación puede ser el resultado de un sesgo en el muestreo hacia estadíos larvales tempranos (post-saco vitelino, preflección). La relación entre abundancia larval y reclutamiento ha sido examinada experimentalmente en un arrecife sin depredadores. Suponiendo que un conjunto de depredadores residentes elimina un alto porcentaje de los nuevos reclutas, se sacaron mensualmente todos los peces de un arrecife aislado. Se compararon las tasas de asentamiento en el arrecife con las abundancias observadas en el plancton. Dos especies, *Lythrypnus dalli* y *Artedius creaseri*, mostraron cierta relación entre la abundancia larval y el reclutamiento; este método permitiría relacionar estos dos conjuntos de observaciones. A futuro, un muestreo más extenso del reclutamiento y un aumento en el conocimiento de la longevidad larval deberían aumentar la utilidad de esta información.

INTRODUCTION

The assemblage of fishes at King Harbor, California, has been studied since 1974 (Terry and Stephens 1976; Ellison et al. 1979; Stephens and Zerba 1981; Stephens et al. 1984). During this 12-year period, major environmental perturbations have occurred (Cayan 1979; Smith and Eppley 1982; McLain 1984). At the origin of this study, temperatures were anomalously cold, but in 1978-79 a small El Niño event occurred, followed in 1982-84 by a major El Niño. These thermal events produced concomitant changes in the fish assemblage at King Harbor (Stephens and Zerba 1981; Stephens et al. 1984). The alterations probably resulted from a combination of adult emigration and changes in spawning or recruitment success. We have monitored the egg and larval abundance at

King Harbor stations monthly during this study and have recorded juveniles of 63 of the 105 species observed in the harbor. Presently, we have data on about 30 species represented by all three stages (larvae, juveniles, and adults).

Most of the literature on population dynamics of marine fishes has been concerned with migratory pelagic or demersal stocks. These stocks may follow controlled patterns, including timed spawning periods coordinated with oceanographic events—a highly evolved condition (Cushing 1975). Long-term records from selected fisheries have allowed a few time series to be developed from these data. For reef fish assemblages, few such records exist. Further, we know of no data relating larval abundance to recruitment for these fishes, and few studies are available describing larval drift patterns (Ahlstrom 1971, 1972; Leis and Miller 1976). Recently, Brothers et al. (1983) and Victor (1985) have documented larval longevity in some tropical and a few temperate species, but these data are unknown for most species. Because estimates of larval longevity are often long (20-60 days) for reef fishes, it seems probable that no relationship exists between the resident spawning assemblage and recruiting larvae.

A number of recent studies have focused on reef recruitment. The majority of these have dealt with tropical reef assemblages (Sale 1977, 1978, 1980, 1984; Talbot et al. 1978; Williams 1980; Victor 1982, 1983, 1984). These recruitment studies have not simultaneously monitored pelagic larval availability; they report primarily on juvenile success, habitat specificity, etc. We have monitored pelagic larvae as well as juvenile success and adult population fluctuations. Our study also includes two years of experimental data designed to determine the effect of resident fishes on larval settlement. This preliminary report will attempt to integrate these data sources and suggest their roles in reef fish population dynamics.

MATERIALS AND METHODS

Since 1974, regular 5-minute isobathic diver transects have been swum at 3-m depth intervals between 1.5 and 15 m (Terry and Stephens 1976). Species abundance by observable life-history stage has been enumerated at eight stations in King Harbor (Redondo Beach, California). Initially, transects were taken monthly; they became quarterly in 1976. The mean number of transects per year = 147.7 (SD = 56.7), maximum = 314 (1975), minimum = 102 (1978). Ichthyoplankton collections are taken with a standard conical plankton net (333 µ) fitted with a TSK flowmeter. All samples are preserved using a formaldehyde and sodium borate solution. Monthly nighttime surface collections were taken at station DS (Figure 1) from January 1974 to February 1978 and from February 1982 to the present. Station 1S, in close proximity, has been sampled monthly since April 1978; additionally, mid-depth and epibenthic collections have been made at this station since August 1980. The epibenthic collections are diver-assisted and were taken during the day until night benthic sampling began in June 1985. Data from surface stations DS and 1S taken on the same dates were tested for concordance (Kendall's tau) and found to be significantly associated ($P < .05$). We have therefore combined surface data from these two stations (1974-85). Since 1974, 2,173 samples have been taken, and 1,186 have been completely sorted and identified, including all surface samples from stations DS and 1S.

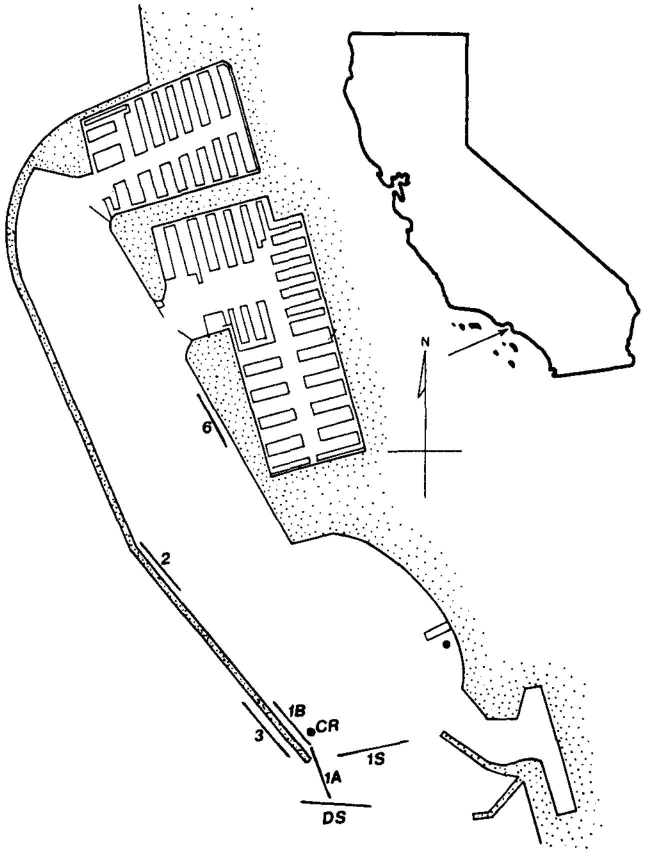


Figure 1. King Harbor study site. 1A, 1B, 2, 3, 6 = diver isobathic transect stations; 1S, DS = plankton stations; CR = cable reef.

Resident fishes were first removed from Cable Reef in July 1984. This small rock isolate, 5 m in circumference and 1.5 m high, is located at a depth of 11 m just inside the harbor entrance and 20 m from the breakwater. Since 1984 the reef has been sampled monthly by anesthetizing the fish with quinaldene and vacuuming the surface with an air lift fitted with 333-µ mesh bags. Samples are preserved in Formalin except where otolith data are to be analyzed: these samples are preserved in 95% ethanol. Temperature profile data are

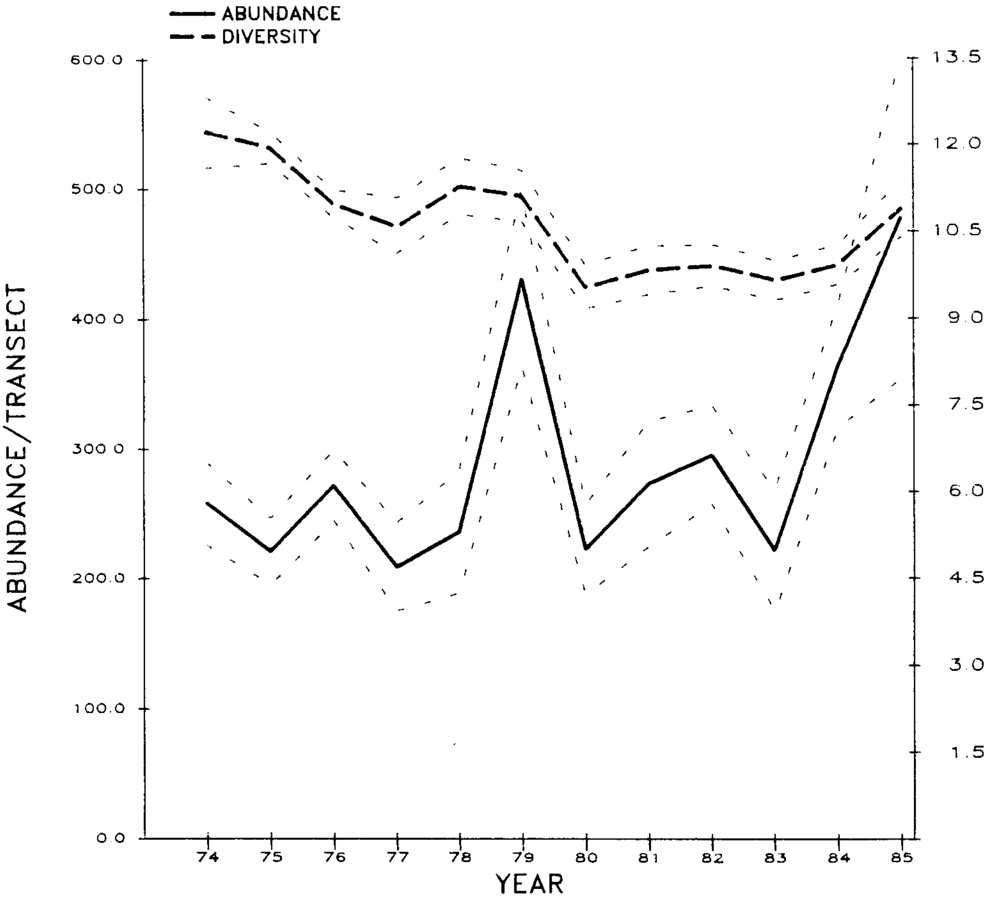


Figure 2. Yearly mean number of species transect^{-1} and mean abundance of fish transect^{-1} (dashes indicate 95% confidence limits).

taken during all field sampling with diver thermometers and YSI telethermometers. Data are entered and stored in Occidental's Prime 550 computer.

CHANGES IN KING HARBOR FISH POPULATIONS (1974-85)

Generally during this study period, the fish assemblage as described by annual abundance of fishes and by annual mean number of species has remained relatively stable (Figure 2). The highest mean number of species per transect was recorded in 1974 (13.1), the lowest in 1980 (9.7), and the mean for this 12-year period was 11.1 (SD = 1.22). The highest mean number of fish per transect was recorded in 1985 (450), the lowest in 1980 (117.4), with a 12-year mean of 154.8 (SD = 126.0). The numbers of individuals have fluctuated considerably but suggest a nonsignificant increasing trend ($y = 214.8 + 10.95x$, $r = 0.5$). The number of species has decreased slightly but significantly ($y = 11.87 - .19x$, $r = .75$, $.01 < P < .05$). Individually, a number of species have disappeared from the study site, and new ones have replaced them. In fact, the existing assemblage is significantly different today from the one originally present in 1974 (Stephens and Zerba 1981).

When the annual abundance is broken down by adults, juveniles, and larvae, and these categories are compared over the 12-year period (Figure 3), the abundance of larvae decreases ($r = .64$, $.01 < P < .05$), while the abundance of adults increases ($r = .71$, $.01 < P < .05$). Juvenile abundance shows no significant correlation ($r = .39$). The larval diversity data (Figure 4) agree closely with the pattern of larval abundance. These latter data suggest that increases or decreases in abundance reflect addition or substraction of species.

We have related adult abundance to changes in thermal conditions (Stephens and Zerba 1981; Stephens et al. 1984) and have attempted to relate changes in larval abundance to the major temperature shifts. Overall larval abundance was greater during cooler years, as indicated by comparison to annual minimal monthly temperatures (Figure 4). The decline of some species during the study period may be related to decreased larval or spawning success with increased water temperatures, though adult emigration may have occurred. The species that have increased are those favoring warmer conditions. These changes in abundance of dominant King Harbor species are presented in Figures 5-10. Table 1 presents linear

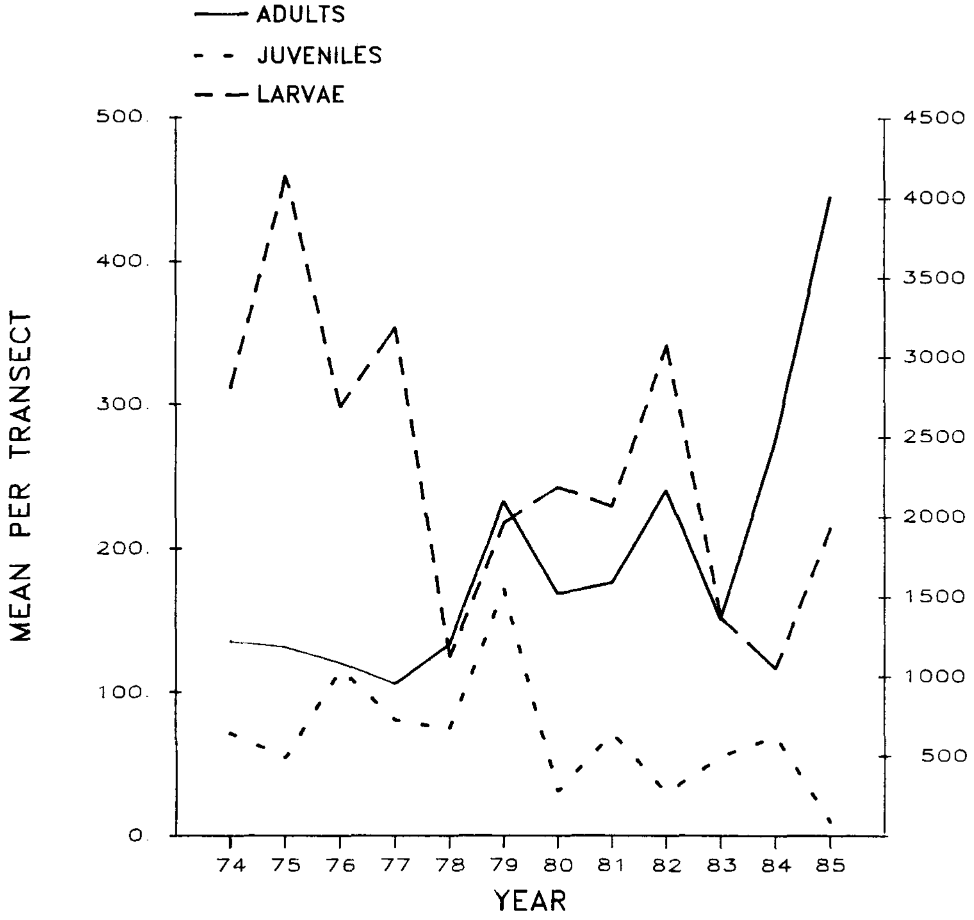


Figure 3. Annual abundance of adults-subadults, juveniles, and larvae at King Harbor.

regression data and Pearson's correlation coefficients for these species. *Chromis punctipinnis, Girella nigricans, Halichoeres semicinctus, Lythrypnus dalli,* and *Paralabrax nebulifer* show significant positive correlations (1974-85), whereas *Cymatogaster aggregata, Embiotoca jacksoni, Hypsurus caryi, Oxylebius picta, Phanerodon furcatus, Rhacochilus vacca, Sebastes mystinus,* and *S. serranoides* show significant negative correlations during this period. These data generally agree with the species' thermal characteristics as tested in laboratory gradient experiments (Ehrlich et al. 1979; Shrode et al. 1982, 1983; Hose et al., in prep.).

Some of the above-cited species are represented by adequate larval and/or juvenile data for preliminary recruitment analysis (Table 2). The viviparous embiotocids lack larval stages and the concomitant vagaries of planktonic existence. Parturition occurs at the study site. All five species that were abundant at King Harbor in 1974—*C. aggregata* (Figure 6), *E. jacksoni* (Figure 6), *H. caryi* (Figure 7), *P. furcatus* (Figure 9), and *R. vacca* (Figure 9)—have declined in abundance, and all have shown reduced juvenile abundance since the last cold anomaly (1975-76). The maximum abundance of embiotocid juveniles was in 1974-75 (Table 2). A linear decline in abundance for more than ten years would result from lack of adequate recruitment and adult attrition in resident long-lived species like *E. jacksoni* (Hough 1981). The other species are more often wanderers or have seasonal migration patterns (e.g., *Cymatogaster* [Wiebe 1968]) and may not fit this scenario.

The ovoviviparous rockfishes (*Sebastes*) show a similar pattern. The blue *S. mystinus* (Figure 10) and olive *S. serranoides* (Figure 10) were extremely abundant as juveniles and yearlings in King Harbor during the pre-El Niño period but declined precipitously in warm-water years, with juveniles being absent or very rare since 1980. The calico *S. dalli* (Figure 9) recruited well in 1975 and 1979. Following the initial recruitment, the population declined about 25% per year, and this small, relatively short-lived species appears to survive four to five years from a single recruitment event. Following 1979, however, adults disappeared, apparently in response to warm water. Rockfishes in general have not recruited well to shallow water since the onset of the 1978-79 El Niño (Mearns et al. 1980). Both recruitment failure and emigration may have occurred.

TABLE 1
Linear Regressions and Correlation Coefficients for 1974-1986 Data

	Linear regression	*r*	Significance
Anisotremus davidsonii	$y = 0.30 + 0.13x$	0.41	NS
Atherinops affinis	$y = 43.90 - 2.28x$	−0.42	NS
Chromis punctipinnis	$y = 2.33 + 14.20x$	0.85	.001
Citharichthys stigmaeus	$y = 0.72 - 0.08x$	−0.57	NS
Coryphopterus nicholsii	$y = 0.44 - 0.18x$	−0.28	NS
Cymatogaster aggregata	$y = 47.00 - 4.81x$	−0.73	.01
Embiotoca jacksoni	$y = 16.10 - 0.46x$	−0.58	.05
Girella nigricans	$y = 5.38 + 1.37x$	0.85	.001
Halichoeres semicinctus	$y = -2.25 + 0.82x$	0.82	.01
Heterostichus rostratus	$y = 0.32 + 0.05x$	0.55	NS
Hyperprosopon argenteum	$y = 7.81 - 0.60x$	−0.33	NS
Hypsurus caryi	$y = 8.60 - 0.66x$	−0.80	.01
Hypsypops rubicundus	$y = 3.49 + 0.03x$	−0.41	NS
Lythrypnus dalli	$y = -4.82 + 1.29x$	0.77	.01
Medialuna californiensis	$y = 1.28 - 0.06x$	−0.31	NS
Oxyjulis californica	$y = 20.56 + 0.44x$	0.14	NS
Oxylebius pictus	$y = 0.58 - 0.04x$	−0.65	.05
Paralabrax clathratus	$y = 6.37 + 0.47x$	0.40	NS
Paralabrax nebulifer	$y = -1.28 + 0.75x$	0.86	.001
Phanerodon furcatus	$y = 5.81 + 0.31x$	−0.68	.05
Rhacochilus toxotes	$y = 0.72 + 0.39x$	0.32	NS
Rhacochilus vacca	$y = 9.44 - 0.59x$	−0.82	.01
Sebastes dallii	$y = 1.51 - 0.13x$	−0.42	NS
Sebastes mystinus	$y = 14.59 - 1.58x$	−0.78	.01
Sebastes serranoides	$y = 6.09 - 0.58x$	−0.74	.01
Semicossyphus pulcher	$y = 0.60 - 0.00x$	−0.03	NS
Trachurus symmetricus	$y = 6.43 + 3.10x$	0.33	NS

TABLE 2
Mean Abundance by Year: Larvae per Thousand Cubic Meters and Juveniles per Transect

		Years											
Species	Stage	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Cymatogaster aggregata	J	16.7	28.6	20.6	1.1	12.3	5.5	0.3	0.4	0.6	0.1	0	0
Embiotoca jacksoni	J	2.1	4.3	2.7	0.5	0.7	1.0	0.7	1.5	1.9	0.2	1.1	1.2
Hypsurus caryi	J	1.1	0.7	0.2	0.2	0.2	0.1	0.1	0	0	0	0.1	0
Phanerodon furcatus	J	0.8	0.6	0.1	0	0	0.1	0.1	0	0*	0	0.1	0.2
Rhacochilus toxotes	J	0.1	0.2	0*	0	0	0	0*	0*	0	0	0	0
Rhacochilus vacca	J	2.4	2.6	0.3	0.2	0.1	0.2	0.5	0.4	0.7	0.1	0.4	0.1
Chromis punctipinnis	L	176.9	0	10.8	0	0	236.2	242.6	0	100.8	12.3	10.4	0
	J	14.3	9.8	56.3	27.5	36.5	81.0	23.7	35.4	20.2	46.0	58.1	29.9
Hypsypops rubicundus	L	0	0	0	91.4	245.7	190.9	384.4	57.2	149.9	80.2	37.1	111.4
	J	0.4	0.7	0.9	1.3	0.9	0.3	0*	0.1	0*	0*	0.1	0.1
Halichoeres semicinctus	L	1.2	0	0	0	0.4	4.4	0.5	0	1.	155	0.9	1.2
	J	0.1	0*	0.1	0.1	0.1	0.9	0.5	0.1	0.2	0.9	3.0	0.4
Oxyjulis californica	L	21.1	130.3	72.8	97.0	0	0	185.6	358.4	151.1	214.9	22.5	32.2
	J	2.4	3.8	7.6	17.6	11.0	17.1	2.4	3.8	0.7	1.6	0.8	1.0
Semicossyphus pulcher	L	10.4	0	0	12.2	0	44.8	0	0	70.1	35.6	10.4	0
	J	0.1	0*	0	0.9	0.5	0.5	0	0	0.1	0	0.1	0*
Cheilotrema saturnum	L	68.8	38.7	279.8	79.4	20.9	45.8	0	71.6	116.5	48.4	45.3	42.7
	J	1.7	0.5	0.7	0.8	2.3	1.5	0.6	1.8	0	0*	1.0	0.3
Anisotremus davidsonii	L	11.6	0	0	0	0	0	0	0	0	21.6	10.4	22.1
	J	0	0.2	0	0.2	0.9	0*	0.3	0.1	0.1	0.2	1.0	0.5
Girella nigricans	L	0	0	11.1	10.6	0	0	0	0	0	0	0	0
	J	2.1	0.7	3.4	0.9	0.4	4.1	0.6	3.6	1.8	1.5	1.2	0.6
Sebastes mystinus	J	21.8	6.9	2.7	4.8	0.6	0.2	0	0	0	0	0	0
Sebastes serranoides	J	5.2	1.9	3.1	7.9	0.1	0.2	0	0	0	0	0.2	0.2
Paralabrax clathratus	J	0.5	0.6	7.1	1.4	5.6	7.0	1.4	3.3	2.0	0.2	1.4	0.9
Paralabrax nebulifer	J	0*	0*	0.8	0*	1.4	1.0	0*	0.1	0.1	0.1	0.7	0.1

* $0 <$ abundance $< .05$ J = juveniles L = larvae

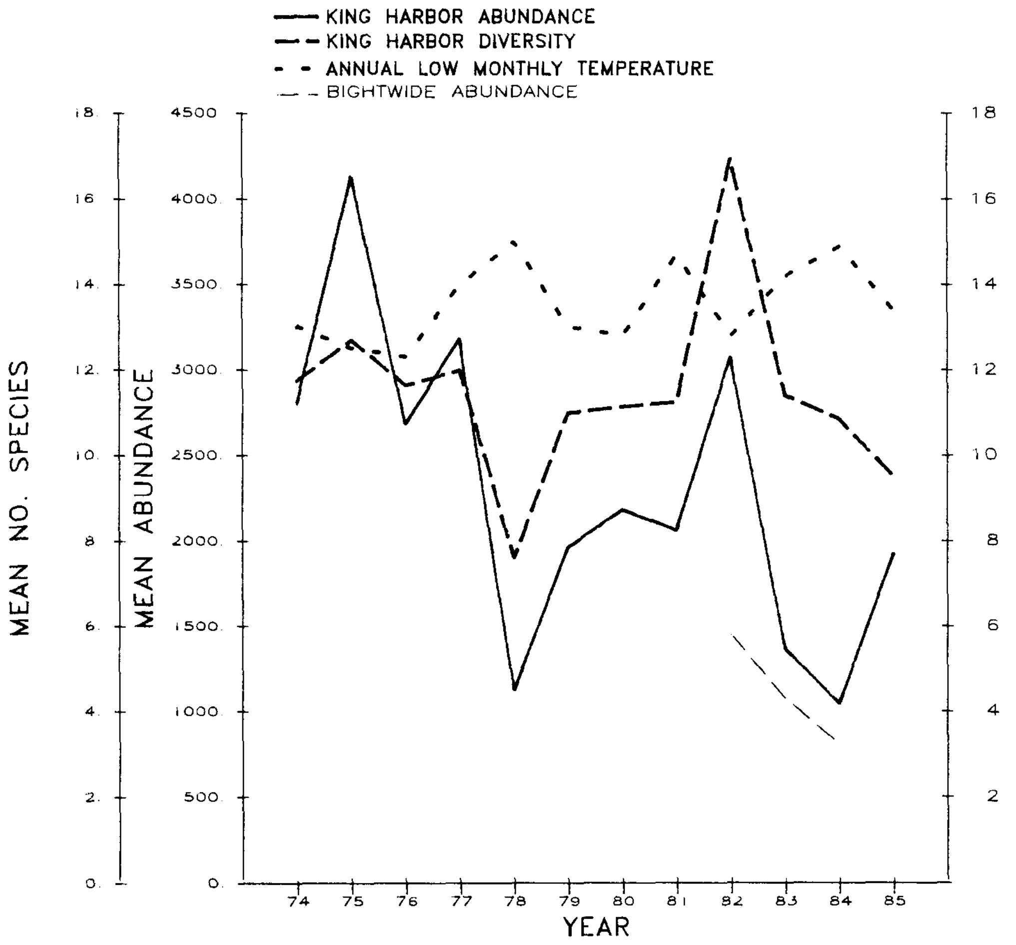


Figure 4. Annual larval abundance and diversity at King Harbor, annual minimal monthly mean temperature, and bightwide larval abundance.

The genus *Paralabrax* includes three species at King Harbor: *P. clathratus*, *P. maculatofasciatus*, and *P. nebulifer*. Their larvae cannot presently be separated. These resident serranids produce pelagic eggs and larvae. Both *P. nebulifer* and *P. clathratus* (Figure 8) have increased with the warm water, but this increase relates only marginally to juvenile abundance and not at all to available larvae (Figure 11). The immigrant stage of *P. nebulifer* may be the subadult, because schools of first-year fish have been observed entering the harbor.

The oviparous wrasses (resident or wandering) have generally increased in El Niño years. As an example, the data for *Halichoeres semicinctus* (Figure 12) may show a direct relationship between larval availability, juvenile recruitment, and adult abundance. Victor (1985) lists 29.9 days as the mean larval life of *H. semicinctus*, certainly long enough for considerable larval transport. Our data suggest a three-year lag between larval abundance and that of adults.

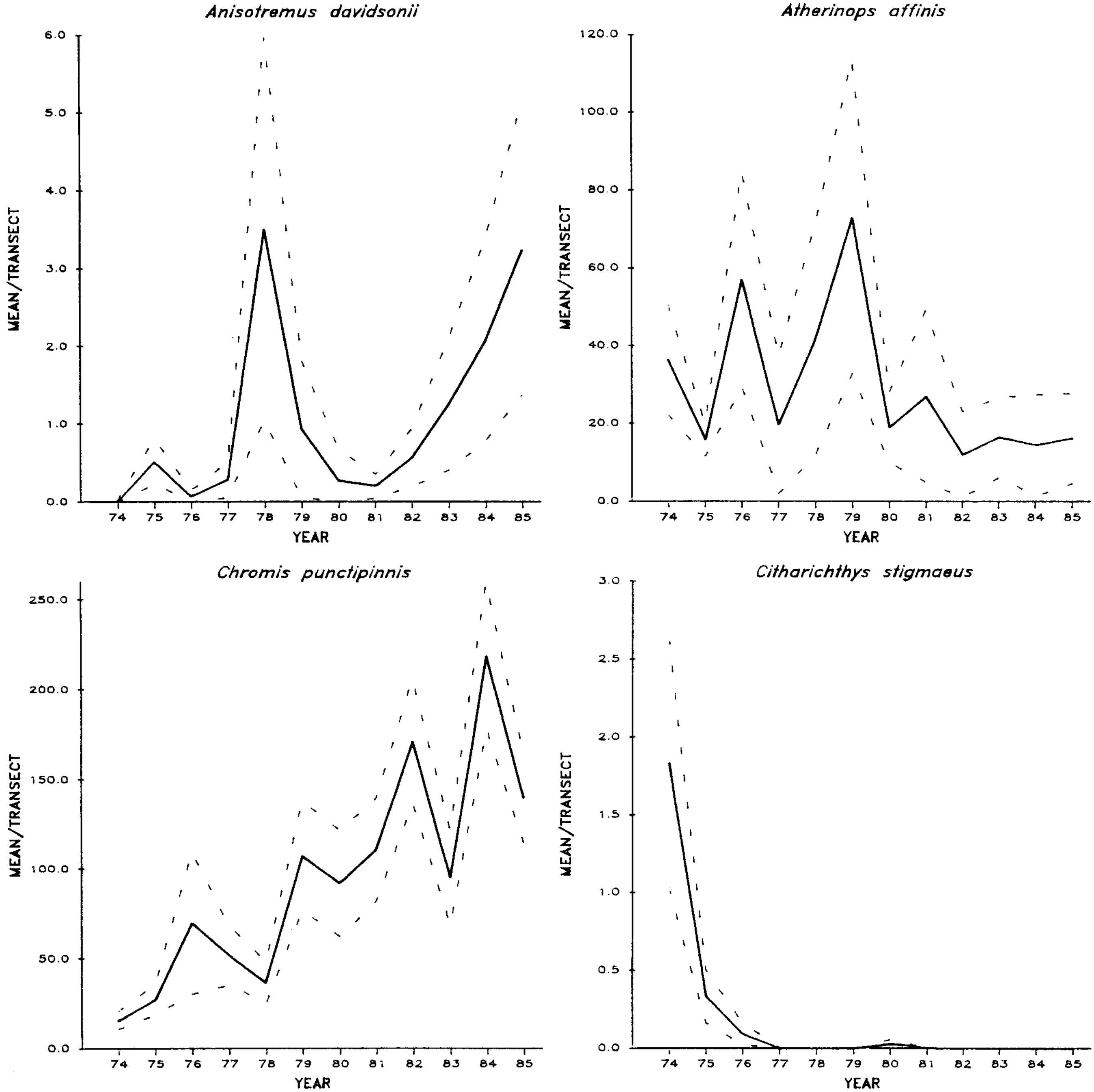
The resident, territorial, nest-guarding pomacentrid *Hypsypops rubicundus* (Figure 13) shows statistically significant correlation between adult and larval abundance ($r = .84$, $P < .01$), and the decrease in larval numbers (1982-84) was directly correlated with the number of nest failures in these years (Singer and Stephens, in prep.). In this long-lived, territorial species (Clarke 1970) successful recruitment may be regulated by adult abundance (Beverton and Holt-type recruitment, Eberhardt 1977).

Finally, the annual or semiannual nest-guarding oviparous goby *Lythrypnus dalli* (Figure 14) shows a significant correlation ($r =$ 81, $.01 < P < .05$) between abundance of adults and larvae. In this case, the fact that adults are short-lived with low fecundity makes the relationship between adults and larvae quite precise.

The above examples indicate that though in some cases there may be a relationship between adult abundance and larval abundance (a fact recognized by fishery egg and larval surveys), larval abundance may, but does not predictably, translate into recruitment (Smith 1981).

LARVAL ABUNDANCE AND JUVENILE RECRUITMENT

The relationship between larval abundance and recruitment should be more intimate if the larvae



Anisotremus davidsonii

Atherinops affinis

Chromis punctipinnis

Citharichthys stigmaeus

Figure 5. Annual abundance transect^{-1} by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

sampled represent later stages of development (flexion or late preflexion). Though these stages are sampled, the majority of the identifiable larvae taken are post-yolk-sac, preflexion stages. Later larvae are not only less numerous (depleted by starvation, predation) but are probably more adept at avoiding nets. More late larvae have been captured in our epibenthic, nocturnal samples, which we began taking in 1985. Table 3 presents the percentage of "returning" late larval stages in the stratified plankton samples. A relatively high

TABLE 3
Percent Late Larval Stages by Depth, June-September 1985

Genus	Surface	Mid-depth	Epibenthic
Hypsoblennius	0.12	0	0.38
Gibbonsia	0	34.5	30.6
Paraclinus	10.5	17.6	15.6
Lythrypnus	0	1.3	0.9
Gobiesox	0	0	22.3
Paralabrax	0	-	2.9

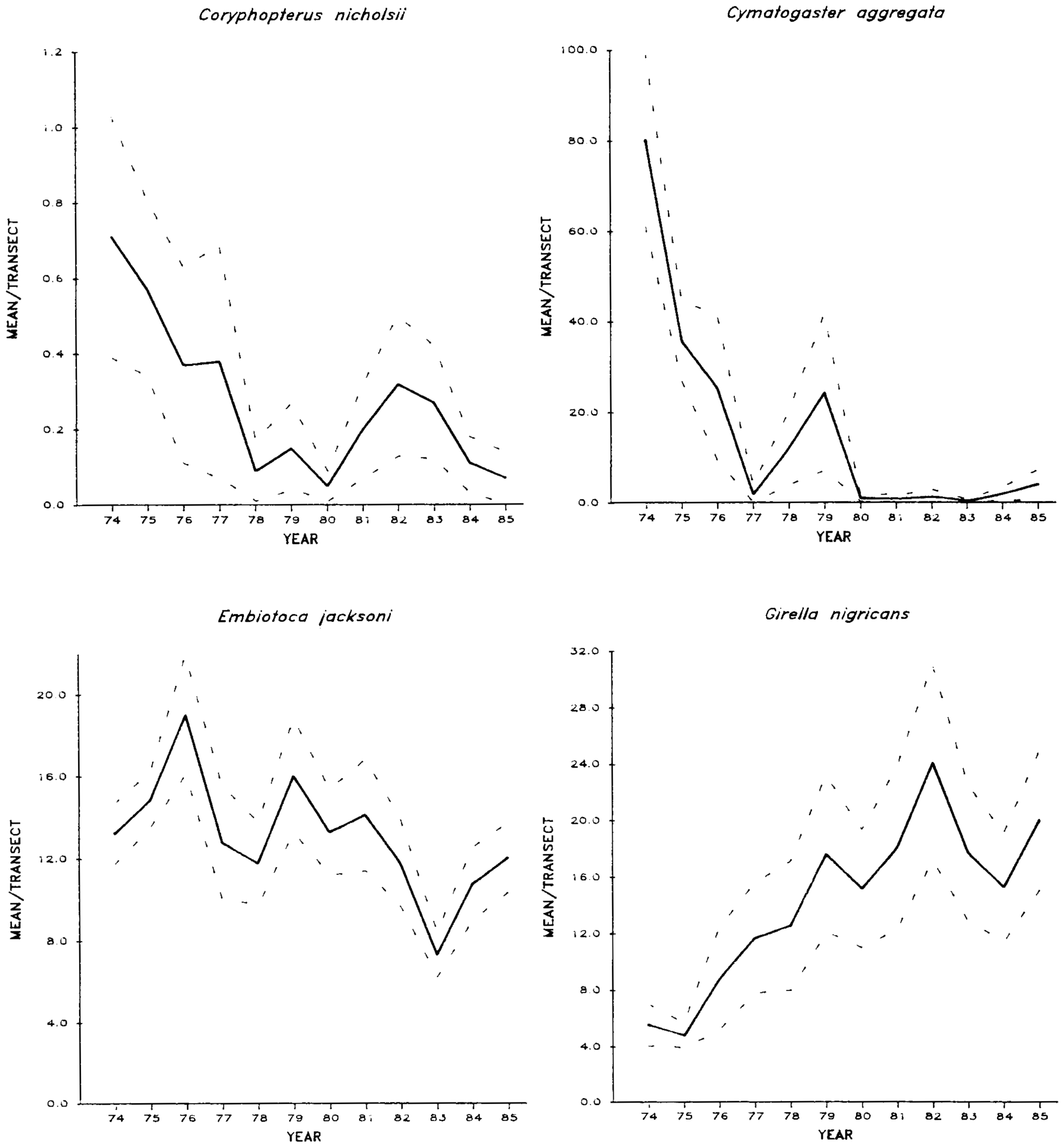


Figure 6. Annual abundance transect^{-1} by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

number of these late larvae are sampled for a few species.

Even if we are able to adequately sample "returning" larvae as they enter the reef environment, they will be subject to increasing numbers of predators as they approach the substrate (Johannes 1978). Only those that survive this "predator gauntlet" will be available for settlement. The correlation between available returning larvae and the abundance of settlers should be affected by the abundance of predators. We feel that small, cryptic resident fishes such as blennies and gobies are important elements of this predator community, and we have begun laboratory experiments to document their removal of settling larvae (Stephens, in

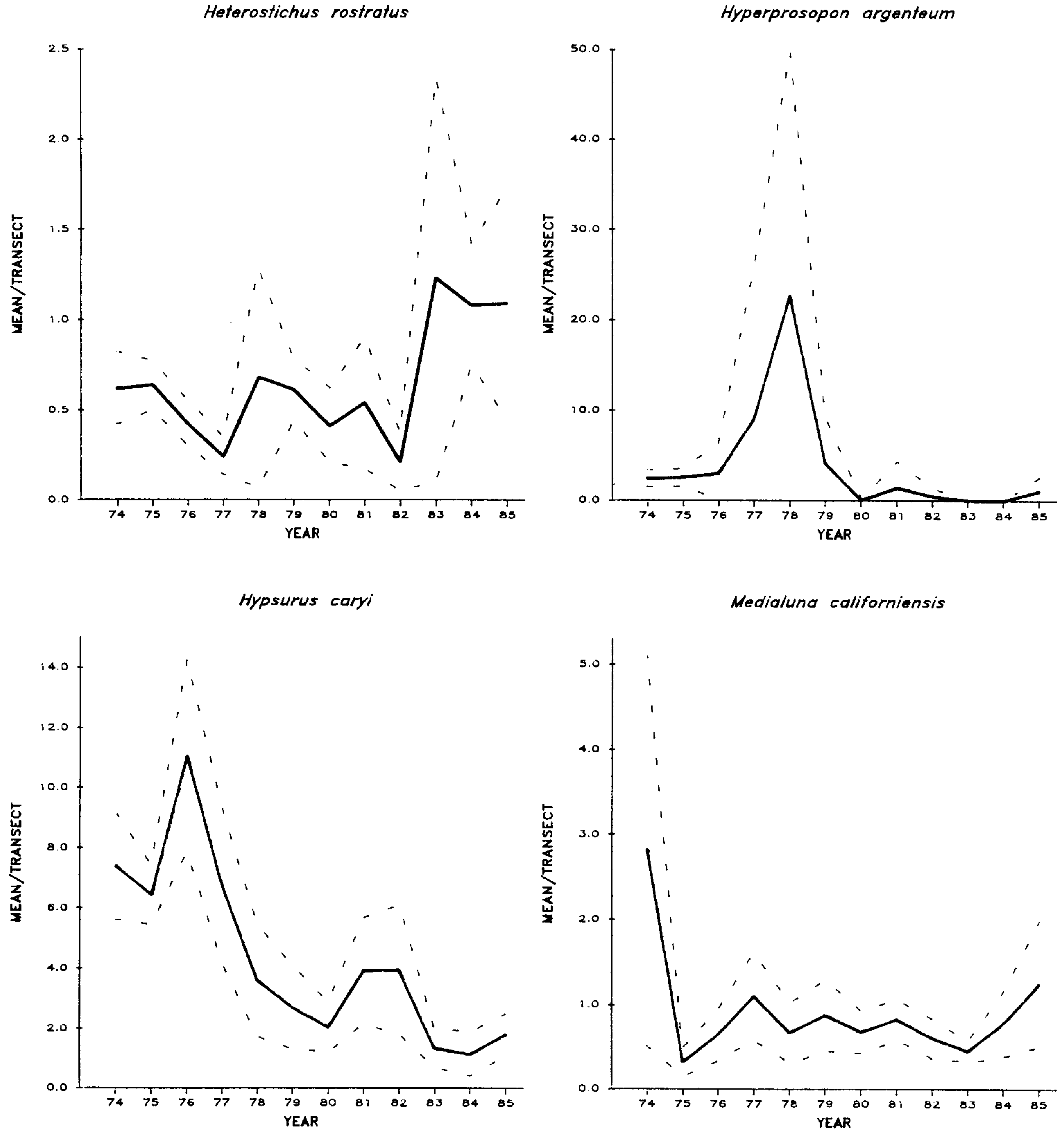


Figure 7. Annual abundance transect^{-1} by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

prep.). Our removal of resident fishes from Cable Reef was designed to test the relationship between larval abundance and the abundance of settlers in the absence of predators.

In the first year's study (July 1984-July 1985) we collected 445 newly settled larvae of 6 species, and 559 immigrants of 21 species on the predator-free reef. The total (1,035) is about ten times the original population (Table 4). After the initial fish removal (July 24, 1984), a high percentage of immigration to the reef occurred from the surrounding shell and some adjacent rocks. From July 1984 to March 1985, larval settling only accounted for an average of 25% of the recruitment. From April 1985 to November 1985, 78% of the re-

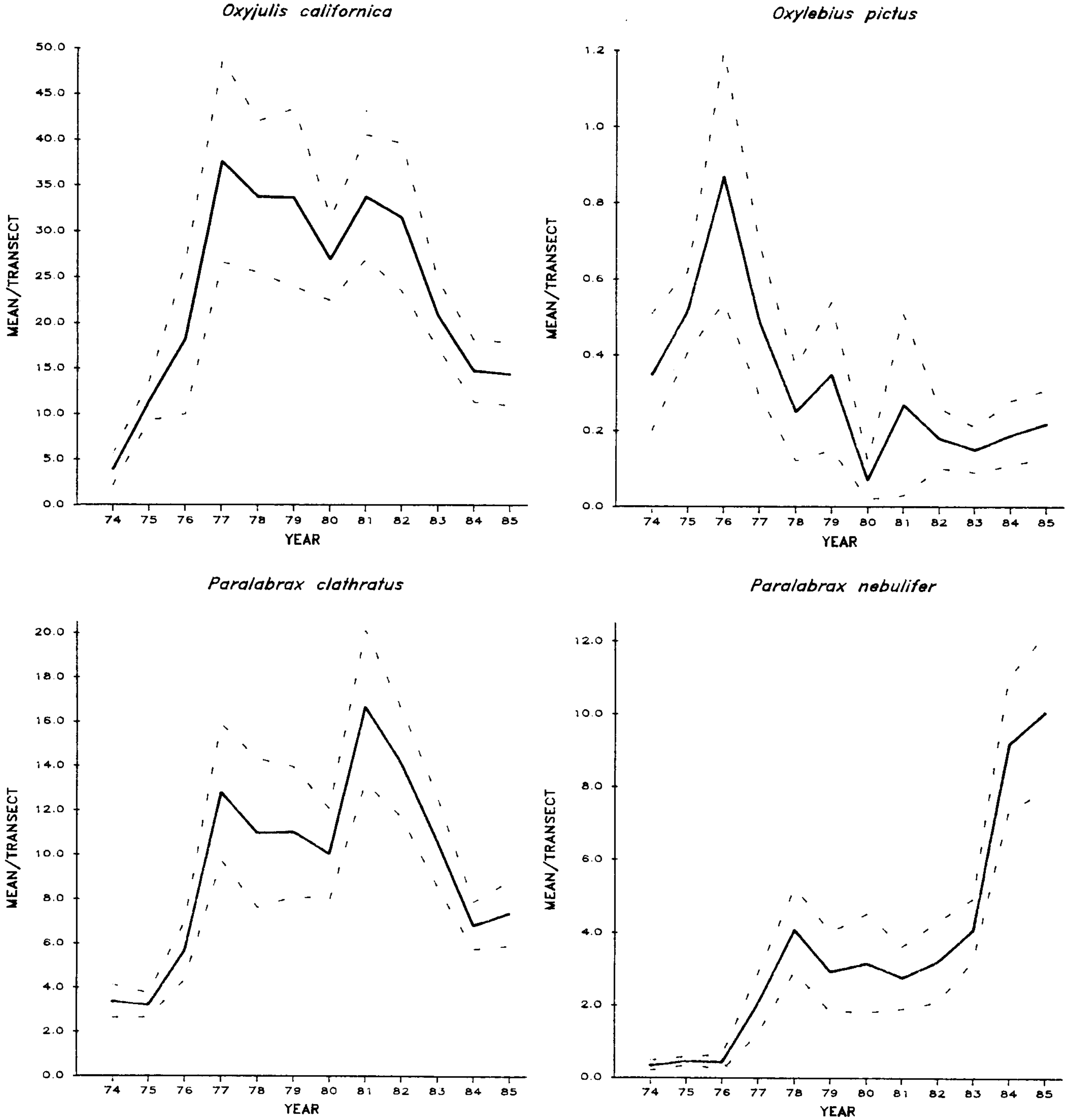
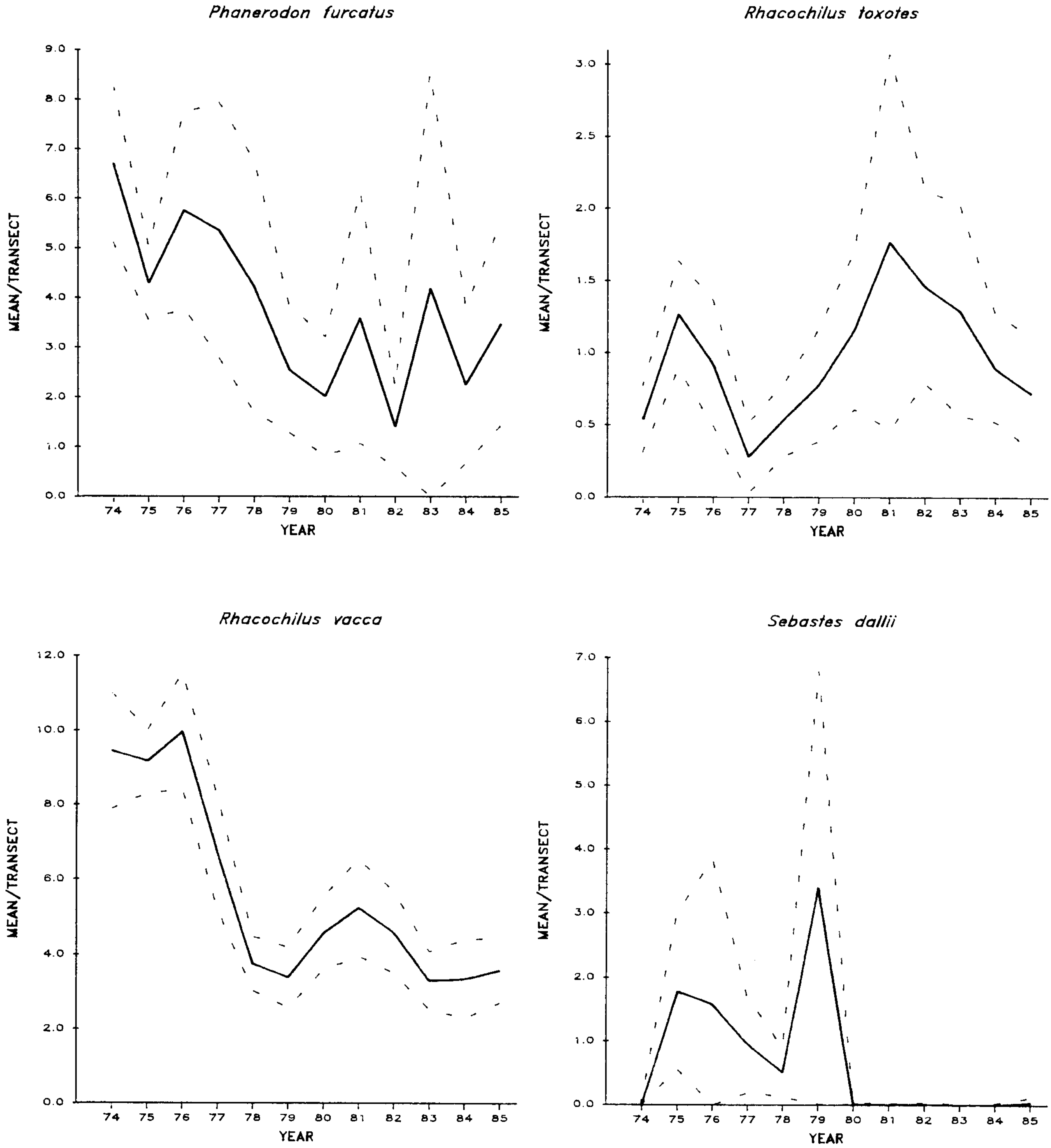


Figure 8. Annual abundance transect^{-1} by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

cruitment was via larval settling. Only two species, the cottid *Artedius creaseri* (winter-spring) and the goby *Lythrypnus dalli* (summer) had obvious settling pulses and showed some tentative correlation to the pelagic larval abundance. A number of species abundant in the plankton and originally present in the habitat (e.g., *Hypsoblennius jenkinsi* and *Paraclinus integripinnis*) were taken only occasionally during this study.

Table 5 presents annual larval abundance data for Cable Reef residents (1974-85). Settling activity was reduced during the summer of 1985. Even *L. dalli*, which had been dominant in the plankton since March 1985, did not recruit to the reef until mid-September, which may reflect later recruitment caused by the breakdown of El Niño. This lack of recruitment was also observed in two samples taken from control reefs


Phanerodon furcatus

Rhacochilus toxotes

Rhacochilus vacca

Sebastes dallii

Figure 9. Annual abundance transect^{-1} by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

at similar depths in July-August. Both control reefs showed only spring recruitment of *A. creaseri*, suggesting that the recruitment pattern observed during our study reflected that of unmodified reefs at the same depth. For the species that did settle, the level of settling was much higher at the predator-free reef, which we conclude resulted from the absence of the predator gauntlet. Our data suggest that this high level of settling might not correlate with the observed planktonic abundance. The number of *A. creaseri* in the plankton during 1985 was not high; the mean annual abundance of 5.3 larvae/1000 m^3 was insignificantly lower

TABLE 4
Fish Removed from Cable Reef

	Original assemblage	1984					1985										
	July	Aug	Sept	Oct	Nov	Dec	Jan	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Total
Alloclinus holderi	1	—	—	—	1	—	—	—	—	—	—	—	1	1	—	—	4
Artedius creaseri	4	4	4	6	1	—	—	5	36	119	14	3	12	2	—	—	210
Chromis punctipinnis	—	2	29	4	2	9	—	—	—	—	—	—	—	—	—	—	46
Coryphopterus nicholsii	—	1	—	—	—	—	—	—	—	—	—	—	2	1	—	—	4
Gibbonsia elegans	4	3	1	1	—	1	—	—	—	—	—	—	1	—	—	—	11
Gobiesox rhessodon	1	2	—	—	—	—	—	1	1	—	—	—	—	1	—	—	6
Hypsoblennius gentilis	—	—	—	1	—	—	—	—	—	—	1	1	2	—	—	—	5
Hypsoblennius jenkinsi	12	11	7	15	5	6	4	1	—	—	—	—	—	2	1	—	64
Lythrypnus dalli	63	111	199	126	75	60	28	14	2	3	—	1	8	67	32	75	864
Neoclinus stephensae	12	8	2	8	1	—	3	2	1	—	—	5	1	—	1	1	45
Odontopyxis trispinosa	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
Orthonopias triacis	5	—	1	1	1	—	—	—	—	6	1	1	2	1	—	1	20
Oxylebius pictus	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Paraclinus integripinnis	6	1	1	—	2	—	—	—	—	—	—	—	—	—	—	—	10
Paralabrax maculatofasciatus	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Paralabrax nebulifer	—	—	—	—	—	2	1	—	1	—	—	—	—	—	—	—	4
Rathbunella sp.	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	1	3
Scorpaena guttata	4	—	—	—	—	1	—	—	—	—	2	—	—	—	—	—	7
Scorpaenichthys marmoratus	4	—	—	—	—	—	—	—	1	2	—	—	2	—	1	—	10
Sebastes auriculatus	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Sebastes miniatus	—	—	—	—	—	—	1	2	1	3	—	—	—	—	—	—	7
Syngnathus sp.	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Total individuals	117	143	245	164	88	79	37	25	43	134	18	12	32	75	35	78	1325
Total species	12	9	9	10	8	6	5	6	7	6	4	6	8	7	4	4	—

(Kruskal-Wallis) than the 11-year mean for 1974-85 (10.1/1000 m^3). The maximum annual larval abundance for this species was 20.6/1000 m^3 in 1982.

Because the number of settled recruits on the predator-free reef was higher than previously observed for this species on unmodified reefs, it appears that removal of resident fish allowed enhanced recruitment. Recruit abundance at the predator-free reef may be more strongly correlated with larval availability than it is at unmodified habitats, a fact that again would appear to support our premise. The temporal relationship between monthly larval abundance and settling for *A. creaseri* is shown in Figure 15. Only with additional paired planktonic and recruitment samples can we determine the concordance between larval abundance and recruitment in the absence of the predator gauntlet.

Lythrypnus dalli recruited very successfully to the predator-free reef in 1984. In this case, the planktonic larvae were quite abundant ($x = 171.6/1000\ m^3$) versus the maximum recorded mean (1985) of 232.1/1000 m^3, whereas the mean for the 11 completely sampled years was 78.4/1000 m^3. The abundance of *L. dalli* as a plankter and a reef inhabitant at King Harbor has been significantly higher since the onset of El Niño in 1978 (Kruskal-Wallis, $P < .05$). This semiannual species maintains its population only with continual recruit-

TABLE 5
Annual Abundance of Larvae per Thousand Cubic Meters for Species Inhabiting Cable Reef

		Years												
		1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	12-yr
Number of tows		19	18	22	26	26	30	21	10	23	24	24	24	$\bar{x}$
Artedius creaseri	$\bar{x}$	6.3	19.5	18.6	0.8	2.7	1.3	16.9	9.0	20.6	11.9	7.3	5.3	10.1
	SD	14.5	38.5	60.2	2.8	5.2	5.2	21.3	18.0	47.0	18.4	14.7	12.6	7.3
Lythrypnus dalli	$\bar{x}$	6.0	4.9	2.4	6.2	18.5	63.9	50.6	35.6	167.6	187.1	171.6	232.1	78.4
	SD	15.2	10.0	8.0	11.6	32.7	140.6	84.7	64.8	235.5	405.0	225.8	491.4	84.7
Gibbonsia elegans	$\bar{x}$	6.7	1.2	1.8	1.1	20.0	17.1	21.0	6.7	4.5	1.4	5.4	2.9	7.5
	SD	11.4	5.2	4.0	5.8	43.6	24.6	41.1	9.5	10.4	5.0	11.0	8.5	7.5
Paraclinus integripinnis	$\bar{x}$	33.1	20.3	5.2	26.3	32.9	271.7	32.4	235.7	68.7	25.6	49.9	20.2	68.5
	SD	66.4	57.4	12.5	69.8	55.4	558.7	55.1	466.4	179.7	54.6	122.8	56.0	88.3
Hypsoblennius sp.	$\bar{x}$	1751.9	946.4	529.8	984.6	320.9	548.9	1009.8	633.8	761.6	410.1	262.4	705.1	738.7
	SD	3261.9	1372.8	705.2	1659.4	562.4	571.2	1353.0	1050.8	1055.0	575.3	459.3	1348.1	405.1
Neoclinus sp.	$\bar{x}$	4.3	7.1	5.7	13.0	4.0	5.7	12.5	1.2	11.2	1.4	0	0.4	5.5
	SD	7.2	20.0	14.5	28.7	9.4	11.6	15.8	3.6	20.2	4.9	0	2.0	4.6

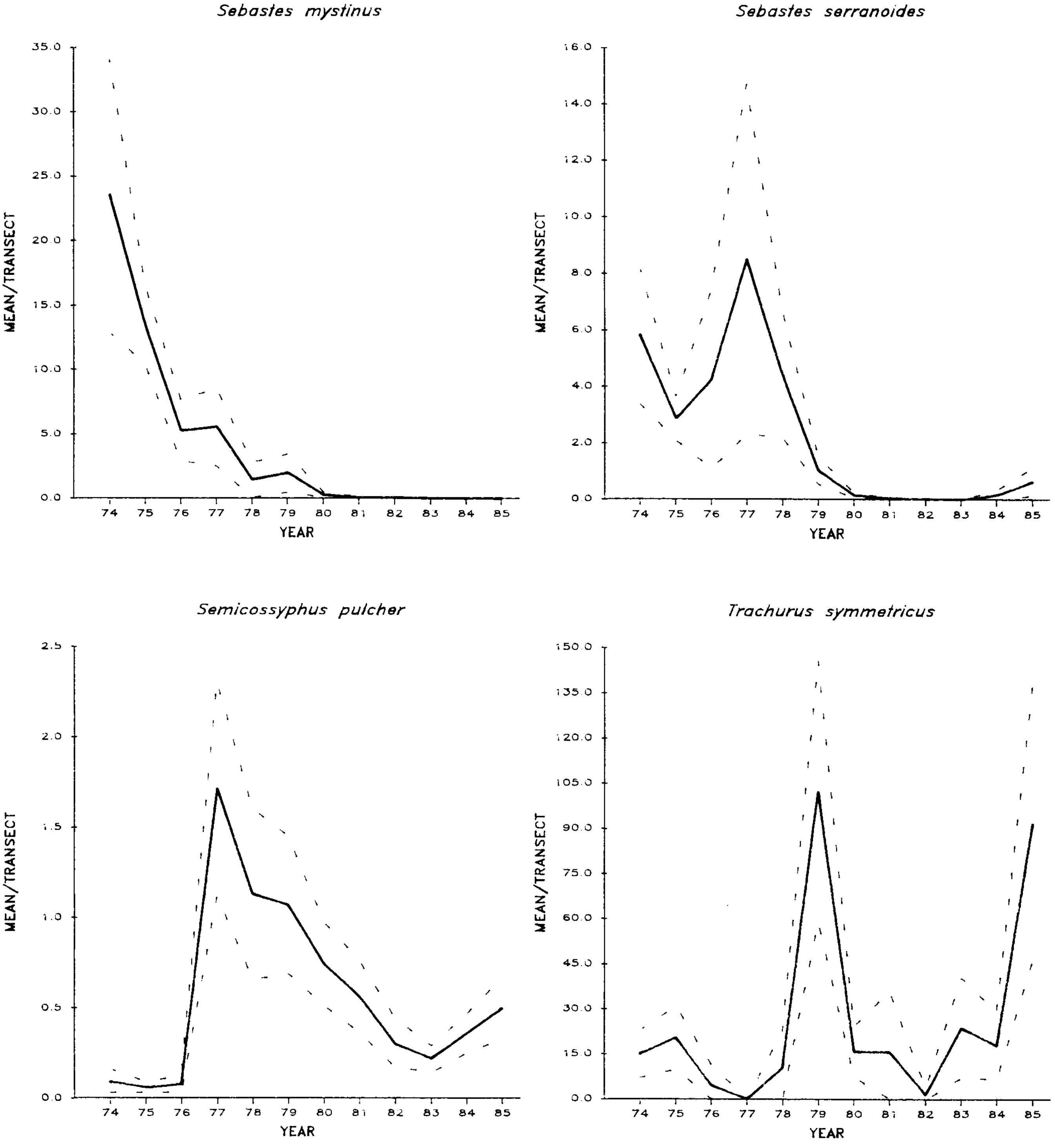


Figure 10. Annual abundance transect^{-1} by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

ment and has been extremely abundant since 1981 (Figure 14). The larval abundance (summer 1985) suggested another very strong recruitment year, but the settling of 234 recruits (September 1985-February 1986) did not quite match the success of 1984 (n = 263), though larval abundance was higher. The temporal relationship between larval abundance and settlement for *Lythrypnus* is presented in Figure 16.

When the experimental reef was first sampled, the blennies *H. jenkinsi*, *Neoclinus stephensae*, *P. integripinnis*, *Gibbonsia elegans*, and *Alloclinus holderi* made up 30% of the assemblage (Table 4). During

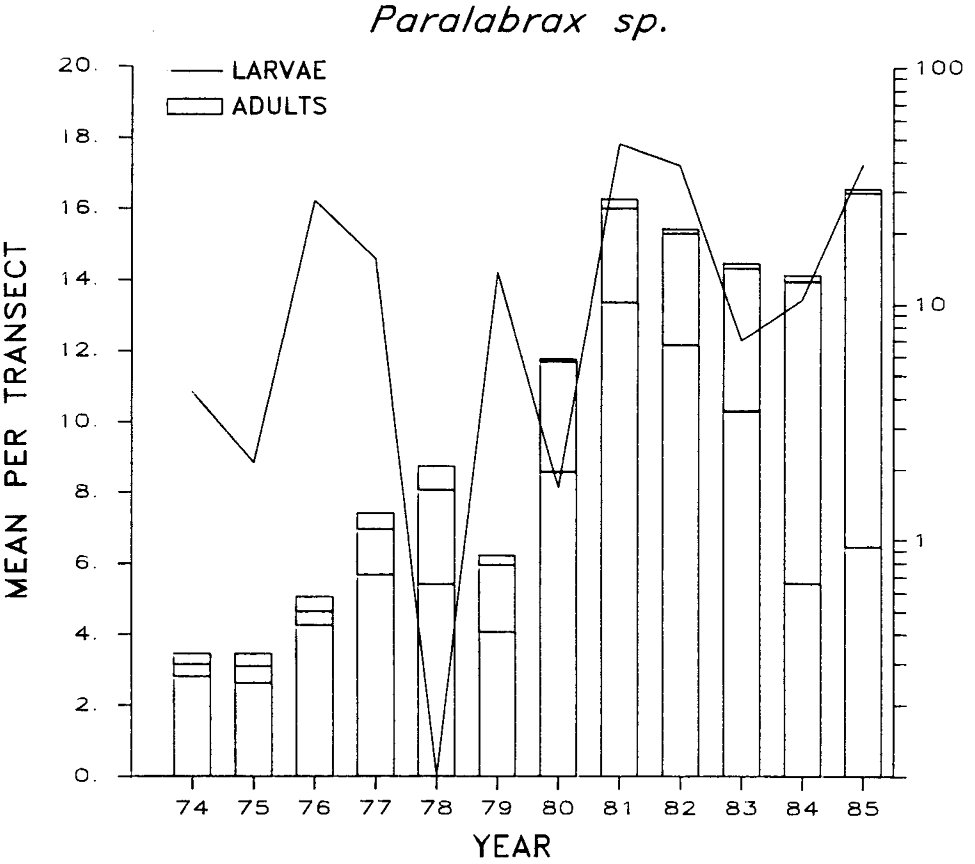


Figure 11. Abundance of larvae, juveniles, and adults of *Paralabrax*. Each bar represents the adults of three species: *P. clathratus* is the base, *P. nebulifer* the center, and *P. maculatofasciatus* the top.

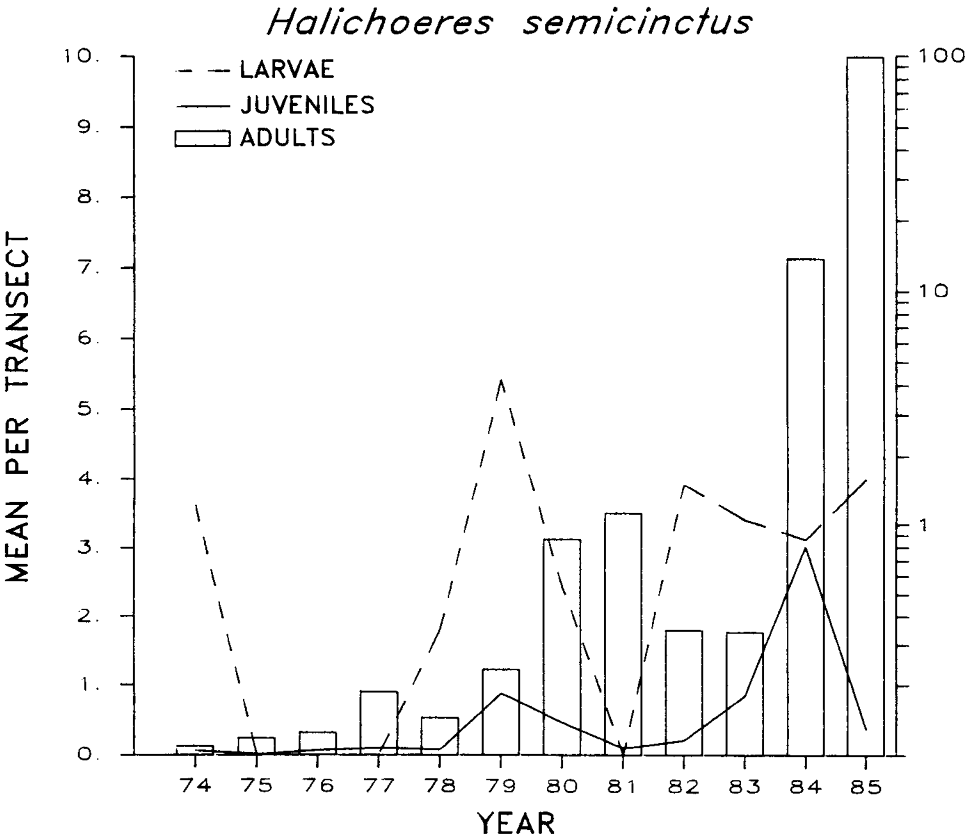


Figure 12. Abundance of adults, juveniles, and larvae of *Halichoeres semicinctus*.

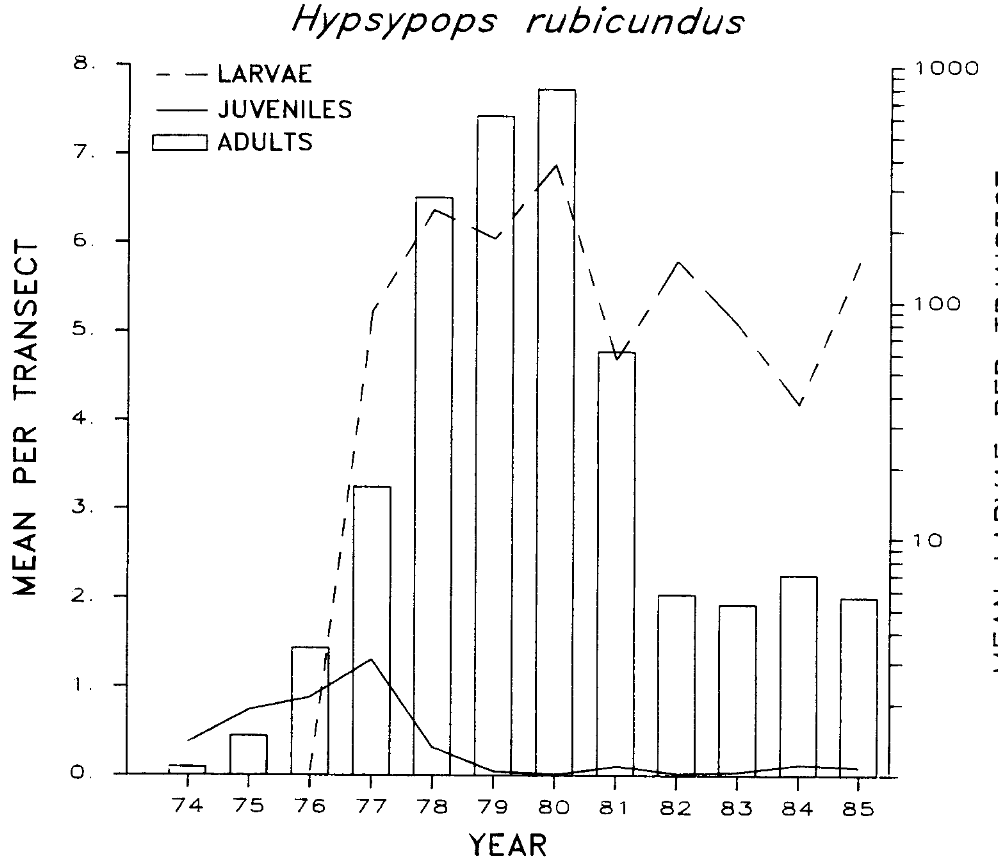


Figure 13. Abundance of adults, juveniles, and larvae of *Hypsypops rubicundus*.

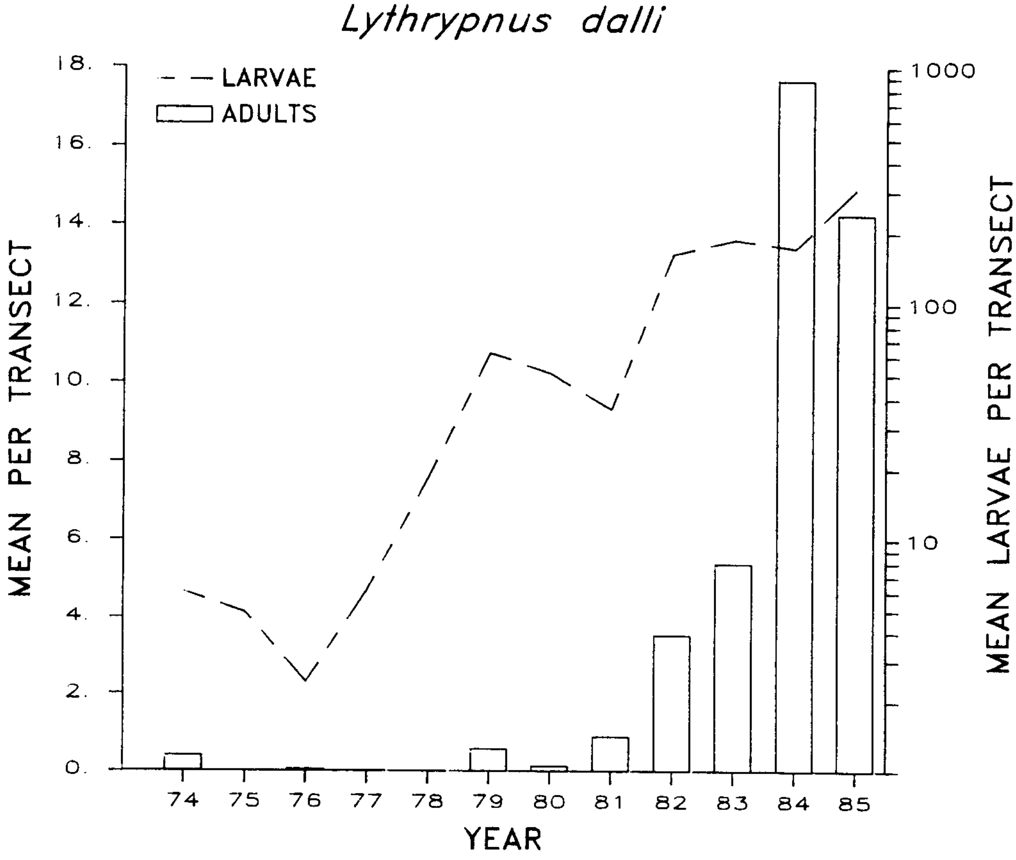


Figure 14. Abundance of larvae and adults of *Lythrypnus dalli*.

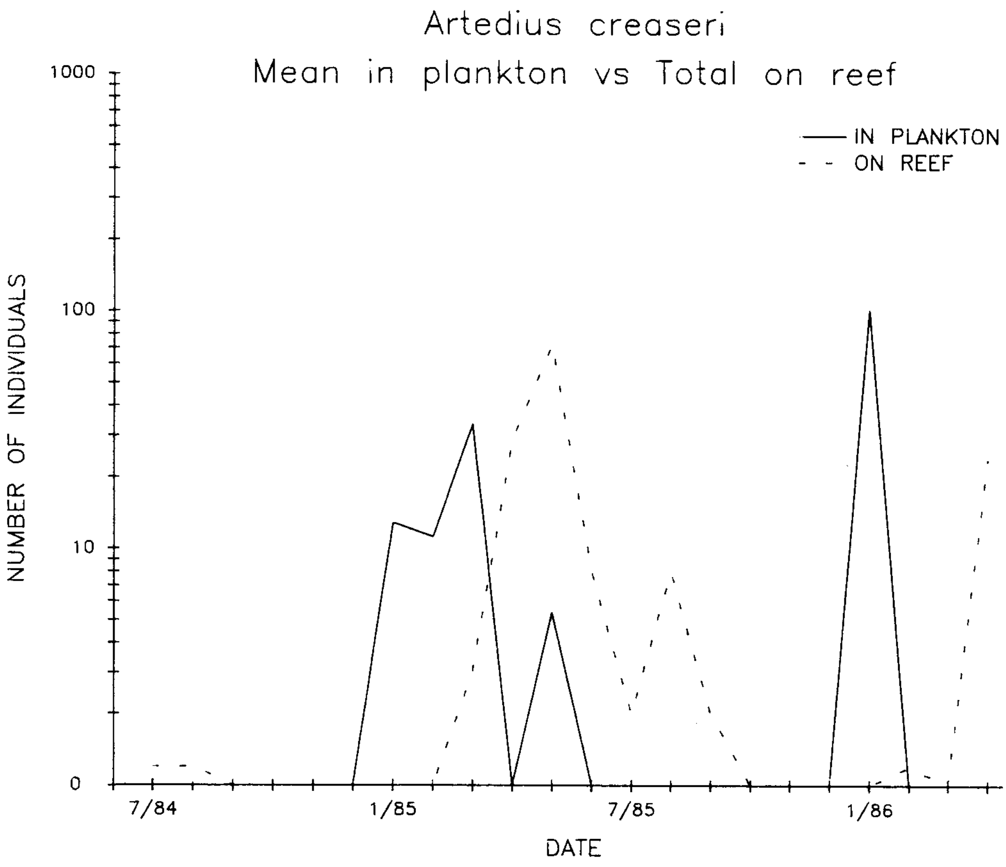


Figure 15. Temporal relationship between larval and recruit abundance, *Artedius creaseri*.

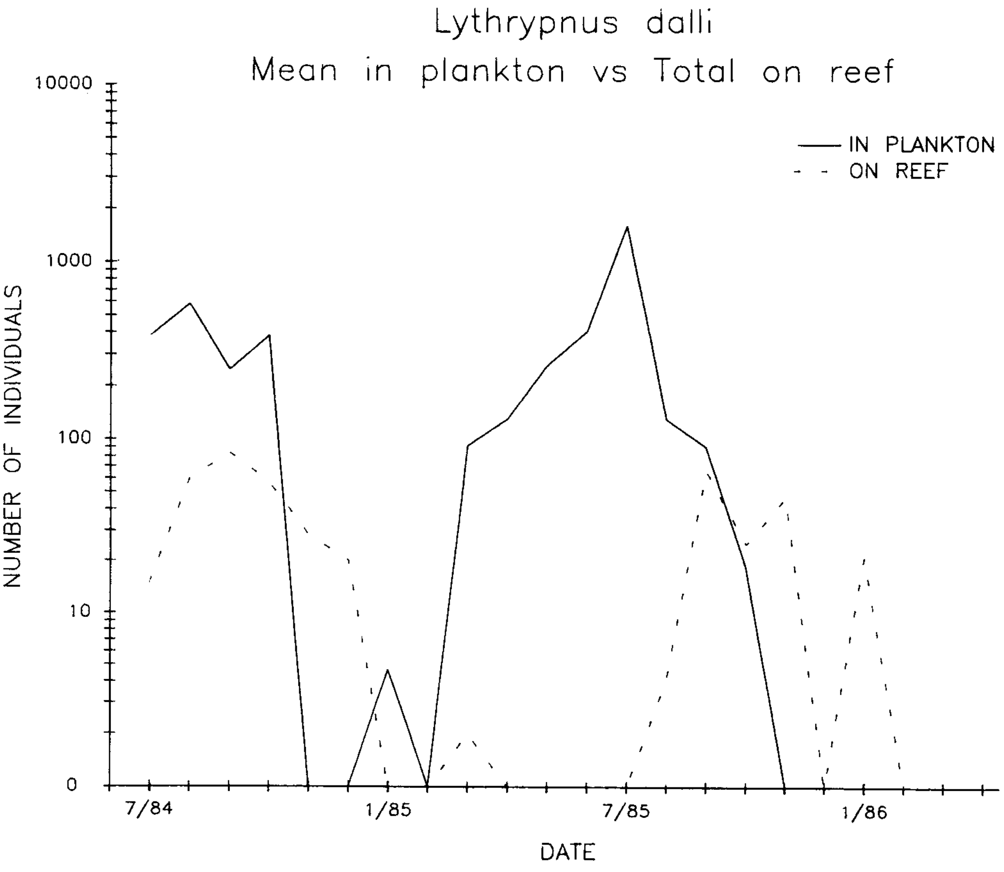


Figure 16. Temporal relationship between larval and recruit abundance, *Lythrypnus dalli*.

summer 1984, both *H. jenkinsi* and *N. stephensae* recruited to the reef at close to replacement levels, while the remaining three species did not recruit. During 1985 only two *H. jenkinsi* and two *A. holderi* settled on the reef, while *N. stephensae* again recruited at about replacement level. Again, *P. integripinnis* and *G. elegans* did not recruit. When these recruitment data are compared to the annual larval abundance for each species (Table 5), all species—with the exception of *Hypsoblennius* (1985)—showed relatively low (below mean) levels of availability (*A. holderi* larvae have not yet been described). The absence of recruitment to the predator-free reef may reflect this lowered larval availability.

By contrast, the almost complete absence of settling of *H. jenkinsi* in 1985 does not appear to correlate to larval density. There are a number of untested possibilities that could explain this situation. Some evidence (La Belle and Nursall 1985) suggests that blenny larvae settle preferentially to reefs occupied by conspecifics. Removal of adults would then cause lower settling. It is also possible that *H. jenkinsi* settles primarily in shallower water: the larvae are surface-orienting, and the center of distribution of adults is <10 m (Stephens et al. 1970). If this is true, the predator-free reef would be a marginal habitat. We have sampled a series of very shallow reefs this last year, and *H. jenkinsi* settlement did occur in these habitats. Our studies now include reefs at 3 and 15 m, bracketing by depth the original study site. A third possibility is that the *Hypsoblennius* larvae that increased in 1985 were not *H. jenkinsi* but congenerics which cannot, at present, be distinguished at preflexion stages.

Finally, a phenomenon of possible interest is suggested from *P. integripinnis* and *A. creaseri* data, which suggest that larval settlement may occur to soft (sandy) substrate. Movement of the cottid *A. creaseri* onto our reef suggests such a phenomenon, and Marliave's (1977) data for a congeneric species, though inconclusive, did show a settling preference for coarse gravel. Our data (Table 6) and that recently published by Barnett et al. (1984) appear to suggest that *Paraclinus*, which is taken abundantly in the epibenthic and midwater plankton at night, drops to low levels in these samples during the day ($x^2 < .01$). Some of this difference could be related to diurnal net avoidance, but we suggest that *Paraclinus* may presettle to the soft substrate during the day. Nocturnal excursions by these settlers into the water column to feed would allow drift to transport the metamorphosing juveniles onto available rock substrate. Compared to planktonic larvae, these presettled individuals might be better developed and more able to avoid the predator gauntlet present in a reef habitat. Further, immigration

TABLE 6
Day/Night Distribution of Selected Larvae/1000 m^3, Summer 1985 (Surface Samples Excluded)

	June		July		August	
	Mid-depth	Bottom	Mid-depth	Bottom	Mid-depth	Bottom
Day						
Hypsoblennius sp.	1,353.9	386.8	389.8	329.4	550.4	206.8
Clinid "A"	20.8	143.7	21.1	270.6/11.8	33.0	82.7/10.3
Paraclinus integripinnis	541.6/62.5[a]	99.5	198.7/10.5	0	539.4/22.0	1,251.3/51.7
Goby "A/C"	166.6	22.1	21.1	235.5	22.0	62.0
Lythrypnus dalli	41.7	33.2	0	11.8	44.0	20.7
Gobiesox rhessodon	41.7	66.2	63.2	270.6	11.0	62.0
Paralabrax sp.	0	44.2	10.5/52.7	47.1	0	10.3
Pleuronichthys verticalis	41.7	11.1	10.5/10.5	188.2/35.3	0	20.7
Heterostichus rostratus	0	0	10.5	0	0	31.0
Hypsypops rubicundus	0	0	0	0	0	0
Night						
Hypsoblennius sp.	776.5	316.1	1,876.3	242.5	2,037.8	1,849.7
Clinid "A"	0/11.8	189.7/115.9	12.1	88.2/22.0	9.8/9.8	74.4/21.3
Paraclinus integripinnis	483.0/82.0	653.3/21.1	2,324.2/363.0	3,681.3/407.8	1,273.6/407.8	435.8/276.4
Goby "A/C"	0	073.8	411.6	407.8	313.5	414.6
Lythrypnus dalli	0	243.3	1,222.6	826.6	215.5/19.6	255.1/10.6
Gobiesox rhessodon	11.8	73.8/21.1	96.8	143.3/44.1	9.8	10.6
Paralabrax sp.	0	10.5	447.9	330.7/11.0	0	21.3
Pleuronichthys verticalis	11.8	21.1	12.1	0	0	0
Heterostichus rostratus	0	21.2	12.1	22.0	0	0
Hypsypops rubicundus	70.8	126.4	254.2	11.0	9.8	10.6

[a] Denominator when present = number of late-stage larvae

would occur at night, which would reduce initial predation, because most discrete plankton feeders are visually orienting (Zaret 1980). Though we have thus far concentrated our epibenthic sampling to above-reef habitats, we are presently building an epibenthic sled to intensively sample the soft substrate (Madenjian and Jude 1985) in order to test this hypothesis.

SOME TENTATIVE CONCLUSIONS FROM THESE PRELIMINARY DATA

The present analysis suffers from a number of shortcomings that we hope to eliminate in the future; primarily, we lack detailed and specific juvenile fish surveys, and have had difficulty in sampling returning larvae. The available data, however, show some interesting relationships. Because we sample predominantly young larval stages before their offshore dilution with the coastal larval pool, there is a reasonable concordance between larval production and local population levels. The relationship between these early larval stages and incipient settlers will depend on a series of factors: the relationship between larval production in the local assemblage to that in the rest of the Southern California Bight, and the distributional pattern of the local larvae.

Little or no data are presently available regarding distributional patterns, but newly available data on larval age at least give us an estimate of the length of planktonic life. Preliminary bightwide data (Figure 4) appear to show the same pattern of total larval abundance for the bight as for King Harbor (1982-84), but the species data are not as clear. If there is annual agreement between larval production on local reefs and throughout the bight, there should be some level of agreement between larval production and incipient settlers. The same situation would obtain if larvae were not dispersed to the coastal pool. The relationship between incipient settlers and recruits depends upon the hazards of settling. Our predator-free experimental reef has demonstrated a close relationship between available larvae and recruitment in *Lythrypnus dalli* and *Artedius creaseri*, but other species have not recruited when expected. Better knowledge of settlement stimuli and wider latitude in available depths and types of predator-free habitats will enhance our continuing studies. We feel that our approach of combining a time series of samples with experimental analysis of recruitment may yield insight into the phenomena regulating fish stability on a temperate reef.

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INSHORE SOFT SUBSTRATA FISHES IN THE SOUTHERN CALIFORNIA BIGHT: AN OVERVIEW

MILTON S. LOVE, JOHN S. STEPHENS, JR., PAMELA A. MORRIS, MICHAEL M. SINGER
Occidental College
Vantuna Research Group
Moore Laboratory of Zoology
Los Angeles, California 90041

MEENU SANDHU
Los Angeles County Natural History Museum
900 Exposition Boulevard
Los Angeles, California 90007

TERRY C. SCIARROTTA
Southern California Edison Company
System Planning and Research
P.O. Box 800
Rosemead, California 91770

ABSTRACT

A series of bimonthly trawls was made at stations off three areas (Ormond Beach, Redondo Beach, and San Onofre) in the Southern California Bight. Three depths (6.1, 12.2, and 18.3 m) were sampled from 1982 to 1984. At all three areas, queenfish (*Seriphus politus*), white croaker (*Genyonemus lineatus*), and northern anchovy (*Engraulis mordax*) dominated the 6.1-m stations. Off the Ormond area, queenfish and white croaker were the important species out to 18.3 m. However, off Redondo and San Onofre, these two species became less dominant in deeper water, giving way to an assortment of flatfishes (particularly speckled sanddab, *Citharichthys stigmaeus*; hornyhead turbot, *Pleuronichthys verticalis*; and fantail sole, *Xystreurys liolepis*). Disregarding seasonality and yearly variation, we found that fish abundances off Redondo and San Onofre decreased with depth, but remained constant at Ormond. This latter phenomenon was due to large numbers of queenfish and white croaker found throughout the Ormond isobaths. For fish one year of age and older (with the partial exception of white croaker and queenfish), there was a decline in mean abundance over the three-year period, particularly from 1983 to 1984. There was an increase in abundance of some species, notably California barracuda (*Sphyraena argentea*) and spotted turbot (*Pleuronichthys ritteri*). Though recruitment of some species such as speckled sanddab and walleye surfperch (*Hyperprosopon argenteum*) declined from 1982 to 1984, a number of species (including queenfish, northern anchovy, California barracuda, and spotted sanddab) appeared relatively unaffected or even enhanced during the El Niño event.

RESUMEN

Una serie de arrastres bimestrales fue realizada en tres áreas (Ormond Beach, Redondo Beach, y San Onofre) en la Bahía del Sur de California. Tres profundidades (6.1, 12.2, y 18.3 m) fueron muestreadas en 1982-1984. En las tres áreas, *Seriphus politus*, *Genyonemus lineatus* y la anchoveta del norte, *Engraulis mordax*, dominaron a 6.1 m de profundidad. Frente a Ormond, *S. politus* y *G. lineatus* fueron las especies más importantes hasta 18.3 m. Sin embargo, frente a Redondo y San Onofre, estas dos especies fueron menos comunes en aguas profundas, siendo reemplazadas por un conjunto de lenguados (especialmente *Citharichthys stigmaeus, Pleuronichthys verticalis,* y *Xystreurys liolepis*). Sin considerar las variaciones estacionales y anuales, las abundancias de peces disminuyeron en profundidad frente a Redondo y a San Onofre aun cuando permanecieron constantes en Ormond. Este último fenómeno se debió al gran número de *S. politus* y *G. lineatus* presentes a todas profundidades. Las abundancias promedio de peces de un año o más (con la excepción parcial de *G. lineatus* y *S. politus*) disminuyeron durante el período de tres años, especialmente entre 1983 y 1984. La abundancia de algunas especies aumentó, en particular la barracuda *S. argentea* y *P. ritteri.* Aun cuando el reclutamiento de algunas especies, como por ejemplo *C. stigmaeus* e *Hyperprosopon argenteum,* disminuyó entre 1982 y 1984, otras especies (incluyendo a *S. politus*, *E. mordax*, *S. argentea*, y *P.*, *ritteri*) parecieron no ser afectadas e inluso favorecidas durante el evento El Niño.

INTRODUCTION

Knowledge of fish assemblages within the Southern California Bight is uneven. A considerable amount is known about pelagic assemblages, both offshore (Mais 1974) and nearshore (Allen and DeMartini 1983). There have been numerous surveys of inshore rocky reef communities (Ebeling et al. 1980; Stephens et al. 1984; Larson and DeMartini 1984), and something is known of the soft substrata fishes from 18 m down to about 900 m (Fitch 1966; Mearns 1979; DeMartini and Allen 1984; Cross[1]). There are no published studies on fish assemblages from the shallowest (< 18 m), open-coast, soft substrata habitats. In 1982 we initiated a survey of this inshore habitat. This report describes the results of this survey from 1982 to 1984.

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[1] Cross, J. MS. Fishes of the upper continental shelf off southern California.

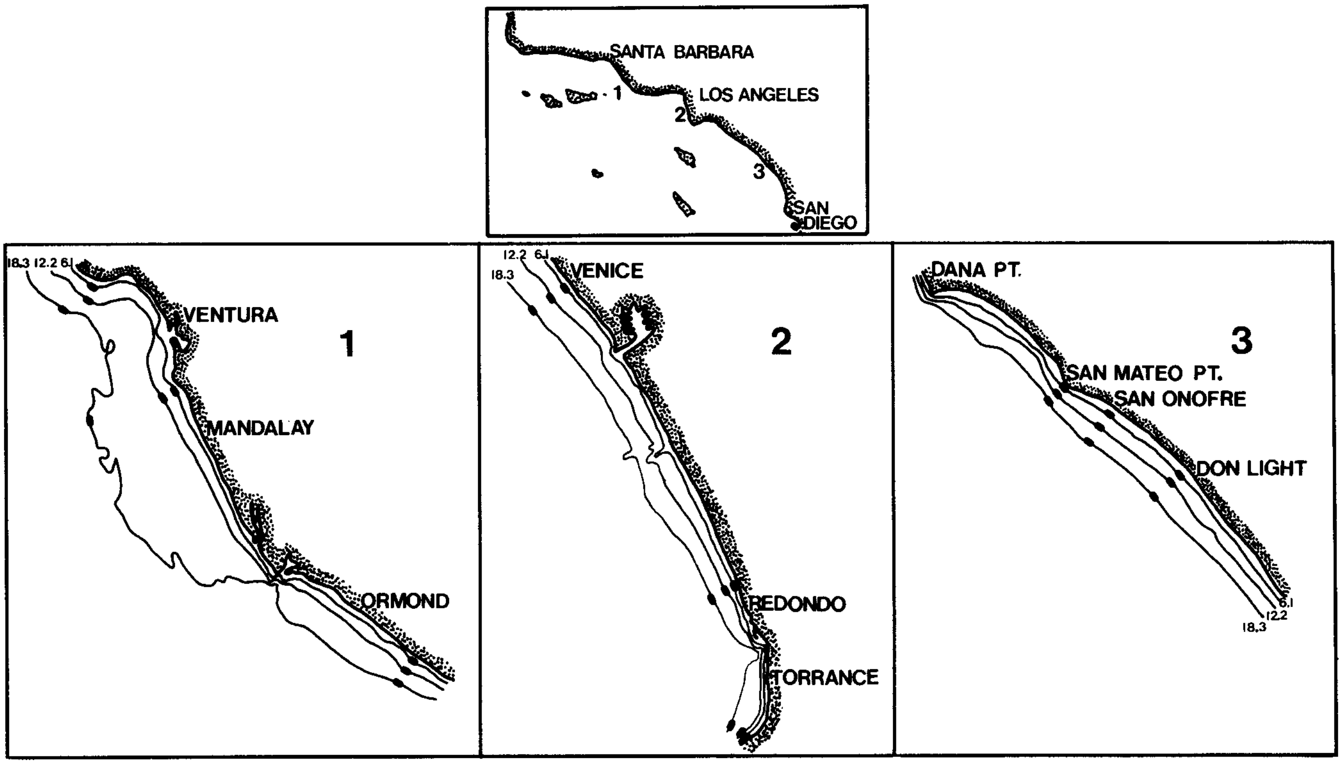

Figure 1. Location of trawling sites within the Southern California Bight. Sampling was conducted in three areas: *1*, Ormond; *2*, Redondo; *3*, San Onofre. Dark ovals indicate the stations—three each along the 6.1-, 12.2-, and 18.3-m isobaths in each area.

METHODS

Sampling was conducted bimonthly from February 1982 to December 1984 off three areas—designated San Onofre, Redondo, and Ormond (Figure 1). Within each area were trawling stations—three each along the 6.1-, 12.2-, and 18.3-m isobaths (Figure 1). In the San Onofre area the stations were San Mateo Point, San Onofre, and Don Light; in the Redondo area they were Torrance, Redondo, and Venice; and in the Ormond area they were Ormond, Mandalay, and Ventura. Table 1 gives precise locations of these stations. Because the study focused on area rather than station, we grouped our results by area. Throughout the paper the word *location* is used interchangeably with *area*.

Each survey consisted of two replicate trawls per day, for two successive days, at each depth and station. As an example, during the February 1982 survey, we made four trawls at 18.3 m off San Mateo Point over two days, two trawls per day. Sampling was conducted during daylight hours with a 7.6-m semiballoon otter trawl towed at two knots for five minutes. Trawls were made along an isobath parallel to shore, in an upcoast direction. All fishes collected were identified (based on Miller and Lea 1972), counted, and measured (standard length).

We used the index of community importance (ICI; Stephens and Zerba 1981) to estimate each species' contribution to its assemblage. ICIs were determined

TABLE 1
Latitude and Longitude of Trawling Stations within the Southern California Bight

Area	Station	Depth (m)	Latitude (N)	Longitude (W)
Ormond	Ventura	6.1	34°16.20′	119°18.34′
		12.2	34°16.03′	119°18.50′
		18.3	34°15.70′	119°18.74′
	Mandalay	6.1	34°13.16′	119°15.72′
		12.2	34°13.18′	119°16.20′
		18.3	13°13.19′	119°17.43′
	Ormond	6.1	34°06.87′	119°09.41′
		12.2	34°06.73′	119°09.61′
		18.3	34°06.30′	119°09.99′
Redondo	Venice	6.1	33°58.64′	118°28.20′
		12.2	33°58.40′	118°28.82′
		18.3	33°58.25′	118°29.24′
	Redondo	6.1	33°51.89′	118°24.39′
		12.2	33°51.76′	118°24.79′
		18.3	33°51.81′	118°24.95′
	Torrance	6.1	33°49.79′	118°23.56′
		12.2	33°49.90′	118°23.72′
		18.3	33°49.43′	118°24.44′
San Onofre	San Mateo	6.1	33°23.50′	117°25.11′
		12.2	33°23.20′	117°36.70′
		18.3	33°22.96′	117°37.13′
	San Onofre	6.1	33°21.19′	117°32.71′
		12.2	33°20.47′	117°34.34′
		18.3	33°21.09′	117°34.01′
	Don Light	6.1	33°19.21′	117°30.43′
		12.2	33°18.83′	117°30.95′
		18.3	33°18.35′	117°31.52′

in the following way. For each assemblage, species were ranked by percent abundance and percent frequency of occurrence. For each species, the two ranks were summed, and the species were reranked based on that sum. The respective ICIs were the sum of the two ranks. We compared the top ten species from each assemblage with Kendall's coefficient of concordance and Kendall's tau coefficient (Siegel 1956).

We tested whether there was an overall seasonal abundance pattern by using a crossed analysis of variance, performed on the log-transformed data for fish abundance (raw count + 1) (Afifi and Azen 1979). Fixed model was assumed with main effects being location, year, and season, with season nested within year. Type III sum of squares was used so that comparison of main effects could be made even in the presence of interactions (Freund and Littell 1981).

Using all data, we noted large interactions, which implied that there was no overall seasonal pattern. We then performed the analysis on three key species—*Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*—and on the rest of the species combined (predominantly various flatfish). In order to take an unbiased approach, we further separated the analyses by water depth (young-of-the-year and 1+ yr fish) and season: winter (December and February) and nonwinter (April, June, August, and October).

We determined fish recruitment patterns (by area, season, and depth) by ascertaining the geometric mean abundance per trawl of small (less than 5 cm SL) individuals by month over the three years. Six species, ranked highest on the ICI, were abundant enough to analyze. Similarly, we wished to exemplify the relative year-class strengths of important species over our three-year study. We selected 12 species and computed the geometric mean abundance per trawl per species, this time of young-of-the-year fishes. Concurrently, we analyzed the abundances of fishes older than one year and plotted this on the same figure.

RESULTS

Species Composition

6.1 m. Midwater, actively swimming species (mainly croakers—Sciaenidae; seaperches—Embiotocidae; and anchovies—Engraulidae) dominated the shallowest isobath and constituted most of the top ten ICI species (Table 2). In all, 82 species and 104,564 individuals were captured.

Queenfish (*Seriphus politus*) had the highest ICI ranking, followed by white croaker (*Genyonemus lineatus*) and northern anchovy (*Engraulis mordax*). These three species composed 86.9% of all fish captured on the 6.1-m isobath. However, *E. mordax*, though taken in high numbers, was encountered in about one-third of all trawls, far less often than *S. politus* or *G. lineatus*. When *E. mordax* was captured, it was often found in large numbers, as many as 7,000 per trawl. Both walleye seaperch (*Hyperprosopon argenteum*) and California halibut (*Paralichthys californicus*), though taken in comparatively low numbers, were caught with greater frequency.

12.2 m. Compared to 6.1 m, slightly more species (87) but far fewer individuals (53,594) were captured along the 12.2-m isobath (Table 3). Some midwater species, particularly *S. politus* and *G. lineatus*, were again very important constituents of this assemblage. However, benthic fishes (flatfishes and the California lizardfish, *Synodus lucioceps*) gained in importance among the top ten ICI species.

Seriphus politus and *G. lineatus* composed 76.8% of all fish taken. However, *S. politus* was not the overwhelmingly dominant species, as it had been in 6.1 m. Here it was the most abundant species (though only about half as many fish were taken as were taken in 6.1 m), but it was encountered less often than along the shallower isobath (44.5% vs 66.6% of all trawls). *G. lineatus* occurred with about the same frequency as in the shallow depth, with somewhat greater abundance. Greatly increasing in frequency of occurrence and abundance over 6.1 m, the specklefin sanddab (*Citharichthys stigmaeus*) was an important member of this assemblage, having the same ICI as the former two species.

18.3 m. Fewest species (80) and lowest total abundance (39,178) occurred along the 18.3-m isobath (Table 4). Flatfishes, continuing the trend begun in 12.2 m, were the group most common among the top ten ICI species; six of the ten were flatfishes. Overall, midwater fishes declined in both abundance and frequency of occurrence.

Citharichthys stigmaeus, ranked first on the ICI, occurred in 64.1% of all trawls, though its percent abundance (7.2%) was nowhere near that of *Genyonemus lineatus*. *G. lineatus* was the most abundant species, constituting 43.4% of all fishes taken, though its frequency of occurrence dropped from what it had been at the 12.2-m stations (33.2% vs 51.6% of all trawls). *Paralichthys californicus*, though not as abundant as six other species, ranked third on the ICI because of its high frequency of occurrence (54.3%). *Seriphus politus*, second in total abundance (19.4%), was nonetheless far less abundant or frequently taken along this isobath than in shallower waters. A number of species (*S. lucioceps*; hornyhead turbot, *Pleuronichthys verticalis*; spotted turbot, *P. ritteri*; fantail sole, *Xystreurys liolepis*; and California tonguefish, *Symphurus atricauda*) that were uncommon in 6.1 m

TABLE 2
Composition of Trawl Catches in 6.1 m, off Three Areas in the Southern California Bight, 1982-84

Species	Numbers	Percent number	Percent frequency of occurrence	ICI
Seriphus politus	48,610	46.49	66.5	2.0
Genyonemus lineatus	11,528	11.02	52.3	5.0
Engraulis mordax	30,702	29.36	34.3	7.0
Hyperprosopon argenteum	2,257	2.16	39.5	8.0
Paralichthys californicus	949	0.91	41.0	9.0
Amphistichus argenteus	768	0.73	32.3	15.0
Phanerodon furcatus	867	0.83	24.9	15.0
Citharichthys stigmaeus	657	0.63	27.2	17.0
Anchoa compressa	2,084	1.99	12.3	19.0
Menticirrhus undulatus	497	0.48	23.9	22.0
Peprilus simillimus	810	0.77	9.7	23.0
Umbrina roncador	516	0.49	14.6	23.0
Syngnathus leptorhynchus	394	0.38	18.9	26.0
Cymatogaster aggregata	537	0.51	9.6	27.0
Pleuronichthys ritteri	213	0.20	14.5	31.5
Platyrhinoidis triseriata	158	0.15	14.5	32.5
Sphyraena argentea	343	0.33	9.4	34.5
Synodus lucioceps	255	0.24	8.8	38.0
Rhinobatos productus	139	0.13	9.4	38.5
Paralabrax nebulifer	113	0.11	9.3	43.0
Heterostichus rostratus	123	0.12	7.1	45.5
Urolophus halleri	106	0.10	7.5	47.0
Embiotoca jacksoni	90	0.09	7.1	50.5
Etrumeus teres	425	0.41	2.2	52.0
Cheilotrema saturnum	107	0.10	4.4	54.0
Roncador stearnsii	135	0.13	3.4	55.0
Cynoscion nobilis	57	0.05	5.6	56.0
Syngnathus californiensis	72	0.07	5.0	57.0
Xystreurys liolepis	45	0.04	5.6	57.0
Myliobatis californica	40	0.04	5.6	58.0
Sardinops sagax	104	0.10	3.1	61.0
Otophidium scrippsi	62	0.06	3.9	61.5
Hysopsetta guttulata	34	0.03	4.2	65.0
Atherinopsis californiensis	35	0.03	3.9	65.5
Paralabrax clathratus	31	0.03	3.0	71.0
Xenistius californiensis	22	0.02	2.6	73.5
Trachurus symmetricus	22	0.02	2.3	74.5
Rhacochilus vacca	17	0.02	2.0	79.0
Micrometrus minimus	19	0.02	1.8	79.5
Brachyistius frenatus	15	0.01	1.8	82.0
Pleuronichthys verticalis	15	0.01	1.7	83.5
Triakis semifasciata	12	0.01	1.5	87.0
Heterodontus francisci	10	0.01	1.5	90.5
Rhacochilus toxotes	11	0.01	1.2	91.5
Scianidae juveniles (unident.)	400	0.38	0.1	91.5
Squatina californica	11	0.01	1.1	94.0
Anisotremus davidsonii	12	0.01	0.7	95.5
Mustelus henlei	9	0.01	1.4	95.5
Hypsurus caryi	9	0.01	0.9	101.5
Leptocottus armatus	8	0.01	1.1	103.0
Pleuronichthys coenosus	8	0.01	1.1	103.0
Symphurus atricauda	7	0.01	1.1	104.5
Atherinops affinis	9	0.01	0.6	105.0
Scomber japonicus	9	0.01	0.6	105.0
Paralabrax maculatofasciatus	9	0.01	0.4	110.5
Sebastes auriculatus	4	<0.01	0.6	115.0
Squalus acanthias	4	<0.01	0.6	115.0
Oxyjulis californica	9	0.01	0.3	116.5
Gibbonsia elegans	5	<0.01	0.4	117.5
Stereolepis gigas	5	<0.01	0.4	117.5
Chromis punctipinnis	4	<0.01	0.4	120.5
Scorpaena guttata	4	<0.01	0.4	120.5
Mustelus californicus	3	<0.01	0.4	123.5
Porichthys myriaster	3	<0.01	0.4	123.5
Halichoeres semicinctus	2	<0.01	0.3	134.0
Parophrys vetulus	2	<0.01	0.3	134.0
Raja binoculata	2	<0.01	0.3	134.0
Scorpaenichthys marmoratus	2	<0.01	0.3	134.0
Chilara taylori	2	<0.01	0.1	144.5
Citharichthys sordidus	2	<0.01	0.1	144.5
Porichthys notatus	2	<0.01	0.1	144.5
Amphistichus koelzi	1	<0.01	0.1	154.0
Glyptocephalus zachirus	1	<0.01	0.1	154.0
Gobiesox rhessodon	1	<0.01	0.1	154.0
Gymnura marmorata	1	<0.01	0.1	154.0
Hypsoblennius gentilis	1	<0.01	0.1	154.0
Hypsoblennius gilberti	1	<0.01	0.1	154.0
Icelinus quadriseriatus	1	<0.01	0.1	154.0
Leuresthes tenuis	1	<0.01	0.1	154.0
Platichthys stellatus	1	<0.01	0.1	154.0
Raja inornata	1	<0.01	0.1	154.0
Sebastes rastrelliger	1	<0.01	0.1	154.0
Sebastes serranoides	1	<0.01	0.1	154.0
Nothing retrieved		5.36		
Total	104,564			

and 12.2 m were more abundant and more frequently encountered in 18.3 m.

Rank correlation tests between assemblages indicate a high degree of similarity between adjacent depths (6.1 vs 12.1, 12.1 vs 18.3 m), but little similarity between 6.1 and 18.3 m (Table 5). The tau coefficient showed close to zero relationship between the 6.1 and 18.3-m depths. Between 6.1 and 18.3 m, only five species were held in common among the top ten in ICI (*C. stigmaeus*, *G. lineatus*, *P. californicus*, *S. politus*, and *E. mordax*). Of these, only *G. lineatus*, *P. californicus*, and *S. politus* were found in the top five at both depths. As Table 6 indicates, there is not a significant relationship in the assemblages by depth. In general, there was a shift with depth from actively swimming, schooling species to benthic, solitary forms. Associated with this decline in schooling species was a decrease in the number of fish taken.

Kendall's coefficient of concordance was computed to determine whether the top ten species were the same for each of the years. It is obvious from Table 6 that the fish assemblages were similar to each other over the

TABLE 3
Composition of Trawl Catches in 12.1 m, off Three Areas in the Southern California Bight, 1982-84

Species	Numbers	Percent number	Percent frequency of occurrence	ICI
Citharichthys stigmaeus	1,727	3.2	57.4	5.0
Genyonemus lineatus	15,255	28.5	51.6	5.0
Seriphus politus	25,900	48.3	44.5	5.0
Paralichthys californicus	960	1.8	57.1	8.0
Phanerodon furcatus	1,428	2.7	29.7	11.0
Engraulis mordax	2,703	5.0	21.4	12.0
Pleuronichthys ritteri	409	0.8	31.2	14.0
Hyperprosopon argenteum	574	1.1	22.3	15.0
Synodus lucioceps	855	1.6	19.9	17.0
Xystreurys liolepis	290	0.5	22.2	20.0
Heterostichus rostratus	303	0.6	16.9	24.0
Paralabrax nebulifer	281	0.5	19.1	24.0
Pleuronichthys verticalis	201	0.4	18.8	27.0
Peprilus simillimus	306	0.6	8.9	29.0
Plathyrhinoidis triseriata	150	0.3	16.3	31.0
Cymatogaster aggregata	240	0.4	9.0	31.5
Syngnathus leptorhynchus	109	0.2	10.8	34.5
Rhinobatos productus	97	0.2	10.8	36.5
Menticirrhus undulatus	103	0.2	9.0	37.5
Embiotoca jacksoni	90	0.2	7.0	44.5
Amphistichus argenteus	77	0.1	7.8	46.0
Hypsopsetta guttulata	63	0.1	8.7	49.0
Symphurus atricauda	85	0.2	6.0	49.0
Halichoeres semicinctus	85	0.2	5.5	50.5
Scorpaena guttata	71	0.1	7.0	50.5
Anchoa compressa	165	0.3	3.0	53.5
Otophidium scrippsi	74	0.1	5.4	54.5
Paralabrax clathratus	73	0.1	5.4	55.5
Pleuronichthys coenosus	48	0.1	6.0	58.5
Xenistius californiensis	123	0.2	2.7	58.5
Myliobatis californica	45	0.1	6.3	59.0
Syngnathus californiensis	50	0.1	4.3	61.5
Cheilotrema saturnum	56	0.1	3.2	65.0
Rhacochilus vacca	45	0.1	4.1	66.0
Sphyraena argentea	50	0.1	3.2	66.5
Rhacochilus toxotes	34	0.1	3.8	72.0
Raja binoculata	26	<0.1	3.3	76.0
Hypsurus caryi	30	0.1	3.2	77.0
Oxyjulis californica	45	0.1	2.2	78.0
Umbrina roncador	35	0.1	2.7	79.5
Urolophus halleri	21	<0.1	3.0	82.5
Brachyistius frenatus	36	0.1	1.1	85.5
Porichthys notatus	23	<0.1	2.2	87.0
Gibbonsia elegans	17	<0.1	2.2	89.0
Anisotremus davidsonii	14	<0.1	1.7	92.0
Heterodontus francisci	11	<0.1	1.4	94.0
Cynoscion nobilis	9	<0.1	1.1	97.5
Citharichthys sordidus	10	<0.1	0.8	103.0
Sebastes auriculatus	7	<0.1	0.9	103.0
Mustelus henlei	6	<0.1	0.9	106.0
Sebastes miniatus	6	<0.1	0.9	106.0
Stereolepis gigas	6	<0.1	0.9	106.0
Porichthys myriaster	7	<0.1	0.8	106.5
Etrumeus teres	31	0.1	0.3	112.0
Roncador stearnsii	5	<0.1	0.8	113.0
Raja inornata	6	<0.1	0.6	114.0
Parophrys vetulus	8	<0.1	0.5	115.5
Atherinopsis californiensis	5	<0.1	0.6	117.5
Paralabrax maculatofasciatus	5	<0.1	0.6	117.5
Sciaenidae juveniles (unident.)	39	0.1	0.2	119.0
Gymnura marmorata	4	<0.1	0.6	121.5
Sardinops sagax	4	<0.1	0.6	121.5
Squatina californica	4	<0.1	0.6	121.5
Scorpaenichthys marmoratus	4	<0.1	0.5	127.5
Semicossyphus pulchrum	4	<0.1	0.5	127.5
Atherinops affinis	3	<0.1	0.5	133.0
Hyperprosopon anale	3	<0.1	0.5	133.0
Leptocottus armatus	3	<0.1	0.5	133.0
Chromis punctipinnis	3	<0.1	0.3	139.5
Pleuronichthys decurrens	3	<0.1	0.3	139.5
Citharichthys xanthostigma	2	<0.1	0.3	145.5
Sebastes rastrelliger	2	<0.1	0.3	145.5
Trachurus symmetricus	2	<0.1	0.3	145.5
Triakis semifasciata	2	<0.1	0.3	145.5
Sebastes paucispinis	3	<0.1	0.2	150.5
Chilara taylori	2	<0.1	0.2	156.5
Hypsoblennius gilberti	2	<0.1	0.2	156.5
Caulolatilus princeps	1	<0.1	0.2	165.0
Clupea harengus pallasii	1	<0.1	0.2	165.0
Gibbonsia metzi	1	<0.1	0.2	165.0
Girella nigricans	1	<0.1	0.2	165.0
Medialuna californiensis	1	<0.1	0.2	165.0
Neoclinus uninotatus	1	<0.1	0.2	165.0
Odontopyxis trispinosa	1	<0.1	0.2	165.0
Squalus acanthias	1	<0.1	0.2	165.0
Stellerina xyosterna	1	<0.1	0.2	165.0
Torpedo californica	1	<0.1	0.2	165.0
Zalembius rosaceus	1	<0.1	0.2	165.0
Nothing retrieved		2.8		
Total	53,594			

three years. Similarly, it was found that the three areas (Ormond, Redondo, and San Onofre) were significantly similar in their fish assemblages (Table 6).

Description of Species Assemblages by and between Areas

Ormond area. Seriphus politus and *Genyonemus lineatus* were the dominant species in trawls along the three isobaths: *Seriphus* first in 6.1 m, *Genyonemus* in 12.2 and 18.3 m, (Table 7). Both species remained abundant throughout the depth ranges, *Genyonemus* increasing with depth, *Seriphus* decreasing. *Engraulis mordax*, *Paralichthys californicus*, and *Citharichthys stigmaeus* were important species at all depths. There was a gradual displacement of shallow-water species (such as *Amphistichus argenteus* and *Hyperprosopon*

TABLE 4
Composition of Trawl Catches in 18.3 m, off Three Areas in the Southern California Bight, 1982-84

Species	Numbers	Percent number	Percent frequency of occurrence	ICI
Citharichthys stigmaeus	2,830	7.2	64.1	5.0
Genyonemus lineatus	17,022	43.4	33.2	8.0
Paralichthys californicus	729	1.9	54.3	9.0
Seriphus politus	7,598	19.4	27.5	10.0
Synodus lucioceps	1,555	4.0	35.8	10.0
Pleuronichthys verticalis	651	1.7	44.6	11.0
Pleuronichthys ritteri	1,088	2.8	35.3	12.0
Xystreurys liolepis	624	1.6	39.2	13.0
Engraulis mordax	4,096	10.5	16.1	14.0
Symphurus atricauda	415	1.1	21.0	19.0
Pleuronichthys coenosus	383	1.0	18.5	21.0
Phanerodon furcatus	287	0.7	13.6	24.0
Otophidium scrippsi	212	0.5	8.5	30.0
Syngnathus leptorhynchus	110	0.3	10.4	30.0
Paralabrax nebulifer	106	0.3	10.6	31.5
Scorpaena guttata	107	0.3	8.7	33.0
Citharichthys xanthostigma	112	0.3	5.5	34.0
Peprilus simillimus	158	0.4	5.1	36.5
Hypsopsetta guttulata	62	0.2	9.3	37.0
Cymatogaster aggregata	106	0.3	5.1	41.0
Platyrhinoidis triseriata	55	0.1	7.6	41.0
Heterostichus rostratus	48	0.1	5.4	45.0
Citharichthys sordidus	72	0.2	3.3	50.0
Hippoglossina stomata	43	0.1	4.9	52.0
Porichthys notatus	69	0.2	3.0	52.5
Raja binoculata	35	0.1	5.2	53.0
Hyperprosopon argenteum	45	0.1	4.1	54.0
Pleuronichthys decurrens	46	0.1	3.6	55.0
Myliobatis californica	40	0.1	4.4	56.0
Porichthys myriaster	41	0.1	4.0	57.5
Rhinobatos productus	32	0.1	4.3	59.0
Paralabrax clathratus	41	0.1	2.2	64.5
Urolophus halleri	25	0.1	3.0	66.5
Rhacochilus toxotes	21	0.1	2.5	70.0
Menticirrhus undulatus	22	0.1	1.9	72.0
Parophrys vetulus	17	<0.1	2.4	72.5
Syngnathus californiensis	17	<0.1	1.6	75.5
Sardinops sagax	54	0.1	0.5	78.5
Icelinus quadriseriatus	14	<0.1	1.1	83.0
Sebastes miniatus	13	<0.1	1.3	83.0
Chilara taylori	16	<0.1	0.9	83.5
Heterodontus francisci	10	<0.1	1.3	84.5
Sebastes auriculatus	8	<0.1	1.1	88.0
Zalembius rosaceus	13	<0.1	0.8	90.0
Hypsurus caryi	7	<0.1	0.9	92.0
Amphistichus argenteus	8	<0.1	0.8	93.0
Brachyistius frenatus	27	0.1	0.3	94.0
Rhacochilus vacca	6	<0.1	0.8	96.5
Raja inornata	5	<0.1	0.8	98.0
Mustelus henlei	5	<0.1	0.6	102.0
Anchoa compressa	7	<0.1	0.5	103.0
Chitonotus pugetensis	4	<0.1	0.6	105.0
Squatina californica	4	<0.1	0.6	105.0
Torpedo californica	4	<0.1	0.6	105.0
Etrumeus teres	4	<0.1	0.5	109.0
Caulolatilus princeps	3	<0.1	0.5	112.0
Semicossyphus pulchrum	14	<0.1	0.2	114.0
Cheilotrema saturnum	2	<0.1	0.3	122.0
Cynoscion nobilis	2	<0.1	0.3	122.0
Embiotoca jacksoni	2	<0.1	0.3	122.0
Neoclinus uninotatus	2	<0.1	0.3	122.0
Platichthys stellatus	2	<0.1	0.3	122.0
Xenistius californiensis	2	<0.1	0.3	122.0
Sebastes dallii	3	<0.1	0.2	130.0
Zaniolepis latipinnis	2	<0.1	0.2	134.5
Chromis punctipinnis	1	<0.1	0.2	145.5
Coryphopterus nicholsii	1	<0.1	0.2	145.5
Glyptocephalus zachirus	1	<0.1	0.2	145.5
Gobiesox rhessodon	1	<0.1	0.2	145.5
Halichoeres semicinctus	1	<0.1	0.2	145.5
Hydrolagus colliei	1	<0.1	0.2	145.5
Lepidogobius lepidus	1	<0.1	0.2	145.5
Leptocottus armatus	1	<0.1	0.2	145.5
Mustelus californicus	1	<0.1	0.2	145.5
Odontopyxis trispinosa	1	<0.1	0.2	145.5
Paralabrax maculatofasciatus	1	<0.1	0.2	145.5
Scorpaenichthys marmoratus	1	<0.1	0.2	145.5
Sphyraena argentea	1	<0.1	0.2	145.5
Squalus acanthias	1	<0.1	0.2	145.5
Stereolepis gigas	1	<0.1	0.2	145.5
Nothing retrieved		0.0		
Total	3,978			

argenteum) by *Synodus lucioceps*, *Pleuronichthys verticalis*, and *Symphurus atricauda*.

Redondo area. As in the Ormond survey, *S. politus* and *G. lineatus* were the highest ranked species in 6.1 m (Table 8). *Paralichthys californicus, H. argenteum,* and *E. mordax* were also important. *Engraulis,* though second most abundant, was very patchy in its distribution. Most of the fish we report here were caught in a few trawls that captured thousands of individuals.

In contrast to the Ormond area, *S. politus* and *G. lineatus*, though important species in 6.1 m, were not dominant through all depths (Table 8). In 12.2 m, *C. stigmaeus* joined *G. lineatus* as the highest ranked on the ICI, though *Seriphus*, ranked fourth, was still most abundant. Flatfish dominated 18.3 m, with six species among the top ten. *C. stigmaeus* was again ranked first, though *Pleuronichthys ritteri* was taken with greater frequency (86.2%). In fact at Redondo in 18.3 m, *P. ritteri* was taken with the greatest frequency of any species at any area in our study. *Paralichthys californicus*, *Pleuronichthys coenosus*, and *S. lucioceps* were also important species. *Seriphus* and *Genyo-*

TABLE 5
Comparisons of Species Rankings (Using the Index of Community Importance) between Depths, All Areas and Years Combined

Depth vs Depth		Kendall's tau	*P*
6.1	12.2	0.372	0.002*
6.1	18.3	0.069	0.604
12.2	18.3	0.421	0.0002*

*Significant at $P \leq 0.5$

TABLE 7
Composition of Ormond Area Trawl Catches (Top Ten Species, Based on Index of Community Importance), 1982-84

Species	Number	Percent number	Percent frequency of occurrence	ICI
6.1-m isobath				
1. *Seriphus politus*	10,088	44.2	73.6	2.0
2. *Genyonemus lineatus*	4,871	21.3	62.0	5.0
3. *Engraulis mordax*	4,883	21.4	34.6	7.0
4. *Hyperprosopon argenteum*	866	3.8	54.3	7.0
5. *Amphistichus argenteus*	498	2.1	48.6	9.0
6. *Paralichthys californicus*	125	0.5	27.4	14.0
7. *Phanerodon furcatus*	224	0.9	26.0	14.0
8. *Citharichthys stigmaeus*	122	0.5	25.4	17.0
9. *Peprilus simillimus*	304	1.3	13.4	19.0
10. *Syngnathus leptorhynchus*	92	0.4	19.2	20.0
12.2-m isobath				
1. *Genyonemus lineatus*	9,597	42.0	71.3	2.0
2. *Seriphus politus*	9,471	41.5	66.5	4.0
3. *Citharichthys stigmaeus*	419	1.8	50.4	7.0
4. *Engraulis mordax*	1,075	4.7	33.4	10.0
5. *Hyperprosopon argenteum*	351	1.5	37.8	11.0
6. *Phanerodon furcatus*	374	1.6	35.4	11.0
7. *Paralichthys californicus*	161	0.7	43.6	13.0
8. *Synodus lucioceps*	236	1.0	18.4	18.0
9. *Peprilus simillimus*	269	1.1	17.9	18.5
10. *Pleuronichthys verticalis*	91	0.4	24.7	19.0
18.3-m isobath				
1. *Genyonemus lineatus*	13,374	57.9	59.7	2.0
2. *Seriphus politus*	5,780	25.0	55.3	4.0
3. *Citharichthys stigmaeus*	940	4.0	47.5	8.0
4. *Engraulis mordax*	804	3.4	36.8	11.0
5. *Paralichthys californicus*	209	0.9	53.3	11.0
6. *Pleuronichthys verticalis*	248	1.0	51.9	11.0
7. *Symphurus atricauda*	354	1.5	41.7	12.0
8. *Synodus lucioceps*	356	1.5	27.7	13.0
9. *Otophidium scrippsi*	174	0.7	22.8	19.0
10. *Phanerodon furcatus*	125	0.5	19.4	22.0

nemus were near or at the bottom of the top ten species. *Seriphus*, while still second in abundance, was infrequently (10.5) encountered.

San Onofre area. As at Ormond and Redondo, *Seriphus* and *Genyonemus* ranked first and second among species captured in 6.1 m (Table 9). *Engraulis mordax* ranked third; second in abundance (behind *Seriphus*); and was taken more consistently (40% of the trawls) than at the more northern stations. California corbina, *Menticirrhus undulatus*; deepbody anchovy, *Anchoa compressa*; and yellowfin croaker, *Umbrina roncador* (all ranked in the top ten at San Onofre) were absent from this list at Ormond and Redondo.

Citharichthys stigmaeus and *G. lineatus* tied for first ranking in 12.2 m (Table 9), though *Seriphus* was by far the most abundant. However, its frequency of occurrence declined markedly from 74.5% in 6.1 m to 39.8% in 12.2 m. *Paralichthys californicus*, as at every isobath and area, was an important constituent, and was taken in over half of the trawls (53.0%). As in 12.2 m, *C. stigmaeus* was ranked first in 18.3 m, followed by *Synodus lucioceps* and *G. lineatus*. *Genyonemus* was most abundant, though taken only about 28% of the time. As at Redondo, flatfishes (such as *P. verticalis*, *Xystruerys liolepis*, and *P. californicus*) were the most commonly taken group.

Compared to fish assemblages in 6.1 m, those of 12.2 m were somewhat more heterogenous. While *Seriphus* and *Genyonemus* continued to be dominant (both numerically and in occurrence) off Ormond, they were not as important off San Onofre and Redondo. They remained the most abundant, but were no longer the most frequently encountered species (these were *Citharichthys sordidus*, *P. californicus*, and also *P. ritteri* off Redondo).

TABLE 6
Comparisons of the Top Ten Species (Index of Community Importance) between Locations, Years, and Depths, Using Kendall's Coefficient of Concordance

	W	K	*N*	X^2	DF	*P*	*R*
Location	.66	3	13	23.8	12	.022	.49
Year	.68	3	13	24.6	12	.025	.52
Depth	.50	3	15	21.1	14	.100	.25

In 18.3 m, densely aggregating, midwater fishes continued to decrease in abundance at Redondo and San Onofre. Off Redondo, *C. stigmaeus* was most abundant, and *P. ritteri* was third, close behind *Seriphus politus* (which was captured only 10.5% of the time). Off San Onofre, *G. lineatus* was taken in highest numbers, though captured in only 28.3% of the trawls. Five species (*C. stigmaeus*, *S. lucioceps*, *P.*

TABLE 8
Composition of Redondo Area Trawl Catches (Top Ten Species, Based on Index of Community Importance), 1982-84

Species	Number	Percent number	Percent frequency of occurrence	ICI
6.1-m isobath				
1. *Seriphus politus*	17,393	45.9	51.4	3.0
2. *Genyonemus lineatus*	1,668	4.4	43.3	6.0
3. *Paralichthys californicus*	620	1.6	55.7	6.0
4. *Hyperprosopon argenteum*	995	2.6	35.7	9.5
5. *Engraulis mordax*	13,834	36.5	28.0	10.0
6. *Citharichthys stigmaeus*	429	1.1	35.7	11.5
7. *Phanerodon furcatus*	341	0.9	29.0	16.0
8. *Pleuronichthys ritteri*	195	0.5	37.6	16.0
9. *Sphyraena argentea*	240	0.6	13.8	21.5
10. *Paralabrax nebulifer*	82	0.2	19.5	25.0
12.2-m isobath				
1. *Citharichthys stigmaeus*	814	6.4	61.4	6.1
2. *Genyonemus lineatus*	1,613	12.7	36.6	6.0
3. *Paralichthys californicus*	550	4.3	74.2	7.0
4. *Seriphus politus*	5,724	45.3	27.6	9.0
5. *Pleuronichthys ritteri*	306	2.4	62.3	10.0
6. *Phanerodon furcatus*	669	5.3	23.3	13.0
7. *Heterostichus rostratus*	242	1.9	35.2	14.0
8. *Xystreurys liolepis*	174	1.3	33.3	16.5
9. *Synodus lucioceps*	492	3.8	20.9	17.0
10. *Paralabrax nebulifer*	174	1.3	30.4	17.5
18.3-m isobath				
1. *Citharichthys stigmaeus*	1,141	14.8	71.4	4.0
2. *Pleuronichthys ritteri*	1,032	13.4	86.1	5.0
3. *Paralichthys californicus*	356	4.6	66.1	10.0
4. *Pleuronichthys coenosus*	377	4.9	52.8	10.0
5. *Synodus lucioceps*	439	5.7	32.8	11.5
6. *Xystreurys liolepis*	286	3.7	50.4	13.0
7. *Pleuronichthys verticalis*	176	2.2	32.8	16.5
8. *Seriphus politus*	1,125	14.6	10.4	18.0
9. *Scorpaena guttata*	105	1.3	25.2	19.0
10. *Genyonemus lineatus*	265	3.4	12.3	21.5

TABLE 9
Composition of San Onofre Area Trawl Catches (Top Ten Species, Based on Index of Community Importance), 1982-84

Species	Number	Percent number	Percent frequency of occurrence	ICI
6.1-m isobath				
1. *Seriphus politus*	21,129	48.0	74.5	2.0
2. *Genyonemus lineatus*	4,989	11.3	51.8	5.0
3. *Engraulis mordax*	11,985	27.2	40.2	6.0
4. *Menticirrhus undulatus*	362	0.8	41.2	10.0
5. *Anchoa compressa*	2,070	4.7	31.9	11.0
6. *Hyperprosopon argenteum*	396	0.9	29.1	14.0
7. *Paralichthys californicus*	204	0.4	39.8	17.0
8. *Amphistichus argenteus*	183	0.4	32.8	19.0
9. *Syngnathus leptorhynchus*	272	0.6	25.0	19.0
10. *Umbrina roncador*	299	0.6	24.5	19.0
12.2-m isobath				
1. *Citharichthys stigmaeus*	494	2.7	60.1	5.0
2. *Genyonemus lineatus*	4,045	22.2	47.2	5.0
3. *Seriphus politus*	10,705	58.9	39.8	5.0
4. *Paralichthys californicus*	249	1.3	53.2	8.0
5. *Phanerodon furcatus*	385	2.1	30.5	10.0
6. *Engraulis mordax*	972	5.3	19.9	13.0
7. *Paralabrax nebulifer*	103	0.5	24.5	15.0
8. *Synodus lucioceps*	127	0.6	20.3	17.0
9. *Pleuronichthys ritteri*	78	0.4	22.6	19.0
10. *Xystreurys liolepis*	81	0.4	21.2	19.0
18.3-m isobath				
1. *Citharichthys stigmaeus*	749	8.9	72.6	5.0
2. *Synodus lucioceps*	760	9.0	46.2	6.5
3. *Genyonemus lineatus*	3,383	40.2	28.2	7.0
4. *Pleuronichthys verticalis*	227	2.7	49.0	9.0
5. *Xystreurys liolepis*	246	2.9	46.2	9.5
6. *Paralichthys californicus*	164	1.9	43.5	13.0
7. *Seriphus politus*	693	8.3	17.5	13.0
8. *Engraulis mordax*	1,624	19.3	8.7	16.0
9. *Citharichthys xanthostigma*	111	1.3	15.7	18.0
10. *Symphurus atricauda*	52	0.6	18.0	18.0

verticalis, *X. liolepis*, and *P. californicus*) were taken more frequently. *Genyonemus* and *Seriphus* were still the major species off Ormond, constituting 82.9% of all fishes taken. *Genyonemus* was captured more often in 18.3 m (57.9%) than along the shallower isobaths; *Seriphus* (25.0%) dropped in occurrence. *Paralichthys californicus*, as at every isobath and area, was among the top ten species. It did not contribute large numbers, but was usually taken in at least 50% of the trawls.

Abundance

Off San Onofre and Redondo (discounting variability in fish sizes and seasonal abundances), fishes were most abundant in 6.1 m, declining sharply in 12.2 and 18.3 m (Figure 2). In contrast, fish abundances were constant through the three isobaths off Ormond. As discussed previously, *Seriphus* and *Genyonemus lineatus* were the dominant species in 6.1 m throughout the bight, accounting for an overwhelming percentage of the total catch. Off San Onofre and Redondo, these species declined in importance with depth, and no other species replaced them in numbers. Off Ormond, croakers remained abundant at all three isobaths. However, there was a shift with depth in the relative number of *Seriphus* and *Genyonemus*. *Seriphus* was most common in 6.1 m, and *Genyonemus* in 18.3 m.

Discounting seasonal variability, abundance along

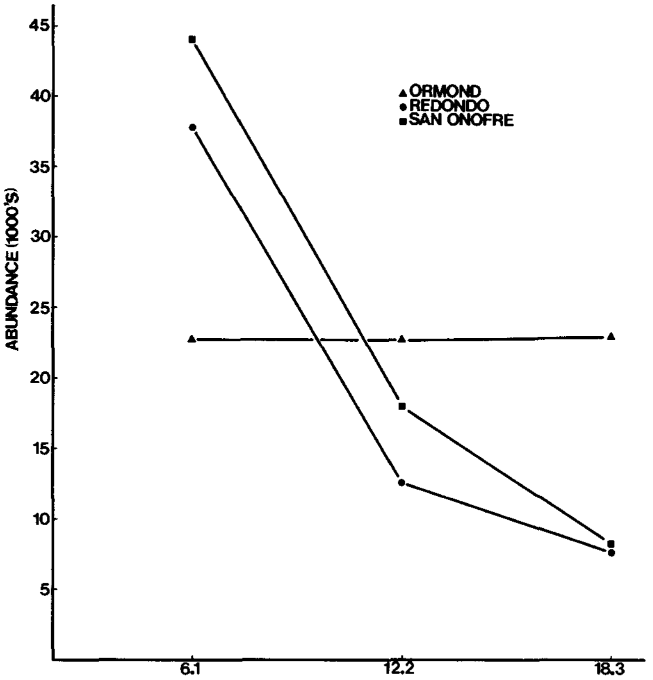

Figure 2. Abundance of fishes taken by trawl at the Ormond, Redondo, and San Onofre areas, along three isobaths—all years combined.

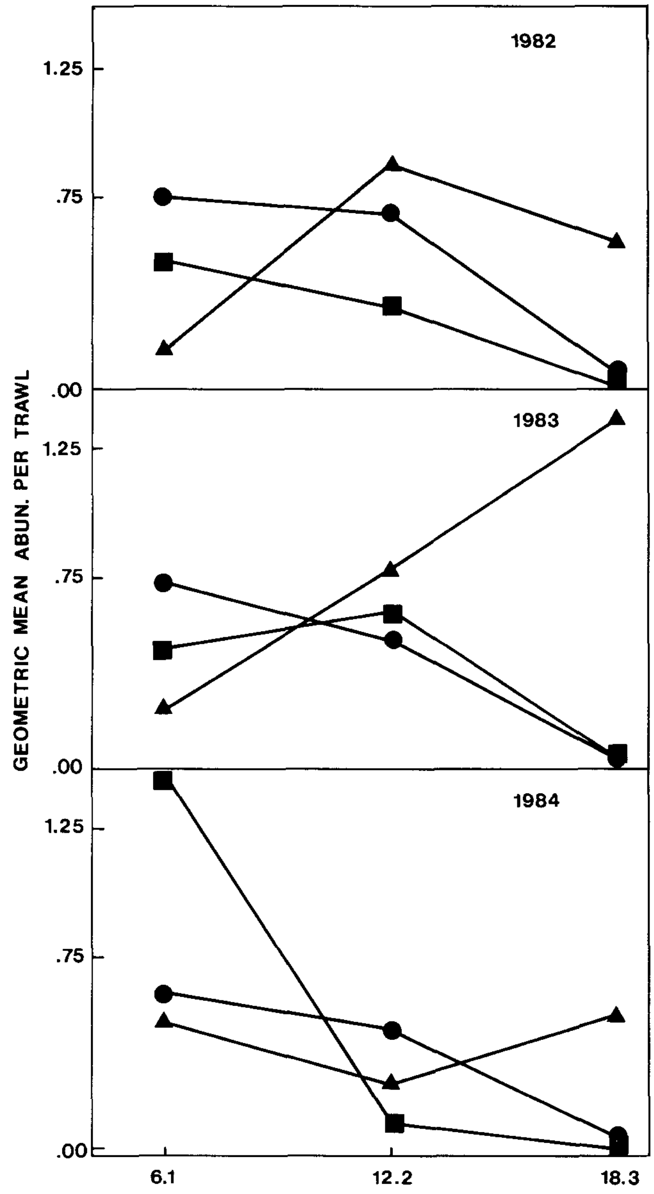

Figure 3. Yearly abundances of fishes taken by trawl, along three isobaths, all areas combined.

these isobaths varied with year and area (Figure 3). With a few exceptions, there was little consistency in these patterns. In all years, catches were highest in 12.2 and 18.3 m off Ormond. In these two depths, catches off Redondo and San Onofre tended to be similar. Overall, catches were lowest in 1984, with the exception of 6.1 m off San Onofre, where there was a strong recruitment of *S. politus*, *E. mordax*, and *G. lineatus*.

The cross-nested analysis of variance (Tables 10-13) represent the main effects—location or area (San Onofre, Redondo, Ormond), year (1982-84), and season (nonwinter, winter)—nested within year, and the amount of interactions between these effects. Interactions tend to be significant where patterns are not consistent at every level, i.e., where trends are not parallel (e.g., Figure 4, Table 10, *S. politus*, young-of-the-year, 12.2 m). Inconsistencies such as these sometimes suppress the interpretation of main effects, whereas nonsignificant interactions (e.g., Figure 4, Table 10, *S. politus*, young-of-the-year, 6.1 m) help interpret the main effects. We also performed the Duncan multiple range test (Steel and Torrie 1980) to gain better insight of the ANOVA; this test is presented in the Appendix.

Table 10 (*S. politus*, young-of-the-year, 6.1 m) indicates that all main effects are significant. At each location, *S. politus* young-of-the-year showed similarity in mean abundance within season. Generally, fewer fish inhabited these waters in winter; the fish were significantly most abundant off San Onofre (Figure 4; Appendix). By contrast, a less coherent pattern was evident with significant interactions in 12.2-and 18.3-m depths. There were some seasonal similarities for both depths, particularly off Ormond and Redondo (Figure 4; Appendix). This reverse of the 6.1-m pattern implies that young-of-the-year *S. politus* may seek the deeper isobath during winter off Ormond and Redondo. However, this was not seen for San Onofre, perhaps because of the relatively few fish taken off this location.

Seriphus politus of 1+ yrs exhibited a pattern similar to younger fish in 6.1 m; in most cases, winter lows (Figure 4; Table 10) were significantly greater in 1982 and 1984 (Appendix). Mean abundances off San

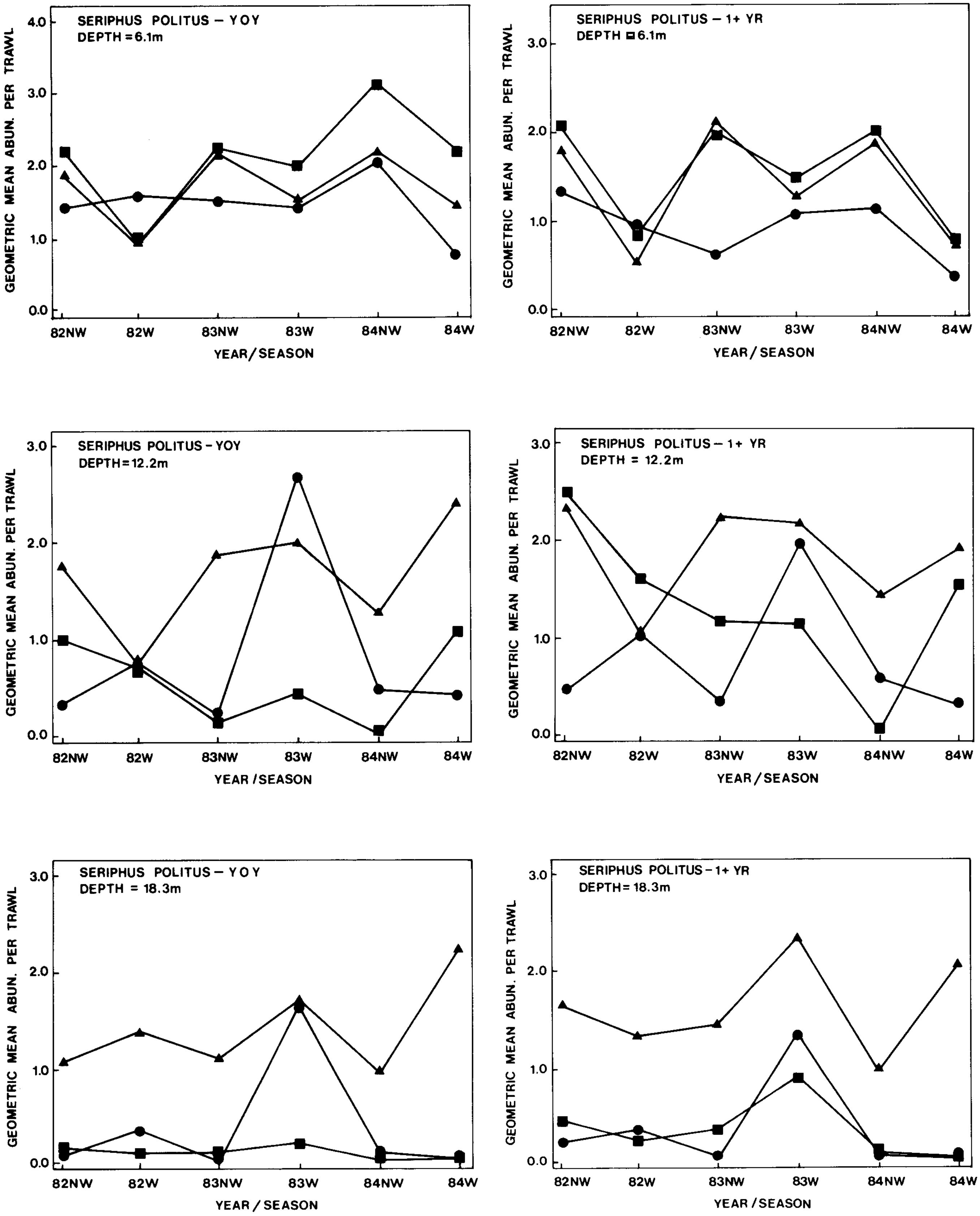

Figure 4. Catch per trawl of young-of-the-year and 1+ yr *Seriphus politus* at three areas and three depths during winter (December and February) and nonwinter (April, June, August, October) 1982-84. Squares = San Onofre, circles = Redondo, triangles = Ormond.

TABLE 10
Cross-Nested ANOVA of *Seriphus politus* (Young-of-the-Year and 1+ Yr) Log Abundance, Southern California Bight, 1982-84

	1+ yr				YOY			
Source	DF	Sum of squares	Mean square	*F* value	DF	Sum of squares	Mean square	*F* value
6.1-m depth								
Location	2	37.33		6.12 **	2	38.76		5.78 **
Year	2	6.68		1.09 NS	2	22.55		3.36 **
Season(year)	3	99.41		10.86 ****	3	72.98		7.26 ****
Location*year	4	10.58		0.87 NS	4	24.88		1.86 NS
Location*season(year)	6	23.60		1.29 NS	6	25.34		1.26 NS
Model	17	209.50	12.32	4.04 ****	17	204.90	12.05	3.59 ****
Error	616	1880.26	3.05	—	616	2065.28	3.35	—
12.2-m depth								
Location	2	102.85		18.82 ****	2	123.31		33.82 ****
Year	2	31.73		5.81 **	2	12.24		3.36 **
Season(year)	3	39.42		4.81 **	3	68.47		12.52 ****
Location*year	4	44.34		4.06 **	4	49.72		6.82 ****
Location*season(year)	6	83.45		5.09 ****	6	77.56		7.09 ****
Model	17	403.15	23.72	8.68 ****	17	339.59	19.98	10.96 ****
Error	614	1678.00	2.73	—	614	1119.20	1.82	—
18.3-m depth								
Location	2	198.79		76.40 ****	2	169.52		80.60 ****
Year	2	27.30		10.49 ****	2	7.81		3.71 **
Season(year)	3	43.88		11.24 ****	3	37.32		11.83 ****
Location*year	4	2.26		0.43 NS	4	15.24		3.62 **
Location*season(year)	6	18.11		2.32 **	6	33.96		5.38 ****
Model	17	299.28	17.60	13.53 ****	17	239.33	14.08	13.39 ****
Error	614	798.84	1.30	—	614	645.72	1.05	—

**** $P < .0001$
** $P < .05$
NS $P > .05$

Onofre and Ormond were quite similar, whereas Redondo was significantly lower. For 12.2 and 18.3 m, interactions were significant, and not too many patterns emerged (Table 10). But among years, average abundance was significantly lower for 1984 and, in 18.3 m, Ormond was considerably higher (Figure 4; Appendix).

Young-of-the-year *G. lineatus* exhibited a pattern similar to *S. politus* in 6.1 m. Again there were winter lows and nonwinter peaks, and young fish were higher in mean abundance off San Onofre (Table 11; Figure 5; Appendix). Young-of-the-year mean abundance decreased in 12.2 and 18.3 m, except off Ormond, where it was significantly higher than in the other two areas. There was no single seasonal pattern in 12.2 m, and too few fish were taken at San Onofre and Redondo in 18.3 m. However, as with *S. politus*, *G. lineatus* young-of-the-year had higher mean abundance in 6.1 m.

There was relatively little similarity in abundance of 1+ yr *G. lineatus* between areas over time (Figure 5). Redondo did not exhibit cycles similar to the other areas, and—as can be noted from the ANOVA (Table 11)—the interaction was significant. Mean abundance is significantly greater for Ormond and generally lower in winter (Appendix). For 12.2 m, the only pattern apparent is that Ormond has significantly higher mean abundance (Appendix). In 18.3 m, mean abundance patterns were generally similar over time, since there were no interactions (Table 11). The multiple range test yielded significance in mean abundance for winter 1983 and for Ormond. The most striking finding for *G. lineatus*, 1+ yr, is that Ormond was the highest in mean abundance at all depths and generally at all locations.

Young-of-the-year *E. mordax* exhibited similar patterns off Ormond and Redondo, generally having winter lows (Figure 6). The ANOVA showed interactions, and the multiple range test revealed that San Onofre was higher in mean abundance and that abundances in 1982 were significantly lower (Table 12, Appendix). In general, *E. mordax* increased in abundance in 1983.

For the remaining species, the ANOVA showed that, although there were interactions, the main effects were interpretable (Table 13). The strongest pattern was that for both young-of-the-year and 1+ yr fishes there were consistently lower mean abundances for the

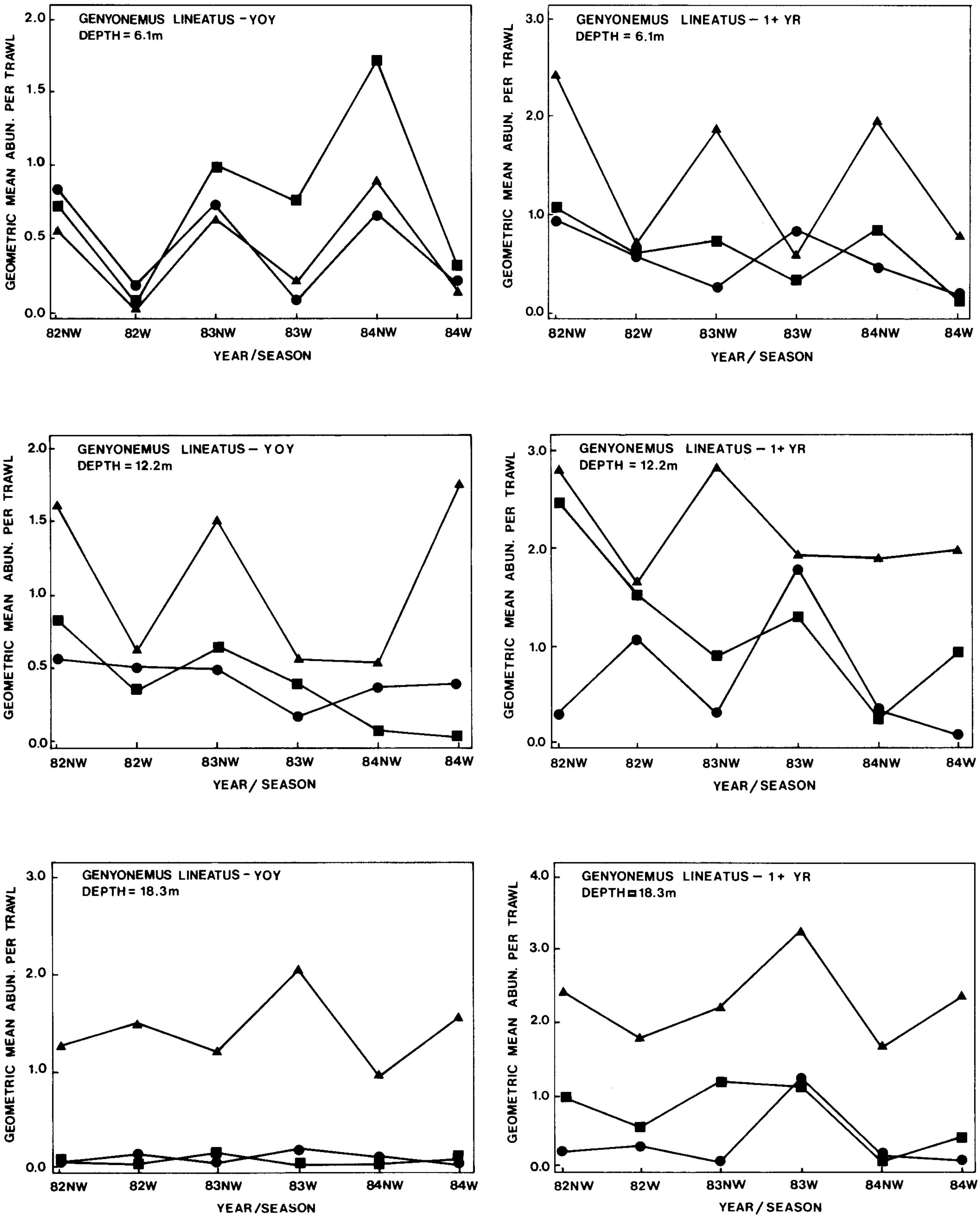

Figure 5. Catch per trawl of young-of-the-year and 1 + yr *Genyonemus lineatus* at three areas and three depths during winter (December and February) and nonwinter (April, June, August, October) 1982-84. Squares = San Onofre, circles = Redondo, triangles = Ormond.

TABLE 11
Cross-Nested ANOVA of *Genyonemus lineatus* (Young-of-the-Year and 1+ Yr) Log Abundance, Southern California Bight, 1982-84

Source	1+ yr DF	1+ yr Sum of squares	1+ yr Mean square	1+ yr *F* value	YOY DF	YOY Sum of squares	YOY Mean square	YOY *F* value
6.1-m depth								
Location	2	76.75		23.50 ****	2	13.94		5.13 **
Year	2	11.03		3.38 **	2	7.53		2.77 NS
Season(year)	3	64.09		13.08 ****	3	61.72		15.13 ****
Location*year	4	2.00		0.31 NS	4	8.73		1.60 NS
Location*season(year)	6	49.80		5.08 ****	6	8.48		1.04 NS
Model	17	275.79	16.22	9.94 ****	17	113.89	6.70	4.93 ****
Error	616	1005.79	1.63	—	616	837.70	1.36	—
12.2-m depth								
Location	2	207.83		49.36 ****	2	56.61		21.51 ****
Year	2	49.50		11.75 ****	2	3.57		1.36 NS
Season(year)	3	15.72		2.49 NS	3	30.49		7.72 ****
Location*year	4	35.54		4.22 **	4	7.49		1.42 NS
Location*season(year)	6	87.37		6.92 ****	6	24.65		3.12 **
Model	17	560.42	32.97	15.66 ****	17	139.41	8.20	6.23 ****
Error	614	1292.75	2.105	—	614	808.11	1.32	—
18.3-m depth								
Location	2	387.54		88.00 ****	2	219.00		134.88 ****
Year	2	50.63		11.50 ****	2	2.20		1.36 NS
Season(year)	3	35.14		5.32 **	3	5.76		2.36 NS
Location*year	4	4.75		0.54 NS	4	1.97		0.61 NS
Location*season(year)	6	22.25		1.68 NS	6	12.06		2.48 **
Model	17	571.07	33.59	15.26 ****	17	242.39	14.26	17.56 ****
Error	614	1352.06	2.20	—	614	498.48	0.81	—
					631	740.87		

**** $P < .0001$
** $P < .05$
NS $P > .05$

winter season throughout, and Redondo was generally higher in mean abundance (Figure 7; Appendix).

Over the three years, recruitment patterns varied little throughout the bight (Figure 8). Recruits of nine species were taken in sufficient quantity to assess recruitment patterns with depth (Figure 9). Three patterns emerged. Four species (*S. politus*, *E. mordax*, *Phanerodon furcatus*, and *Hyperprosopon argenteum*) recruited predominantly in 6.1 m. Four other species (*Citharichthys stigmaeus*, *Synodus lucioceps*, *Pleuronichthys verticalis*, *Xystreurys liolepis*) settled out

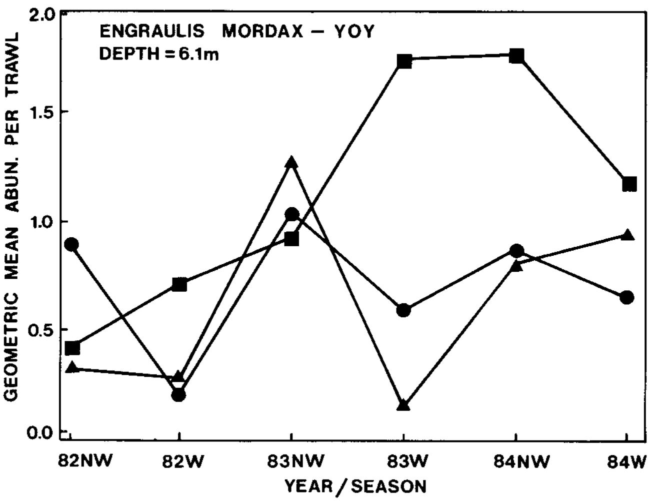

Figure 6. Catch per trawl of young-of-the-year *Engraulis mordax* at three areas and three depths during winter (December and February) and nonwinter (April, June, August, October) 1982-84. Squares = San Onofre, circles = Redondo, triangles = Ormond.

TABLE 12
Cross-Nested ANOVA of *Engraulis mordax* Young-of-the-Year Log Abundance, Southern California Bight, 1982-84

6.1-m depth Source	DF	Sum of squares	Mean square	*F* value
Location	2	27.79		5.29 **
Year	2	38.91		7.40 **
Season(year)	3	6.50		0.82 NS
Location*year	4	9.17		0.87 NS
Location*season(year)	6	45.40		2.88 **
Model	17	137.61	8.09	3.08 ****
Error	616	1618.96	2.63	

****$P<.0001$; **$P<.05$; NS $P>.05$

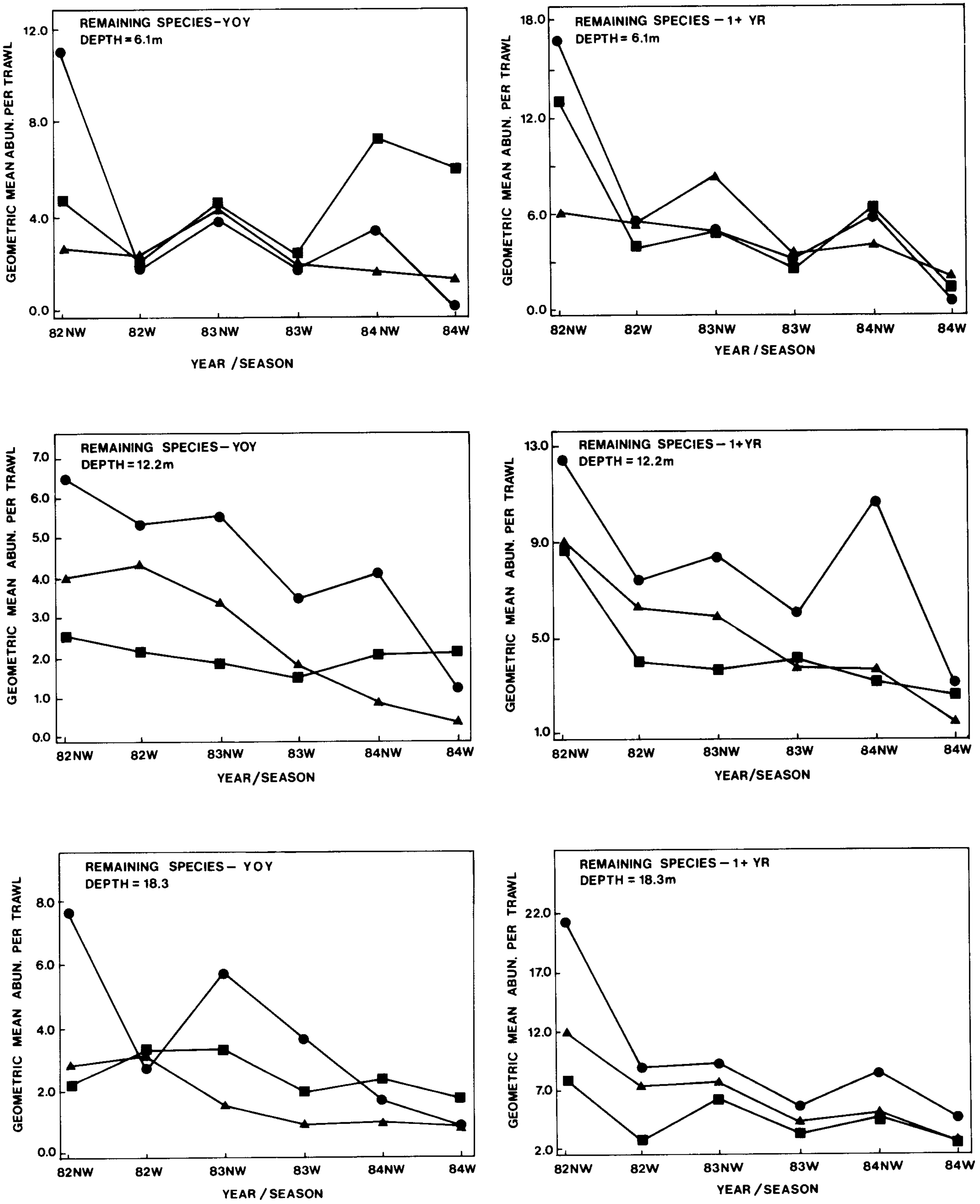

Figure 7. Catch per trawl of young-of-the-year and 1 + yr fishes (except for *Engraulis mordax, Genyonemus lineatus,* and *Seriphus politus*) at three areas and three depths during winter (December and February) and nonwinter (April, June, August, October) 1982-84. Squares = San Onofre, circles = Redondo, triangles = Ormond.

TABLE 13
Cross-Nested ANOVA of Young-of-the-Year and 1+ Yr (Except for *E. mordax, G. lineatus, S. politus*) Log Abundance, Southern California Bight, 1982-84

	1+ yr				YOY			
Source	DF	Sum of squares	Mean square	*F* value	DF	Sum of squares	Mean square	*F* value
6.1-m depth								
Location	2	0.12		0.06 NS	2	20.65		7.07 ****
Year	2	57.53		30.52 ****	2	4.68		1.60 NS
Season(year)	3	87.62		30.99 ****	3	52.78		12.05 ****
Location*year	4	11.98		3.18 **	4	44.79		7.67 ****
Location*season(year)	6	16.99		3.00 **	6	31.67		3.62 **
Model	17	187.49	11.03	11.70 ****	17	163.29	9.60	6.58 ****
Error	616	580.56	0.94	—	616	899.08	1.46	—
12.2-m depth								
Location	2	25.27		17.65 ****	2	29.44		15.23 ****
Year	2	38.62		26.98 ****	2	41.17		21.30 ****
Season(year)	3	30.03		13.99 ****	3	12.01		4.14 **
Location*year	4	3.90		1.36 NS	4	21.13		5.46 **
Location*season(year)	6	9.11		2.12 *	6	7.77		1.34 NS
Model	17	121.06	7.12	9.95 ****	17	118.97	7.00	7.24 ****
Error	614	439.46	0.72	—	614	593.46	0.97	—
18.3-m depth								
Location	2	31.88		23.99 ****	2	19.73		10.33 ****
Year	2	30.85		23.21 ****	2	33.19		17.38 ****
Season(year)	3	46.74		23.44 ****	3	8.60		3.00 **
Location*year	4	7.88		2.96 *	4	17.71		4.64 **
Location*season(year)	6	1.82		0.46 NS	6	13.22		2.31 **
Model	17	131.76	7.75	11.66 ****	17	111.98	6.59	6.90 ****
Error	614	408.02	0.66	—	614	586.11	0.95	—

**** $P < .0001$
** $P < .05$
NS $P > .05$

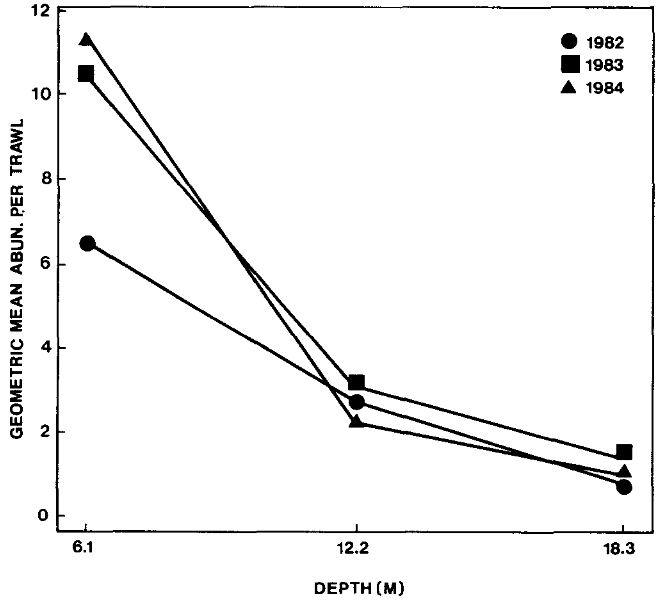

Figure 8. Abundance by depth of recruits taken by trawl, areas and months combined.

primarily in 18.3 m. *Genyonemus lineatus* recruited about equally to 6.1 and 12.2 m, declining somewhat in 18.3.

Generally, the patterns exhibited in Figures 10 and 11 accurately reflect the underlying patterns at all three areas. However, there are two exceptions—*G. lineatus* and *S. politus*. Off San Onofre and Redondo, most *G. lineatus* recruited to 6.1 and (occasionally) 12.2 m (Figure 10). Very few fish settled out in 18.3 m. Recruitment patterns off Ormond were different: here the deeper two stations were favored, with heaviest concentrations in 12.2 m (1982) and 18.3 m (1983-84). Few recruits were taken in 6.1 m in 1982-83. To a certain extent, this phenomenon held true for *S. politus*. At both San Onofre and Redondo, the bulk of recruitment occurred in 6.1 m—generally followed by steep declines in 12.2 and 18.3 m. Off Ormond, this decline was more gradual. In fact, there was no decline in abundance between 6.1 and 12.2 m in 1982 and very little between all depths in 1984.

Additionally, as noted below, there appeared to be

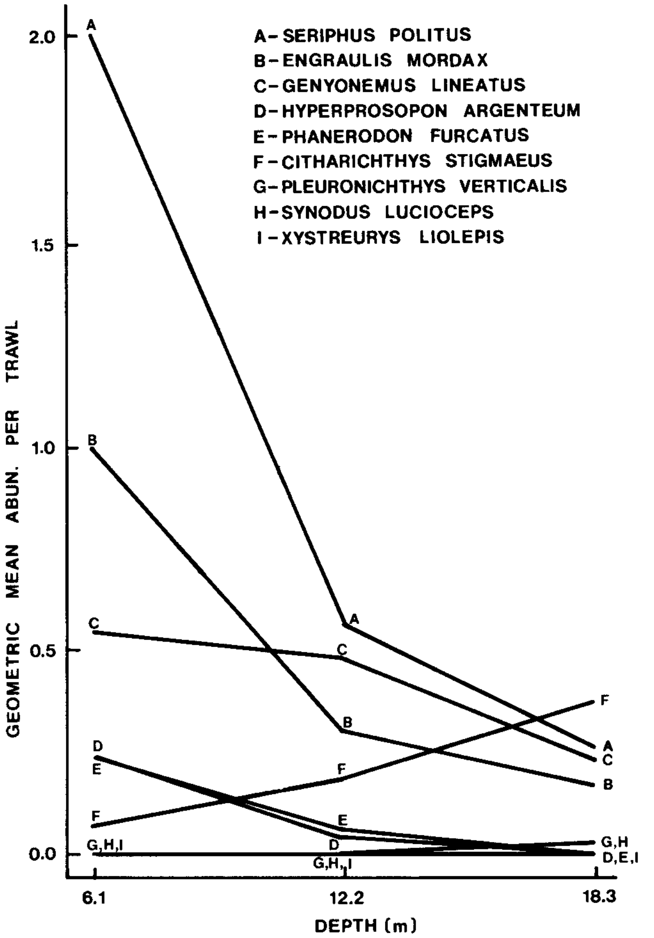

Figure 9. Recruitment depth of nine fish species taken by trawl in the Southern California Bight.

variability between areas in recruitment strength and season (based on Figure 11 only) for many of these species.

Seriphus politus. There was some fluctuation in month of peak recruitment between years. In 1982, we captured almost all small *S. politus* in August (Redondo) or October (San Onofre and Ormond). In 1983, peak catches were in August, whereas in 1984 June was highest off San Onofre and August at Redondo and Ormond. Peak catches off Ormond tended to be later than either Redondo (1982) or San Onofre (1984), or coincided with them (1983). In no year did catches peak off Ormond before the other two areas.

Genyonemus lineatus. Peak catches of small *G. lineatus* occurred between April and August, depending on area and year. In two of three years (1983-84), recruitment peaks were sequential from south to north, beginning at San Onofre, continuing at Redondo, and ending off Ormond. For 1983 and 1984, these peaks occurred in April, June, and August. In 1982, highest catches were again earliest off San Onofre, but both Redondo and Ormond peaked the following month.

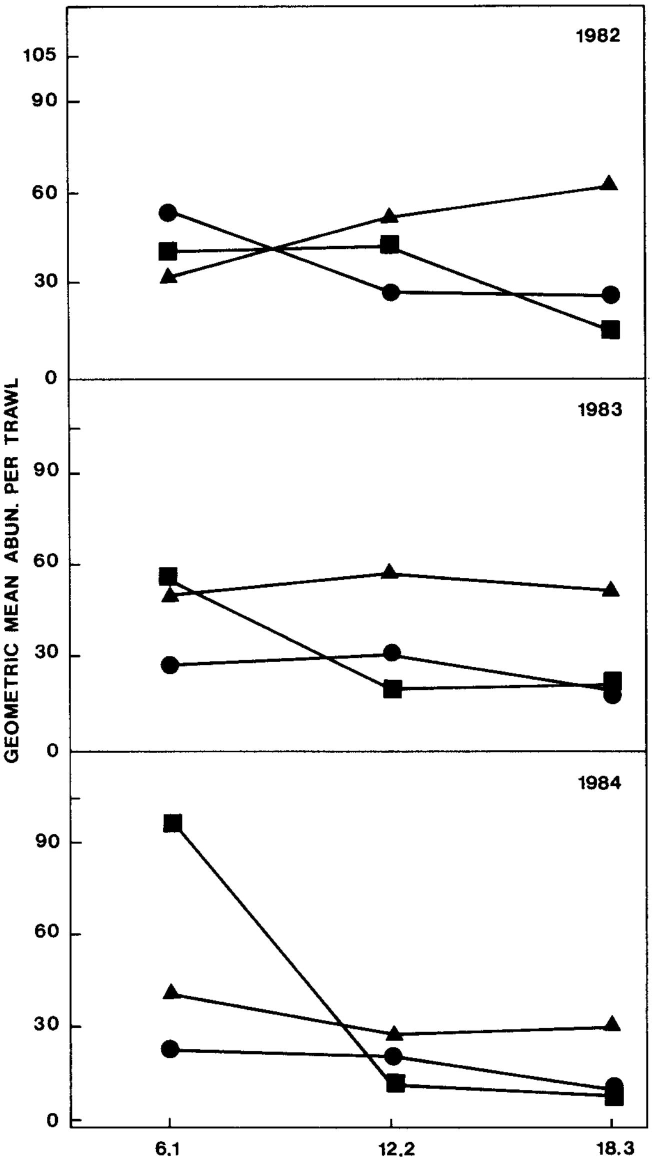

Figure 10. Yearly recruitment depth of *Genyonemus lineatus* off three areas in the Southern California Bight. Squares = San Onofre, circles = Redondo, triangles = Ormond.

Citharichthys stigmaeus. Between 1982 and 1984, most small *C. stigmaeus* were taken off Redondo. Almost all recruitment occurred between June and October. June was the peak month during 1982 and 1983, whereas August catches were highest in 1984. We captured very few small fish in 1984.

Phanerodon furcatus. In all three years *P. furcatus* recruited almost completely during June. Recruitment levels were similar in 1982 and 1983 but were reduced in 1984. No young *P. furcatus* were taken off Ormond in 1984.

Hyperprosopon argenteum. As with *P. furcatus*, recruitment of *H. argenteum* was restricted to a very few, primarily spring, months. April and June were the only

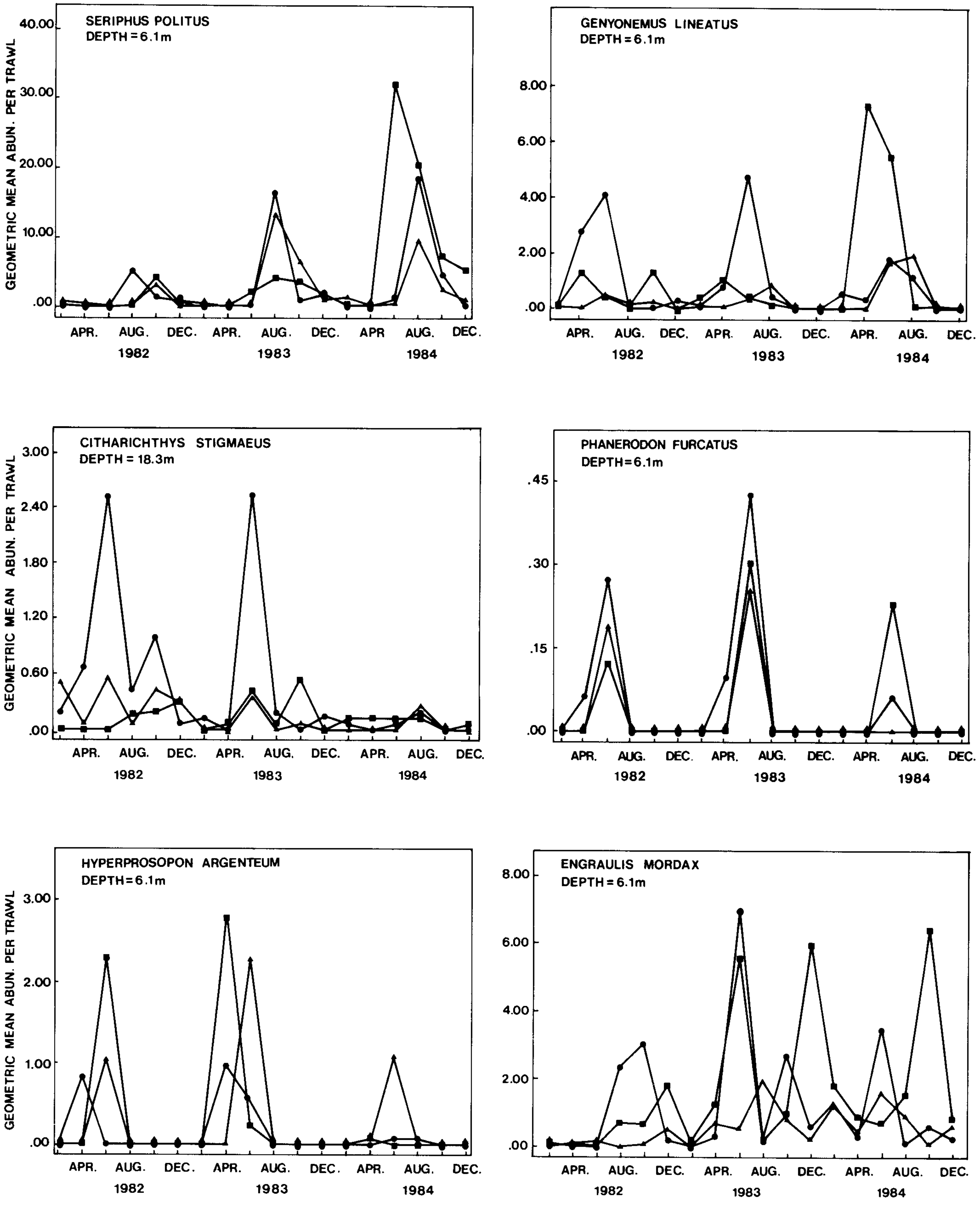

Figure 11. Recruitment strength and season at three areas in the Southern California Bight—all years combined. Depth figured is that where maximum number of recruits were taken.

months in which the youngest fish were taken. As with *P. furcatus*, recruitment was of similar levels in 1982 and 1983, but reduced in 1984. In that year we took young *H. argenteum* off Ormond only.

Engraulis mordax. We took small *E. mordax* in all seasons, though peaks varied with area and year. No single pattern was evident; however, largest catches were made between June and December.

Abundance of 1+ Year and Young-of-the-Year

Of the 12 species we examined, the majority of 1+ yr fishes declined in abundance over the three-year period (based on Figure 12 alone) or at least between 1982 and 1983. *Citharichthys stigmaeus*, *Phanerodon furcatus*, and *Synodus lucioceps* showed sequential declines in abundances from 1982 to 1984 (Figure 12). *Genyonemus lineatus*, *Seriphus politus*, and *Symphurus atricauda* increased in abundance from 1982 to 1983 but declined beginning in mid-1983. The abundance of 1+ yr *Hyperprosopon argenteum* declined gradually from 1982 to 1984. Compared to 1982, 1+ yr *Paralichthys californicus* and *Pleuronichthys verticalis* were less abundant in 1983 but seemed to increase or remain constant in 1984. *Pleuronichthys ritteri* and *Sphyraena argentea* increased in abundance between 1982 and 1984, while 1+ yr *Engraulis mordax* abundance was relatively stable. The *Engraulis* population was not sampled effectively, so this assessment may be inaccurate.

The widespread decline in 1+ yr fishes that began in 1983 was not so apparent in young-of-the-year individuals. Young-of-the-year of several species exhibited stronger first-year classes in 1983, 1984, or both. One species, *G. lineatus*, declined sequentially from 1982 to 1984. *Citharichthys stigmaeus* declined sharply between 1982 and 1983; 1984 levels were similar to 1983. *Hyperprosopon argenteum* declined in mid-1983 and remained low in 1984. The young-of-the-year of the remainder of the 12 species either increased in 1983 or 1984 or remained fairly constant.

DISCUSSION

Between 1982 and 1984, we sampled fishes living on or over the inshore soft substrata of the Southern California Bight. Our analysis indicates that the fish assemblages form a dynamic system with considerable seasonal, annual, and spatial heterogeneity.

The fish assemblages along the 6.1-m isobath are quite similar throughout the bight, dominated by the midwater schooling croakers, *Seriphus politus* and *Genyonemus lineatus*. A number of other species, such as *Engraulis mordax, Hyperprosopon argenteum*, and *Paralichthys californicus*, were common in these assemblages in all survey areas. With increasing depth, bathymetric and geographic differences in species composition occurred. Croakers decreased in importance in 12.2 and 18.3 m off San Onofre and Redondo; they were replaced by various flatfishes (notably *Citharichthys stigmaeus*, *Pleuronichthys* spp., and *Xystreurys liolepis*) and *Synodus lucioceps*. However, these species do not form the large schools characteristic of croakers; hence the total number of fish along the deeper isobaths was low when compared to 6.1 m. In contrast, croakers remained abundant off the Ormond area down to at least 18.3. *Seriphus politus* was abundant in 6.1 m, giving way to *G. lineatus* in 18.3 m. Here too, flatfishes increased their numbers with depth, but they were overshadowed by *Genyonemus*.

Not only were the 6.1-m assemblages similar at all three areas, but many of the fishes also exhibited similar seasonal fluctuations. There were considerable annual fish movements into and out of this isobath all along the Southern California Bight. In 6.1 m, we took very few fish per trawl (occasionally none) during December and February. Catches increased in April and generally peaked in summer and early fall. Most species, both motile midwater and benthic forms, declined in abundance or disappeared from our shallowest stations. It is likely that fishes moved offshore, though we are not sure into what depth. Catches of *S. politus* and *G. lineatus* increased (at least off some areas) during winter, indicating that these species had moved into the 18.3-m isobaths.

It is not completely clear why fishes would leave the shallows during winter. A plausible explanation is that they are driven out as increasing water motion, caused by winter storms, requires greater energy for keeping stations or for finding and capturing prey. It is interesting that zooplankton, the prey of some species (such as *S. politus*) increases in inshore biomass in winter (Barnett and Jahn, in press); thus diminished prey availability may not fully explain the offshore movement.

In tandem with the annual fluctuations in fish numbers along the coast was general movement of many (though not all) species out of inshore waters during 1983 and 1984. It is likely that the El Niño influx of warm water, with attendant environmental perturbations, was responsible. The El Niño phenomenon reached its peak in 1983-84: the maximum temperature anomaly (with surface waters as much as 4°C above normal) began in August 1983 and peaked in October of the same year. Coincident was a decline in total zooplankton abundance; this decline began in 1982 and intensified in June 1983 (Peterson et al. 1986). However, not all zooplankton declined. For instance, although populations of the adult mysid *Metamysidopsis elongata* decreased markedly in August 1983, a num-

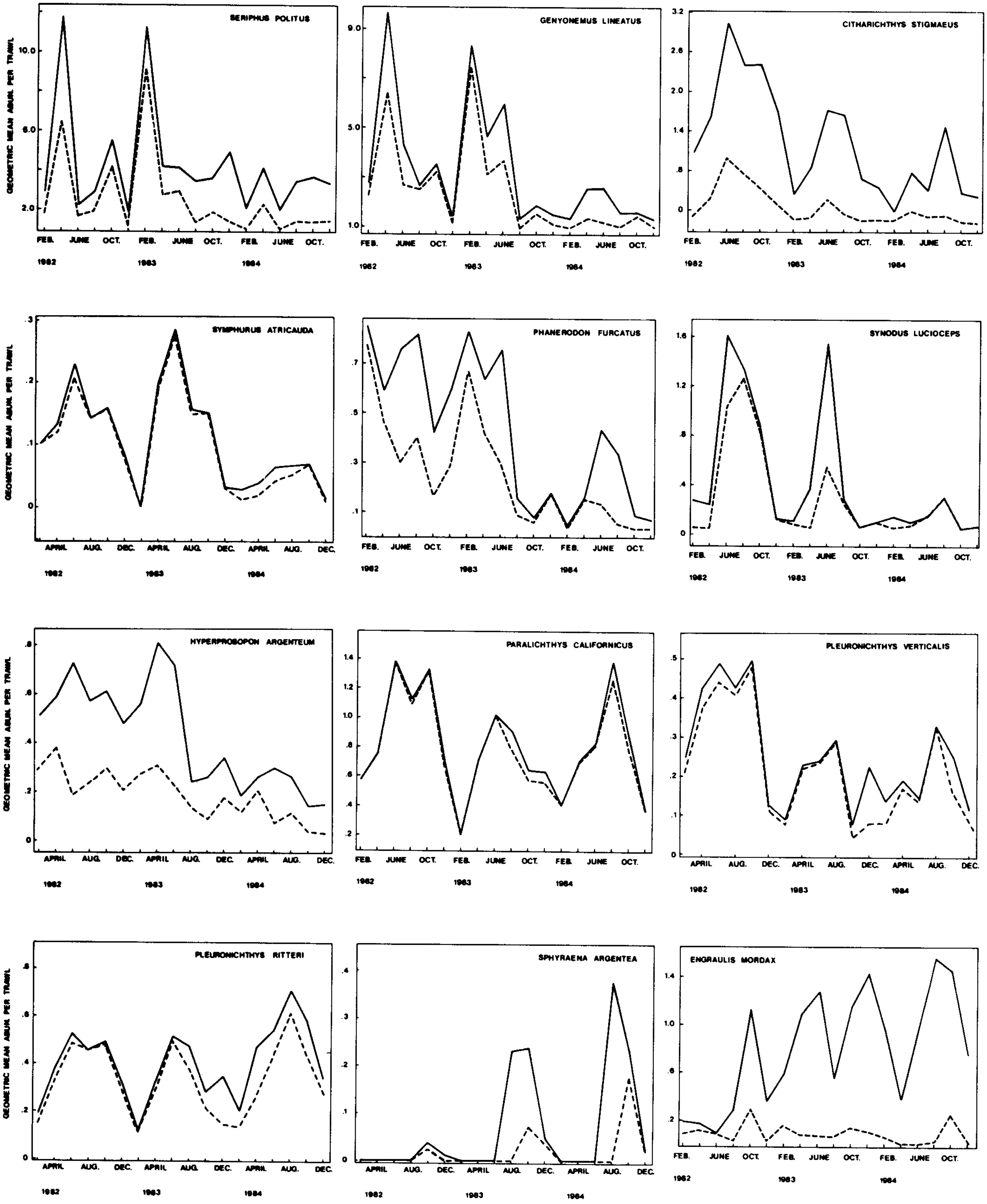

Figure 12. Monthly abundance of young-of-the year and 1+ yr fishes of 12 species, taken by trawl in the Southern California Bight. Broken lines represent abundance of 1+ yr fishes; solid lines represent abundances of both young-of-the-year and 1+ yr fishes. Thus the abundance of young-of-the-year fishes equals the distance between broken and solid lines.

ber of other species did not (A. Barnett, pers. comm.).

It does not seem reasonable to point to any one factor as decisive in this exodus. For instance, it is not clear why a 4° rise in ambient temperature would cause so many fish species to move away. Water 4° above normal is not unusually warm for some of these species and is similar to temperatures encountered in the more southerly parts of their ranges. However, it is possible that the rapid onset of peak temperatures prompted the departure.

Similarly, decreases in food availability might account for some movement, but not all. The species we examined represent a variety of predator types, including midwater planktivores, substrate-oriented microcarnivores, and piscivores. It is unlikely that the prey of all these species declined. Moreover, some fish species, such as *Pleuronichthys ritteri*, increased in abundance. If food availability alone were responsible, we would not expect to see any increases.

Regardless of the reason, it is undeniable that the abundance of older juveniles and adults of many fish species declined markedly during mid-1983. We do not believe this decline was due to die-offs. The temperatures experienced were well within physiological limits, and no die-offs (such as occasionally occur in embayments during dinoflagellate blooms) were observed.

It is more likely that fish moved to cooler conditions. Some may have traveled northward along the coast. From commercial fishery data, there is evidence that adult *Paralichthys* moved north (R. Collins, pers. comm.), because *Paralichthys* landings declined in southern California and increased substantially in central California.

Equally plausible is an offshore movement by some species. If it occurred off San Onofre and Redondo, we can be sure this movement continued into waters deeper than 18.3 m, because we observed no abundance increase in our deepest stations. We do not know how deep the fishes moved. During this period, a similar offshore migration occurred in somewhat deeper waters; E. DeMartini (pers. comm.) noted a bathymetric shift within the bight in populations of pink seaperch (*Zalembius rosaceus*) and Pacific sanddab (*Citharichthys sordidus*). Both species generally inhabit depths below those of our survey; that these species also exhibited offshore movements indicates that warming occurred to considerable depths.

Though the El Niño phenomenon drove many fishes away from the immediate coast within the bight, not all species departed. Species whose populations might have been predicted to remain stable, based on geographic range (i.e., *P. ritteri*, *Sphyraena argentea*) remained stable or increased in numbers. While increases in *P. ritteri* were due to adult movements, increases in *S. argentea* resulted from an unusually successful recruitment of young fishes.

For the species we examined, there was considerable variability among areas in recruitment season and strength. For instance, *C. stigmaeus* recruited primarily to the Redondo area; we captured few recruits off San Onofre and Ormond. At the other extreme, virtually all *Phanerodon furcatus* recruited in June at all three stations during 1982 and 1983.

For at least some species (notably *G. lineatus*), there appears to be sequential recruitment from south to north; fishes tend to settle out earliest at San Onofre, followed by Redondo and Ormond. A similar pattern may exist with the kelp bass, *Paralabrax clathratus*, a southern California reef species (M. Carr, pers. comm.).

There are several possible explanations for this phenomenon. A species may delay spawning in the northern part of the bight if conditions favorable to larval recruitment occur later in the year. Some northeast Pacific rockfishes have later spawning seasons in the northern part of their range than in the south (T. Echeverria, pers. comm.). Second, a species may spawn synchronously throughout the bight, but various factors may differentially affect the larvae. For instance, cooler waters in the northern part of the bight may extend the larval stage, leading to later recruitment. Or perhaps conditions in the north are such that only those larvae spawned late in the season survive. Lastly, recruitment may derive from larvae generated in the southern part of the bight (or even farther south). As the larvae drift north, they leave the plankton later and later. This implies that some species may not spawn in the northern part of the bight (or if they do, their offspring do not survive to recruitment). An example is the moray eel, *Gymnothorax mordax*, which does not spawn in southern California even though abundant there (McGleneghan 1973). Rather, the population is replenished through larvae drifting north from Baja California.

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APPENDIX A
Duncan's Multiple Range Test

	Seriphus politus				*Genyonemus lineatus*			
	1 + Yr		YOY		1 + Yr		YOY	
Depth	*Location*	*Log mean*	*Location*	*Log mean*	*Location*	*Log mean*	*Location*	*Log mean*
6.1m	San Onofre	1.711	San Onofre	2.242	Ormond	1.625	San Onofre	.907
	Ormond	1.595	Ormond	1.832	San Onofre	.708	Redondo	.575
	Redondo	.964	Redondo	1.537	Redondo	.543	Ormond	.524
	Year		*Year*		*Year*		*Year*	
	1983	1.494	1984	2.149	1982	1.185	1984	.846
	1982	1.431	1983	1.885	1984	.842	1983	.669
	1984	1.349	1982	1.600	1983	.827	1982	.507
	Season-year		*Season-year*		*Season-year*		*Season-year*	
	NW82	1.760	NW84	2.465	NW82	1.464	NW82	1.124
	NW84	1.685	NW83	1.994	NW84	1.084	NW83	.801
	NW83	1.583	NW82	1.835	NW83	.953	NW84	.718
	W83	1.304	W83	1.649	NW82	.627	W83	.385
	W82	.773	W84	1.473	W83	.555	W84	.251
	W84	.632	W82	1.132	W84	.326	W82	.086
Depth	*Location*	*Log mean*	*Location*	*Log mean*	*Location*	*Log mean*	*Location*	*Log mean*
12.2m	Ormond	1.915	Ormond	1.648	Ormond	2.306	Ormond	1.144
	San Onofre	1.295	Redondo	.595	San Onofre	1.224	Redondo	.460
	Redondo	.642	San Onofre	.507	Redondo	.514	San Onofre	.454
	Year		*Year*		*Year*		*Year*	
	1982	1.571	1983	1.021	1982	1.700	1982	.833
	1983	1.408	1982	.933	1983	1.446	1983	.751
	1984	.846	1984	.767	1984	.857	1984	.449
	Season-year		*Season-year*		*Season-year*		*Season-year*	
	W83	1.748	W83	1.638	NW82	1.844	NW82	1.002
	NW82	1.745	W84	1.198	W83	1.675	NW83	.905
	NW83	1.252	NW82	1.022	W82	1.412	W84	.652
	W82	1.223	W82	.755	NW83	1.341	W82	.494
	W84	1.208	NW83	.742	W84	.940	W83	.416
	NW84	.675	NW84	.564	NW84	.819	NW84	.353
Depth	*Location*	*Log mean*	*Location*	*Log mean*	*Location*	*Log mean*	*Location*	*Log mean*
18.3m	Ormond	1.526	Ormond	1.254	Ormond	2.226	Ormond	1.304
	San Onofre	.320	Redondo	.234	San Onofre	.714	Redondo	.053
	Redondo	.220	San Onofre	.097	Redondo	.211	San Onofre	.034
	Year		*Year*		*Year*		*Year*	
	1983	.896	1983	.632	1983	1.387	1983	.546
	1982	.728	1982	.494	1982	1.095	1982	.453
	1984	.410	1984	.431	1984	.627	1984	.361
	Season-year		*Season-year*		*Season-year*		*Season-year*	
	W83	1.544	W83	1.151	W83	1.928	W83	.782
	NW82	.769	W84	.624	NW82	1.205	W82	.524
	W82	.644	W82	.619	NW83	1.140	NW83	.439
	NW83	.599	NW82	.432	W82	.875	W84	.431
	W84	.556	NW83	.394	W84	.817	NW82	.418
	NW84	.340	NW84	.340	NW84	.538	NW84	.328

Means with the same bracket are not significantly different. Geometric mean = 2.7182*log mean − 1
NW = nonwinter; W = winter

APPENDIX A (continued)
Duncan's Multiple Range Test

	Remaining species				*Engraulis mordax*	
	1 + Yr		YOY		YOY	
Depth	*Location*	*Log mean*	*Location*	*Log mean*	*Location*	*Log mean*
6.1m	Redondo	1.893	San Onofre	1.710	San Onofre	1.110
	San Onofre	1.838	Redondo	1.488	Redondo	.800
	Ormond	1.815	Ormond	1.259	Ormond	.678
	Year		*Year*		*Year*	
	1982	2.250	1982	1.603	1984	1.103
	1983	1.757	1983	1.488	1983	1.020
	1984	1.524	1984	1.370	1982	.486
	Season-year		*Season-year*		*Season-year*	
	NW82	2.502	NW82	1.848	NW84	1.177
	NW83	1.928	NW83	1.653	NW83	1.100
	NW84	1.863	NW84	1.552	W84	.945
	W82	1.748	W83	1.133	W83	.847
	W83	1.391	W82	1.114	NW82	.537
	W84	.800	W84	.980	W82	.383
Depth	*Location*	*Log mean*	*Location*	*Log mean*		
12.2m	Redondo	2.241	Redondo	1.686		
	Ormond	1.820	Ormond	1.194		
	San Onofre	1.685	San Onofre	1.111		
	Year		*Year*			
	1982	2.244	1982	1.608		
	1983	1.846	1983	1.348		
	1984	1.637	1984	1.019		
	Season-year		*Season-year*			
	NW82	2.410	NW82	1.636		
	W82	1.910	W82	1.551		
	NW83	1.910	NW83	1.460		
	NW84	1.827	NW84	1.138		
	W83	1.704	W83	1.103		
	W84	1.233	W84	.767		
Depth	*Location*	*Log mean*	*Location*	*Log mean*		
18.3m	Redondo	2.384	Redondo	1.514		
	Ormond	2.052	San Onofre	1.252		
	San Onofre	1.791	Ormond	.989		
	Year		*Year*			
	1982	2.397	1982	1.494		
	1983	2.005	1983	1.327		
	1984	1.804	1984	.926		
	Season-year		*Season-year*			
	NW82	2.636	NW82	1.545		
	NW83	2.165	NW83	1.449		
	NW84	1.962	W82	1.393		
	W82	1.918	W83	1.062		
	W83	1.654	NW84	.994		
	W84	1.470	W84	.781		

Means with the same bracket are not significantly different. Geometric mean = 2.7182*log mean − 1
NW = nonwinter; W = winter

Part III

SCIENTIFIC CONTRIBUTIONS

EVALUATING INCIDENTAL CATCHES OF 0-AGE PACIFIC HAKE TO FORECAST RECRUITMENT

KEVIN M. BAILEY, ROBERT C. FRANCIS
Northwest and Alaska Fisheries Center
7600 Sand Point Way NE
Seattle, Washington 98115

KENNETH F. MAIS
California Department of Fish and Game
1301 West 12th Street
Long Beach, California 90813

ABSTRACT

Incidental catches of 0-age Pacific hake (*Merluccius productus*) in California Department of Fish and Game trawl surveys for pelagic fishes were evaluated for use in estimating relative year-class strength. Indices of catch per unit of effort and frequency of occurrence of 0-age hake in surveys from 1965 to 1981 were compared with recruitment at age 3 as determined by cohort analysis. Five strong year classes appeared in the cohort analysis from 1965-81, and these same year classes also were strongest in the pelagic survey catches. We conclude that the surveys are useful for qualitative determination of relative year-class success or failure. Suggestions are made for improving the surveys with respect to hake.

RESUMEN

Capturas incidentales de la merluza del Pácifico de edad cero, en las prospecciones de peces pelágicos del departamento de Fish and Game de California fueron evaluadas, para estimar la dominancia relativa de clases anuales de merluza. Indices de captura por unidad de esfuerzo y frecuencia de ocurrencia de merluza a la edad cero en las prospecciones de 1965-81 fueron comparadas con los reclutamientos a la edad de tres años, determinada por análisis de cohorte. En el análisis de cohorte se observaron cinco generaciones dominantes, las cuales fueron también abundantes en la prospección de peces pelágicos. Concluimos que las prospecciones son útiles para la determinación cualitativa del éxito o fracaso relativo de las clases anuales de edad. Se proponen varias sugerencias para mejorar las prospecciones de merluza.

INTRODUCTION

Surveys for young fish can be useful in forecasting year-class strength (Rauck and Zijlstra 1978; Smith 1981; Burd 1985). Such forecasts can benefit management of fisheries that are heavily dependent on recruiting new fish. Furthermore, surveys for juvenile fish can reveal at what stage relative abundance levels are established, which is information that augments studies on the causes of variations in recruitment.

Juvenile Pacific hake (*Merluccius productus*) are caught as an incidental species during pelagic trawl surveys conducted by the California Department of Fish and Game. In this report, we evaluate these catches for use in forecasting year-class strength.

Pacific hake is the dominant groundfish species in the California Current region of the Pacific west coast. There has been a large foreign fishery on hake since 1966, with annual catches up to 240,000 tons. In recent years a joint-venture domestic fishery has developed. Recruitment to the fishery, which occurs at 3 years of age, is quite variable and possibly influenced by abiotic conditions during early life stages (Bailey 1981). Hake spawn primarily from January through March off the southern and central coast of California. Juveniles generally are distributed from the spawning grounds into southern Oregon. Juvenile hake are the third most frequently occurring fish in pelagic trawl surveys of the California Department of Fish and Game (Mais 1974).

METHODS

The pelagic fish surveys of the California Department of Fish and Game have employed standardized methodology since 1965; in this study we used data from the 1965-84 surveys. A detailed description of survey methodology is presented in Mais (1974). In general, hydroacoustic surveys were conducted during the daytime along predetermined tracklines. At night, the trackline was retraced, and a midwater trawl with a 50- or 60-foot-square mouth opening was deployed, usually for 20 minutes in the upper 15 fathoms of the water column unless the echo sounder indicated that fish were deeper. The mesh size of the cod end was 0.5 inches. Some surveys consisted entirely of trawling at predetermined stations without the use of sonar. The surveys generally extended seaward to the 1,000-fathom depth contour or a minimum of 35 miles offshore.

The number of cruises and tows and the seasons covered are listed in Table 1. In the case of hake, the number of fish caught in the trawl were counted, or estimated if the catch was extremely large; length ranges and sometimes length frequencies were recorded. The length range of 0-age juvenile hake in each season was estimated as: April-May, 10-80 mm; June-

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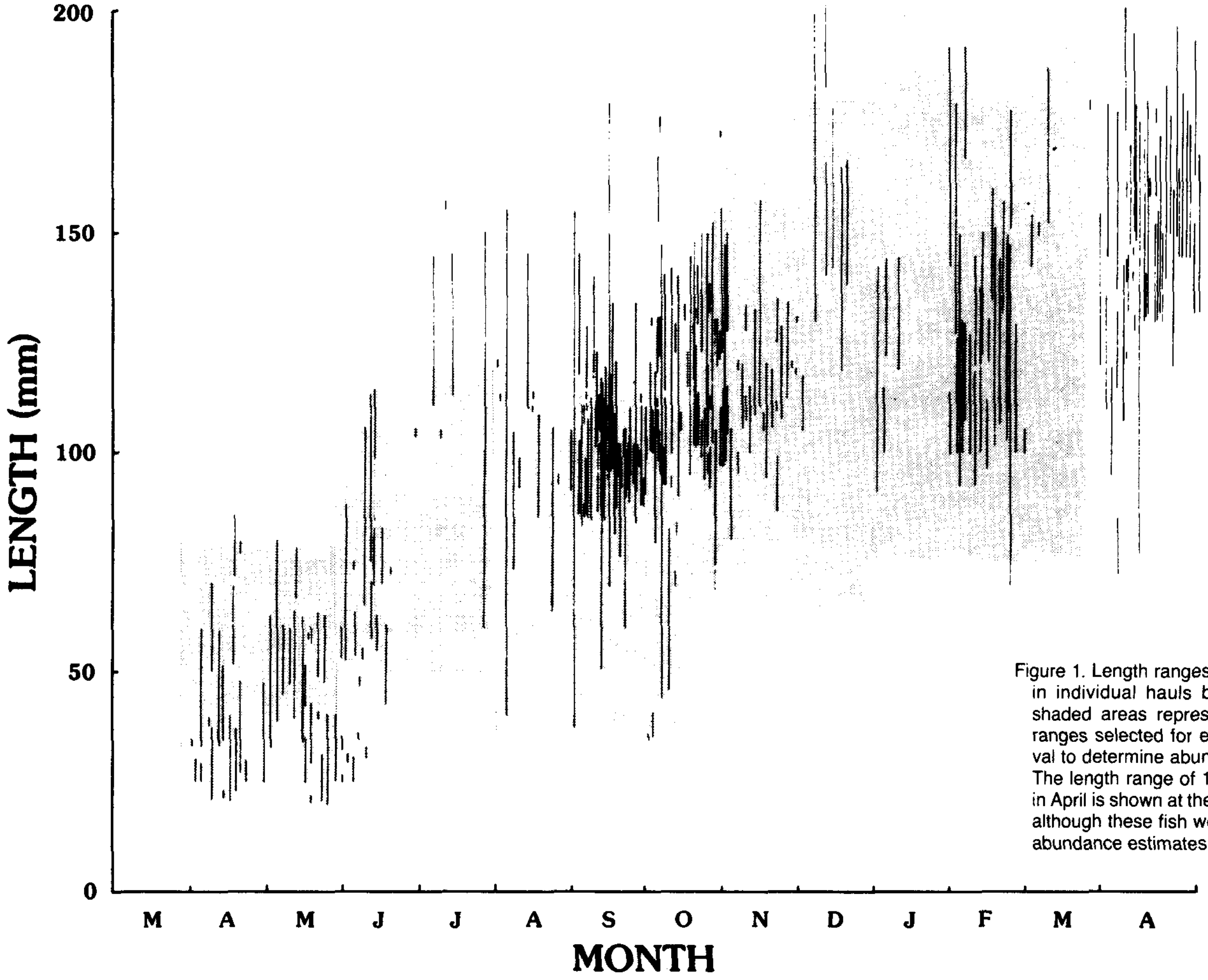

Figure 1. Length ranges of 0-age hake in individual hauls by month. The shaded areas represent the length ranges selected for each time interval to determine abundance indices. The length range of 1-year-old hake in April is shown at the extreme right, although these fish were not used in abundance estimates.

TABLE 1
California Fish and Game Midwater Trawl Surveys Used in This Study

Year class	Number of cruises	Seasons[1]	Number of tons
1965	3	sp, a	96
1966	5	sp, su, a	102
1967	4	sp, a, w	133
1968	4	sp, a	178
1969	5	sp, su, a, w	225
1970	4	sp, a, w	158
1971	3	sp, a	92
1972	3	sp, a, w	91
1973	2	sp, a	72
1974	4	sp, a, w	129
1975	3	sp, a	86
1976	8	sp, a, w	337
1977	6	sp, a, w	229
1978	1	w	60
1979	3	sp, a, w	283
1980	3	a, w	337
1981	4	sp, a, w	506
1982	3	su, a, w	339
1983	2	a	234
1984	1	a	128

[1] sp = spring; su = summer; a = autumn; w = winter

July, 25-120 mm; August-October, 35-150 mm; November-December, 65-180 mm; and January-March, 80-200 mm (Figure 1).

A standardized survey subarea of 30°-35°N was chosen because it was consistently occupied during most surveys. With the exception of numerous catches in Monterey Bay, this appears to be the main area inhabited by 0-age hake (Figure 2).

Catches of 0-age hake were combined for all surveys from April until March of the next year. Percent occurrence was calculated as the percent of all hauls that recorded catches of 0-age hake. Catch per unit of effort (CPUE) for annual estimates of relative 0-age juvenile abundance was calculated as:

$$\text{CPUE} = \sum_{\text{tows}=1}^{n} \ln\left[(\text{number fish/hours trawled}) + 1\right]/n$$

where n is the number of tows. Recruitment was estimated by the number of 3-year-old hake derived by cohort analysis (Francis 1985).

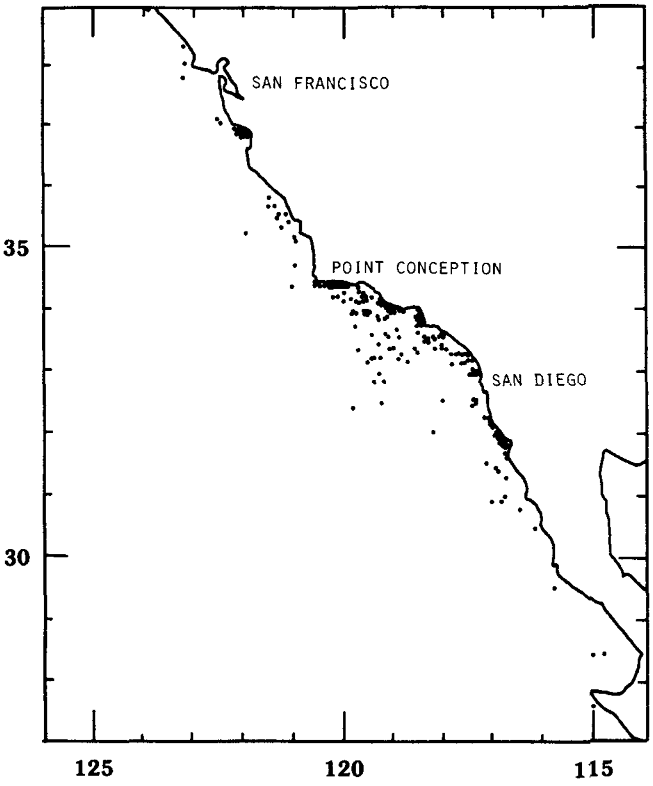

Figure 2. Locations of catches of 0-age hake in midwater trawls of the California Department of Fish and Game used in this study, 1965-84.

RESULTS AND DISCUSSION

The California Fish and Game trawl surveys for pelagic fish resources were not targeting on juvenile hake, but their incidental catches of 0-age hake appear to be useful in forecasting year-class strength of this species. Figure 3 demonstrates the relationship between catches of 0-age hake in the surveys and year-class strength as determined by cohort analysis. During the interval from 1965 to 1981, five large year classes of hake appeared in the population (1967, 1970, 1973, 1977, and 1980). These five year classes were also the most abundant as 0-age juveniles monitored by the surveys.

The surveys apparently are not accurate in ordering the rank of strong year classes when compared with results of the cohort analysis. For example, 0-age hake were more abundant in the 1973 surveys than in the 1970 surveys, but the cohort analysis indicated that the 1970 year class was stronger than the 1973 year class. Predicting strong year classes is important, but in a management context it is equally important to recognize year-class failure; in this analysis all weak year classes were accurately indicated by the surveys.

Since the cohort analysis extends only to the 1981 year class, we can use the 0-age catches in the surveys to forecast the relative recruitment strengths of the

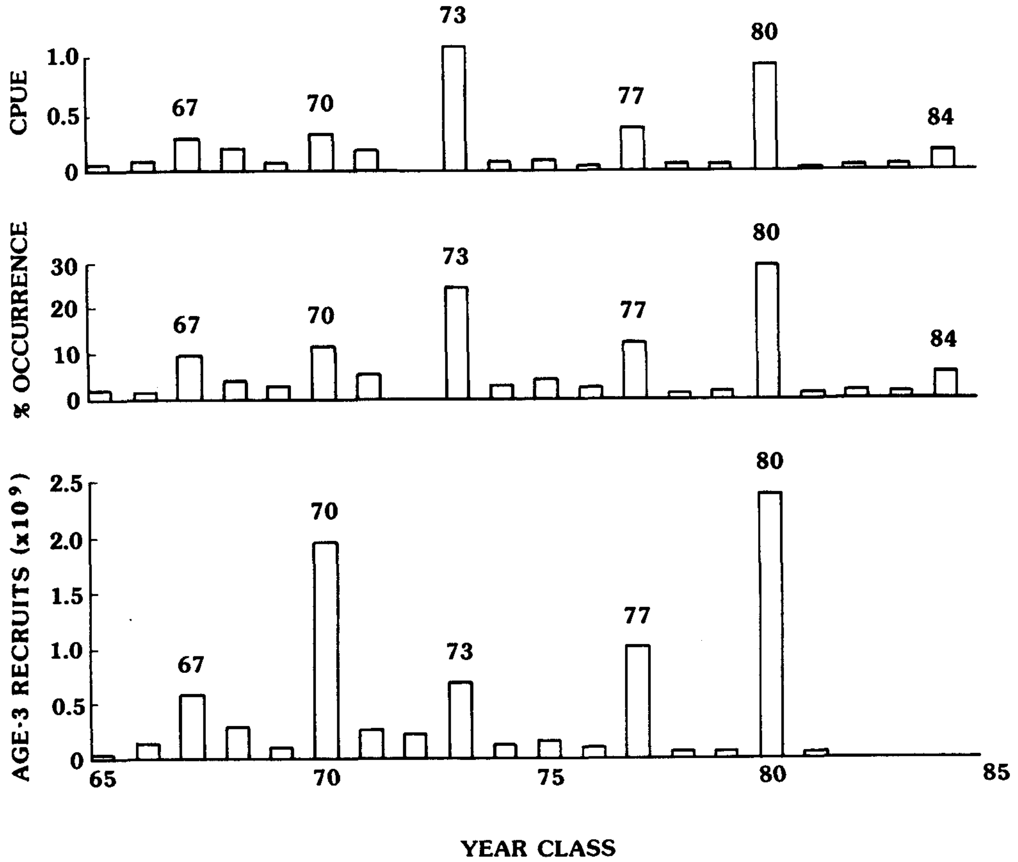

Figure 3. Catch per unit effort (CPUE; *top*) and percent occurrence (*middle*) of 0-age hake in midwater trawl surveys compared with year-class strength determined by cohort analysis (*bottom*).

1982-84 year classes. The juvenile surveys indicate that the 1982-83 year classes will be weak. The 1984 year class may be moderately strong. However, both the 1983 and 1984 surveys may have underestimated the abundance of juvenile hake, because spawning apparently shifted northward during these warm-water years. In fact, there are anecdotal reports of a strong 1984 year class.

From these results it is apparent that the relative recruitment strength of hake year classes is established within the first year of life. Furthermore, the 1967, 1970, 1973, and 1977 year classes were detectable as strong year classes in surveys from April to June in those years. This indicates that relative year-class strength may be established within the first three to five months after spawning (there was no spring survey in 1980). The early establishment of year-class strength may be more apparent for hake than for other species because of the boom-or-bust nature of recruitment to the hake population; survival is either very good or poor.

Because of the close relationship of recruitment success to stock abundance, we consider such surveys to be a valuable and inexpensive asset to stock management. Evaluation and assessment of the hake resource for management of the U.S. fishery is currently based on stock projections that take into account estimates of recruitment up to three years into the future based on the results of the 0-age surveys (Francis 1985). At this stage, the surveys can only be considered rough relative indices of year-class strength, and the precision of the indices cannot be addressed. To improve the assessment of prerecruit abundance of hake, preliminary studies on vertical and geographic distribution and behavior of juveniles are required. These factors may affect catchability and the utility of survey CPUE as a relative index. Further improvement of hake assessment would result from extending the northern boundary of the survey area, and implementing a more statistically rigorous survey design.

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PERUVIAN HAKE FISHERIES FROM 1971 TO 1982[1]

MARCO A. ESPINO
Instituto del Mar del Perú
Apartado 22
Callao, Perú

CLAUDIA WOSNITZA-MENDO
Programa Cooperativo Peruano-Alemán de Investigación Pesquera
Deutsche Gesellschaft für Technische Zusammenarbeit
Instituto del Mar del Perú
Apartado 22
Callao, Perú

ABSTRACT

Past estimates of Peruvian hake biomass calculated by the swept-area method have left some doubts about the size of the stock. With the available monthly catch statistics from 1971 onwards, quarterly age-length keys, and estimates of natural mortality, we applied a cohort analysis that shows much lower biomass estimates than those obtained by the swept-area method. This cohort analysis indicates that spawning stock biomass has been in serious decline since especially heavy exploitation in 1978. Peruvian hake stocks are expected to recover after the 1982-83 El Niño because of light exploitation and possibly good recruitment. A yearly catch of about 100,000 metric tons is proposed; this is much lower than previous estimates of sustainable yield. A yield-per-recruit analysis supports this contention.

RESUMEN

Las estimaciones de biomasa de la merluza peruana obtenidas en los últimos años mediante el método de area barrida han dado resultados dudosos con respecto a la dimensión del stock. En base a la estadística disponible de la pesca mensual desde 1971 en adelante y las claves tamaño-edad, además de los estimados de mortalidad natural, se aplicó el análisis de cohortes que mostró una biomasa mucho menor que aquella obtenida por el método de área barrida. Este análisis de cohortes muestra que la biomasa del stock desovante ha declinado peligrosamente desde la excesiva explotación del año 1978. Se espera que el stock de la merluza peruana se restablezca después de El Niño 1982-83, debido a la escasa explotación y posiblemente al buen reclutamiento. Se propone una pesca anual de 100.000 tons que es mucho menor que las estimaciones anteriores del rendimiento sostenible. Además un análisis de rendimiento por recluta corrobora esta suposición.

INTRODUCTION

The Peruvian hake *(Merluccius gayi peruanus)* is distributed over the continental shelf and farther offshore to more than 500-m depth. As the most abundant demersal species in the Peruvian coastal ecosystem, hake is important both commercially and ecologically. Furthermore, the dynamics and life history of the Peruvian hake may have parallels with the Pacific hake *(Merluccius productus).*

The Peruvian hake grows slightly faster and attains a larger size than the Pacific hake. The Peruvian hake spawns in the austral winter-spring months of August to October over the continental shelf. Fish are recruited to the fishery at age 2 and mature at about age 3 (35 cm). Juveniles are pelagic. However, in contrast to the Pacific hake, adults are demersal and are fished with bottom trawls, whereas Pacific hake are fished mostly with midwater trawls (Bailey et al. 1982).

Before 1972, Peruvian hake was harvested mainly by the coastal demersal fleet off Paita in northern Peru (about 5°S), and catches fluctuated around 20,000 metric tons (MT) annually. In 1973 an intensive fishery by foreign high-seas fleets began (Table 1). Catches of hake reached their highest levels (303,000 MT) in 1978, when the stock apparently changed its habitat from demersal to semipelagic and became accessible to the national purse seine fisheries as well.

In past years, various estimates of Peruvian hake biomass have been made from bottom trawl surveys but have left doubts about the results.

To obtain a better estimate, we applied cohort

TABLE 1
Catches of Peruvian Hake

	Paita (N. Peru) *Coastal fleet* (Metric tons)	Total Peru *Including high-seas fleet* (Metric tons)
1971	24,000	26,000
1972	7,695	12,580
1973	36,386	132,856
1974	20,862	109,318
1975	14,307	84,898
1976	10,230	92,872
1977	5,833	106,799
1978	10,645	303,495
1979	8,163	92,954
1980	8,165	159,376
1981	14,581	64,026
1982	—	33,000*

*Preliminary data

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[1] Publication No. 25 of the Cooperative Peruvian-German Fisheries Research Project (PROCOPA)

analysis (Pope 1972) using catch data from the 12 years between 1971 and 1982.

METHODS

The equations used to calculate stock in number *(N)* and fishing mortality rate *(F)* were the following (Pope 1972):

$$N_i = (C_i + N_{i+1} e^{M/2})\, e^{\mathrm{M}/2} \qquad (1)$$

$$F_i = \ln(\frac{N_i}{N_{i+1}}) - M \qquad (2)$$

where C = catch in number, and
where M = natural mortality rate.

The number of the oldest year class was calculated as:

$$N_t = \frac{C_t}{F_t/(F_t/M)}$$

Natural mortality *(M)* was estimated using the equation from Pauly (1980):

$$\mathrm{Log}_{10} M = -0.0066 - 0.279\ \mathrm{Log}_{10}\ L_\infty + 0.6543\ \mathrm{Log}_{10} K + 0.4634\ \mathrm{Log}_{10} \bar{T}$$

where L_∞ is the asymptotic length (total length, in cm),
K is a growth constant of the von Bertalanffy growth equation; and
$\bar{T}$ is the annual mean temperature (°C) of the water in which the stock lives.

Applying this formula and using the growth parameters from Misu and Hamasaki (1971), we got $M = 0.2$ for females and $M = 0.4$ for males. Using the former estimates, we obtained biomass values for males two times higher than for females.

Because these figures seemed to be unrealistic, and because equal natural mortality for both sexes (at least in the younger age-groups) should be assumed, we used the mean value of $M = 0.3$. This value led to more balanced abundances in age-group II, although some differences remained (Table 2). A value of $M = 0.3$ is similar to values used for other hake stocks around the world (Francis 1983; Terré 1984).

We determined ages by reading otoliths collected from the Paita area. It should be mentioned, however, that for the first years of the study relatively few otoliths existed. Therefore, we established quarterly age-length keys for each year of investigation, taking them as representative of the age distribution of the monthly catch. We also assumed that the high-seas fleet catch had the same age composition as the Paita fleet catches; this assumption appears to be acceptable based on existing length frequencies of the high-seas fleet catches. The annual catch by age for the two sexes is demonstrated in Figure 1. N and F matrices were calculated separately for each sex because of their different growths and terminal lengths.

Preliminary runs indicated a fishing mortality rate of 1.0 for females of age-group V and VI. From this we chose a provisional terminal F of 0.5 and 1.0 for females and males, respectively, supposing that the older age-groups suffer less fishery mortality (Beverton and Holt 1957, p.81).

RESULTS (Table 2)

Biomass, Number of Spawning Stock, and Recruits

Until 1978, there is a continuous increment in biomass; later it diminishes (Figure 2). The total biomass fluctuates between a maximum of 630,500 MT in 1978 and a minimum of 130,000 in 1982; the latter is possibly an underestimation due to the scarce landings made in this El Niño year.

Observing the number of two-year-old recruits (Table 3), we note very low values in the last three years despite a certain underestimation of the 1982 value as explained above. The very good recruitment of the 1974 year class was probably due to the more favorable environmental conditions for hake following the 1972 El Niño (Wosnitza-Mendo and Espino. The impact of "El Niño" on recruitment in the Peruvian hake [*Merluccius gayi peruanus*]. In review.)

Analysis of the Instantaneous Rate of Fishing Mortality (F)

The mean F value for both males and females was low in the first two years (Figure 3), when the stock was being exploited only by the coastal fleet. From 1973 on, with the beginning of the heavy fishery, F for males increased until 1978, at which time it reached 2.08. F diminished in 1979 (1.30) and reached its maximum values in 1980 (2.35) and 1981 (2.48). The latter values are a result of a fishery on a depleted stock at levels higher than sustainable equilibrium yields. In the case of the females, F was maintained between 0.51-0.96 until 1979; in 1980 it reached its maximum (2.14). The F's in females are due, fundamentally, to their higher longevity and presumably to the larger individuals concentrated in deeper water. Analysis of the variation of F values in each year (Figures 4 and 5) shows that in the first two years (1971-72) the main fishing effort was on age-group V (males). Because of the intensive fishery from 1973 on, and the depletion of

TABLE 2
Cohort Analysis of Peruvian Hake

$M = 0.3$; $F_t = 0.5$ (females) $F_t = 1.0$ (males)

Stock in Number (10^6)												
Females	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
II	161.7	171.2	146.2	165.2	192.2	460.3	222.8	187.4	116.0	80.1	76.1*	78.1*
III	73.9	119.8	126.8	100.1	122.2	141.8	340.7	161.7	137.5	81.4	58.1	19.4
IV	34.9	53.0	87.5	80.4	75.3	82.4	98.0	239.3	72.9	88.6	43.9	39.0
V	13.3	19.6	27.4	20.7	10.2	16.6	20.7	17.9	18.1	13.1	13.3	8.9
VI	10.2	7.8	7.2	3.8	3.9	2.4	4.4	7.5	6.3	5.2	1.2	1.3
VII	2.9	6.9	2.8	1.2	1.6	2.7	1.1	2.5	3.7	1.0	0.1	0.2
VIII	—	1.6	4.5	0.8	0.4	1.0	2.0	0.5	1.5	1.4	—	—
	296.9	379.9	402.4	380.2	405.8	707.2	689.7	616.8	356.0	270.8	192.7	146.9
Males												
II	244.8	271.1	233.1	203.5	220.6	616.4	298.6	295.9	211.8	129.6	94.3*	119.9*
III	63.7	181.3	200.8	172.3	150.1	162.8	456.0	215.5	215.8	154.5	94.9	36.9
IV	58.4	45.5	130.6	133.4	113.7	102.5	103.4	316.1	89.0	110.2	60.4	53.7
V	7.8	31.2	11.5	19.2	25.5	14.0	4.4	4.2	3.5	23.7	1.8	1.4
	374.7	529.1	576.0	528.4	509.9	895.7	862.4	831.7	520.1	418.0	251.4	203.9
Fishing Mortality Rates												
Females												
II	0.0003	—	0.0012	—	0.004	0.04	0.011	0.01	0.005	0.03	0.001*	0.02*
III	0.01	0.001	0.05	0.08	0.01	0.05	0.08	0.50	0.10	0.34	0.07	0.04
IV	0.30	0.13	1.13	1.12	1.33	1.36	1.31	2.60	1.03	1.85	1.59	0.82
V	0.37	0.17	1.10	1.88	0.94	1.38	0.91	0.76	0.73	1.84	2.58	1.41
VI	0.29	0.12	0.98	0.83	0.14	0.01	0.48	0.48	0.64	3.38	2.11	0.56
VII	0.29	0.12	0.98	0.83	0.14	0.01	0.48	0.48	0.64	3.33	2.11	0.56
F(III-VII)	0.25	0.11	0.85	0.95	0.51	0.56	0.65	0.96	0.63	2.14	1.69	0.68
Males												
II	—	—	0.0003	0.001	0.006	—	0.008	0.007	0.002	0.001	0.002*	0.002*
III	0.01	—	0.04	0.05	0.12	0.03	0.12	0.54	0.34	0.55	0.30	0.18
IV	0.68	0.21	1.86	1.42	1.67	2.03	2.62	4.45	2.56	4.77	4.38	1.21
V	1.40	0.28	0.68	1.26	0.42	0.94	1.16	1.24	0.99	1.73	2.77	1.00
F(III-V)	0.70	0.16	0.86	0.91	0.74	1.00	1.30	2.08	1.30	2.35	2.48	0.80
Biomass (10^3 MT)												
Females												
II	55.1	58.4	49.9	56.3	65.5	157.0	76.0	63.9	39.6	27.3	26.0*	26.6*
III	30.1	48.8	51.7	44.1	49.8	57.8	138.8	65.9	56.0	34.4	23.7	7.9
IV	19.8	30.1	49.6	45.6	42.7	46.7	55.6	135.7	41.3	50.2	24.9	19.4
V	11.3	16.6	23.2	17.5	8.6	14.1	17.5	15.2	15.3	11.1	11.3	6.7
VI	18.0	13.8	12.7	6.7	6.9	4.2	7.8	13.2	11.1	9.2	2.1	2.6
VII	6.9	16.5	6.7	2.9	3.8	6.5	2.6	6.0	8.9	2.4	0.2	0.5
VIII	—	4.6	13.8	2.5	1.2	3.1	6.1	1.4	4.6	7.4	5.0	—
	141.2	188.8	207.6	175.6	178.5	289.4	304.4	301.3	176.8	142.0	93.2	63.7
Males												
II	70.3	77.9	67.0	58.5	63.4	177.1	85.8	85.0	60.9	37.2	27.1*	32.2*
III	24.1	68.5	76.0	65.2	56.8	61.6	172.5	81.5	81.6	58.4	35.9	11.4
IV	27.7	21.6	62.0	63.2	54.0	48.7	49.1	150.2	42.3	52.4	28.7	22.0
V	4.6	18.4	6.8	11.3	15.0	8.2	2.6	2.5	2.1	14.0	1.1	0.7
	126.7	186.5	211.8	198.2	189.2	295.6	310.0	319.2	186.9	162.0	92.8	66.3

*Preliminary data

Continued on next page

TABLE 2 (continued)
Cohort Analysis of Peruvian Hake

$M = 0.3$; $F_t = 0.5$ (females) $F_t = 1.0$ (males)

Biomass (10^3 MT) (continued)

Females + males	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
II	125.4	136.3	116.9	114.8	128.9	334.1	161.8	148.9	100.5	64.5	53.1*	58.8*
III	54.2	117.4	127.7	109.3	106.6	119.4	311.3	147.4	137.6	92.8	59.6	19.3
IV	47.5	51.7	111.6	108.8	96.7	95.4	104.7	285.9	83.6	102.6	53.6	41.4
V	15.9	35.0	30.0	28.8	23.0	22.3	20.1	17.7	17.4	25.1	12.4	7.4
VI	18.0	13.8	12.7	6.7	6.9	4.2	7.8	13.2	11.1	9.2	2.1	2.6
VII	6.9	16.5	6.7	2.9	3.8	6.5	2.6	6.0	8.9	2.4	0.2	0.5
VIII	—	4.6	13.8	2.5	1.2	3.1	6.1	1.4	4.6	7.4	5.0	—
	267.9	375.3	419.4	373.8	367.7	585.0	614.4	620.5	363.7	304.0	186.0	130.0

*Preliminary data

older fish, the *F* values in age-group IV increased, showing extremely high peaks in 1978, 1980, and 1981. However, mesh size regulations were increased from 70 to 90 mm in 1980, and thus since 1981 *F* has increased on older ages.

For the females, we note a uniform exploitation rate on age-groups IV, V, VI, and VII in the first three years (Figure 5). Between 1974 and 1979, the exploitation rate is very high on age-groups IV and V, especially for age-group IV in 1978. After 1980 the pattern changes because of the increase in mesh size and increasing *F* values for age-groups V, VI, and VII.

Yield per Recruit

Results of the cohort analysis make it possible to calculate the yield per recruit by taking the *F* value of

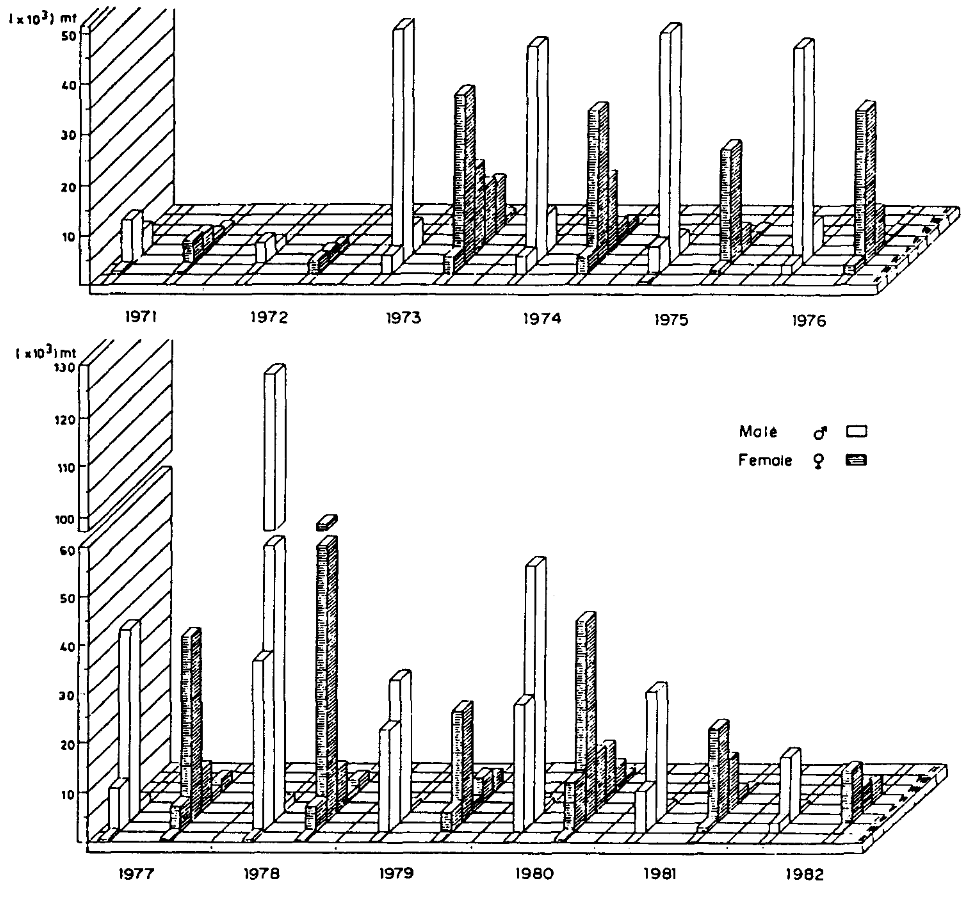

Figure 1. Annual catch by age distribution by sexes of Peruvian hake (*Merluccius gayi peruanus*).

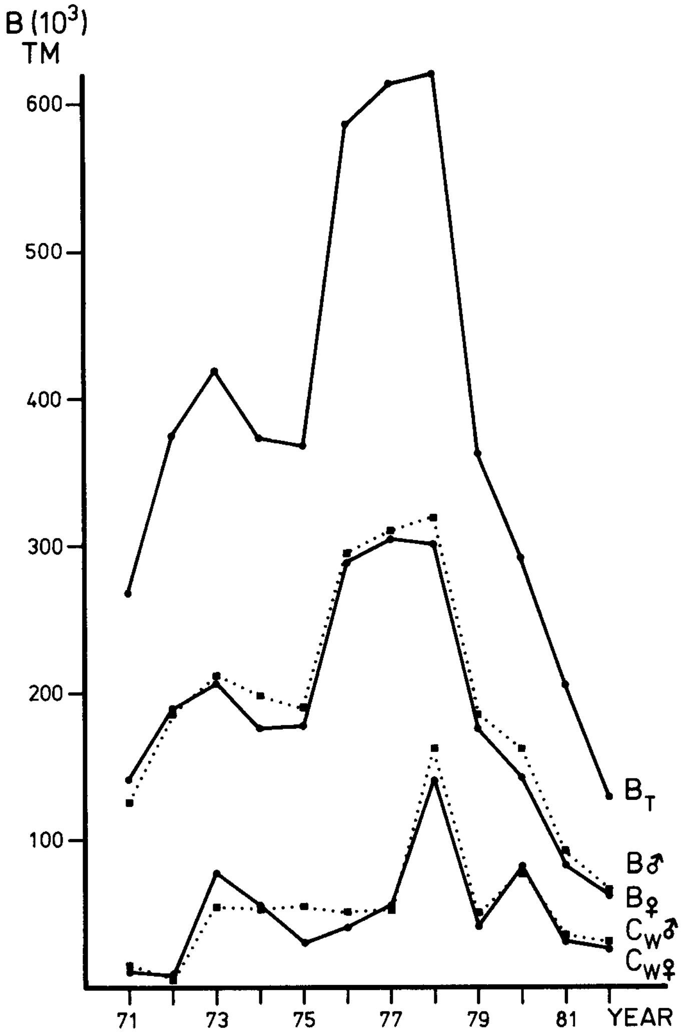

Figure 2. Variation of catches (Cw) and biomass (B) of Peruvian hake, 1971-82.

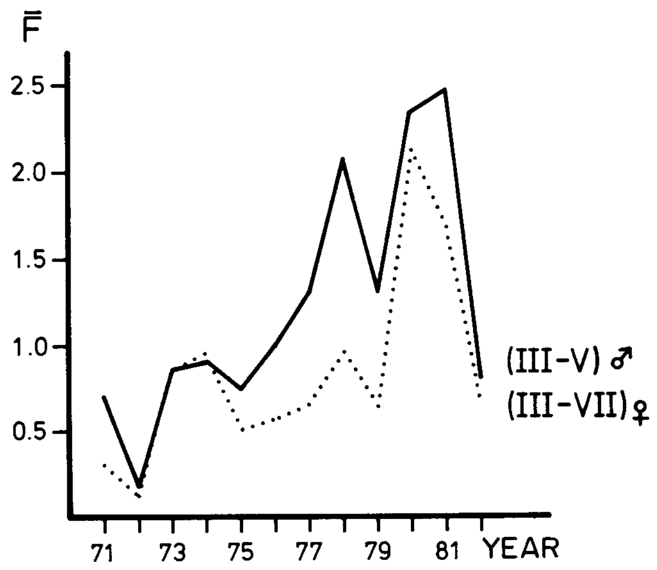

Figure 3. Annual variation of fishing mortality (F̄) for Peruvian hake, 1971-82.

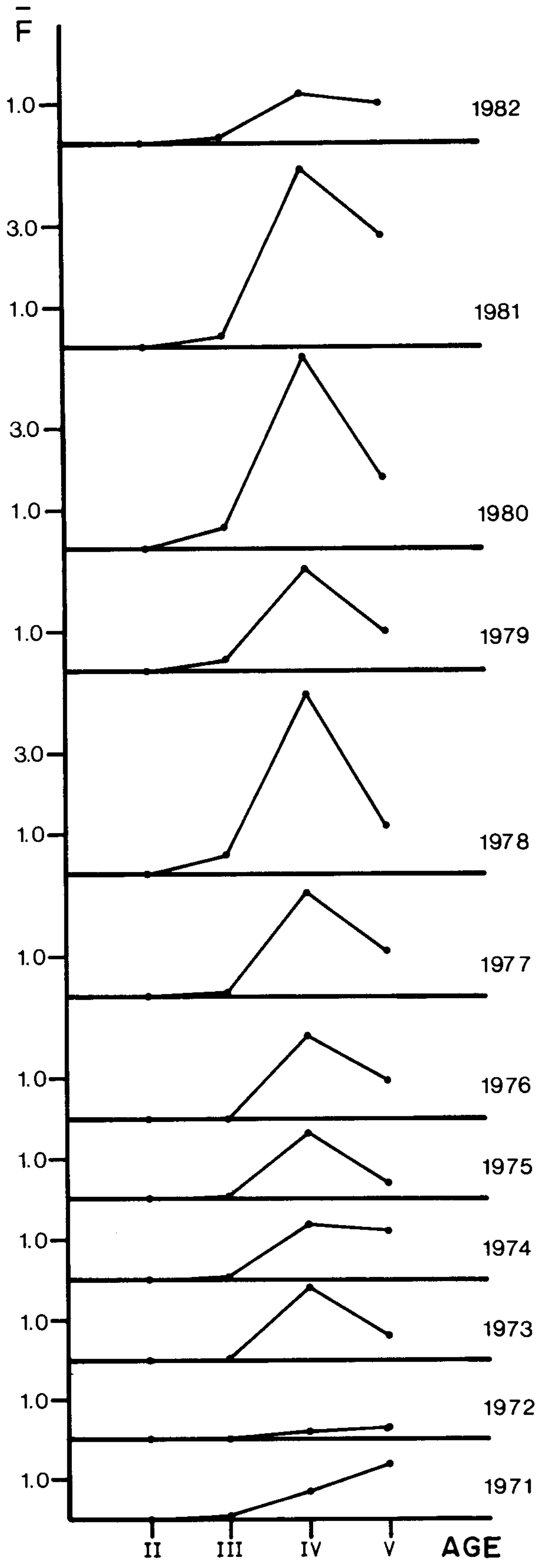

Figure 4. Variation of fishing mortality rate (F̄) for males, 1971-82.

TABLE 3
Number of Two-Year-Old Recruits

	N (II) (Millions)
1971	406.5
1972	442.3
1973	379.3
1974	368.7
1975	412.8
1976	1,076.7
1977	521.4
1978	483.3
1979	337.8
1980	209.7
1981	170.4
1982	198.0

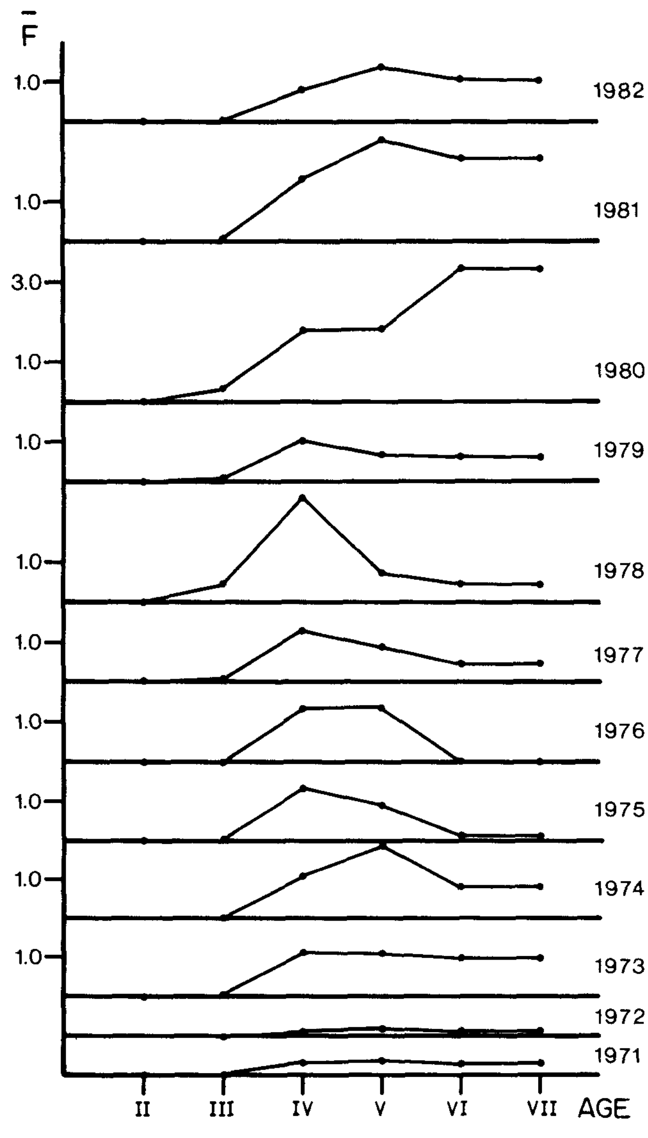

Figure 5. Variation of fishing mortality rate (F̄) for females, 1971-82.

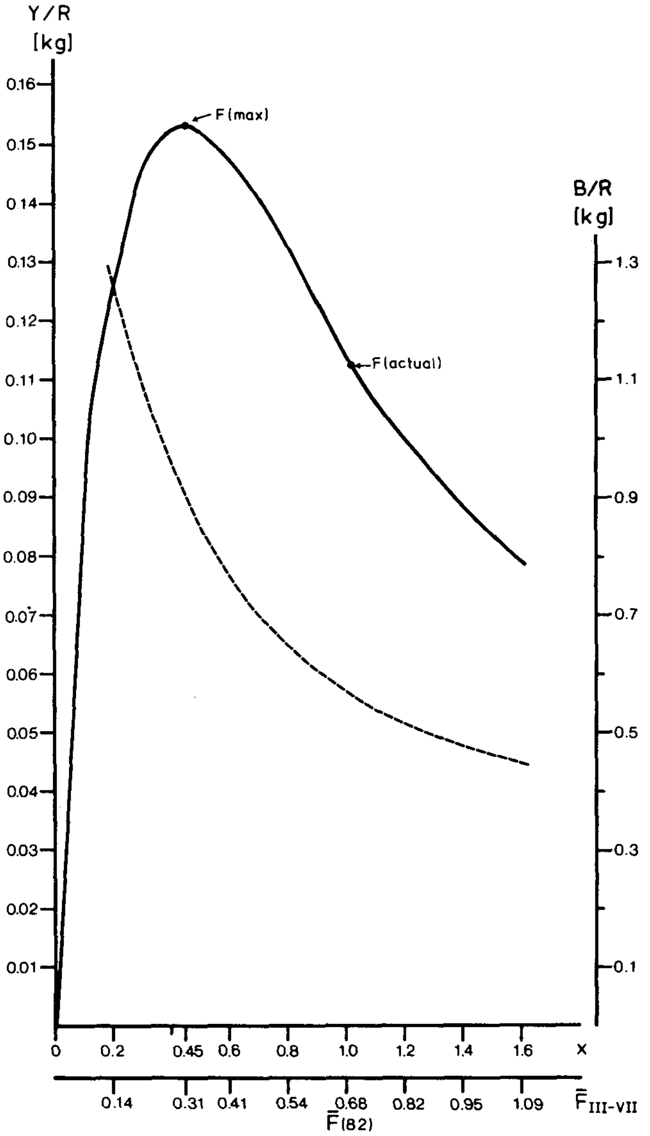

Figure 6. Yield per recruit for females (————). Biomass per recruit for females (-----).

the last year (1982) for each age-group as 100%. *M* is a constant of 0.3. The calculations were made with a unit of 1,000 recruits, leading to yield per recruit for different values of *F* (Figures 6 and 7). In both sexes, we observe that the actual (1982) *F* value is much higher than the value needed to obtain the maximum yield. The actual *F* value for males is 0.80 (age-groups III-V), whereas the optimal *F* should be 0.48, which would mean a 40% decrease in fishing effort. For females, the actual *F* is 0.68 (age-groups III-VII) and should be 0.31 (55% lower).

Because fishing mortality is directly correlated with fishing effort, this would indicate a considerable decrease in fishing effort. But a direct reduction of effort would cause serious socioeconomic consequences; we therefore recommend that the minimum mesh size

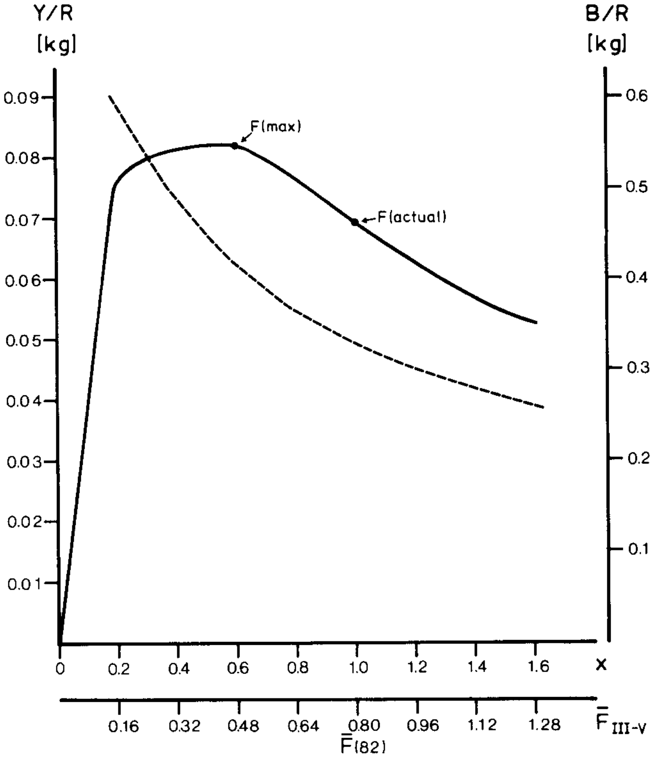

Figure 7. Yield per recruit for males (———). Biomass per recruit for males (-----).

be increased to at least 110 mm. A similar measure was taken in the South African hake fishery in 1974 (Wysokinski 1976). Environmental conditions like El Niño may also act to preserve the stock. In 1982-83 the stock was apparently unavailable to the fishery, because landings did not exceed 33,000 MT.

Exploitation Rate

Because we find very different distribution and concentration of fish stocks off Peru during so-called normal and abnormal years of El Niño, existing production models are not so useful for estimating the equilibrium yield. Therefore, we have taken the catches of "normal" years (1973-76 and 1979) from Table 1 to calculate an average equilibrium yield of 103,300 MT and a biomass of 454,000 MT. This gives us an equilibrium exploitation rate of "*E*" calculated as $\bar{C}/\bar{B}$ of about 0.25 with 95% confidence limits between 0.16 <"*E*" <0.36.

The variation of "*E*" (Figure 8, Table 4) shows low values for the first two years and excessive exploitation in 1978 and 1980. The high exploitation rate in 1978 is a result of the purse seine fishery of the anchovy fleet off Chimbote (9°S); in July and August this fleet concentrates in the spawning area. The high 1980 "*E*" value reflects an effort too high in relation to the already overfished stock.

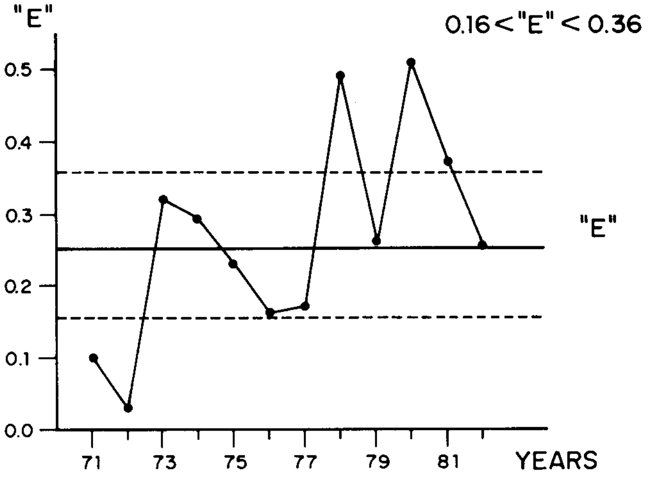

Figure 8. Variation of equilibrium exploitation rate "E" from 1971 to 1982.

DISCUSSION

The Peruvian hake stock between 1971 and 1982 showed marked variability in abundance from highs of 614,000 and 620,000 MT in 1977 and 1978 to lows of less than 200,000 MT in recent years. Whereas the high levels of stock biomass appear to be due to strong recruitment, the decline in biomass seems to result from overexploitation of the resource and relatively poor recruitment. Recruitment dynamics of Peruvian hake are quite marked, varying by some sixfold over a 12-year period. This pattern of great changes in recruitment from year to year is also observed in the Pacific hake (Francis 1983). Strong year classes are especially important to the fishery, as exemplified by the 1974 year class, which constituted about 50% of the stock biomass in 1977-78.

There are several sources of potential error in this study. The cohort analysis may underestimate stock biomass if the initial *F* values are too large. But we believe that using monthly runs minimizes the error. We have done some simulations and found that applying monthly runs and using, for example, $F_t = 1.0$

TABLE 4
Biomass and Equilibrium Yield for Peruvian Hake (in 1,000 Metric Tons)

	Biomass	Yield (*C*) (from Table 1)
1973	419.4	132.9
1974	373.8	109.5
1975	367.7	84.9
1976	585.0	92.5
1977	614.4	106.8
1979	363.7	92.9
	$\bar{B} = 454.0$	$\bar{C} = 103.25$

"*E*" = $\bar{C}/\bar{B}$ = 0.23

instead of 0.5 yields an underestimate of the biomass of 7.4% in the first year and less than 1% in the following years. Applying annual runs yields an underestimate of about 38.5% in the first year, and about 8% and 4% in later years (Wosnitza-Mendo, in prep.)

A second source of underestimation of biomass might be a smaller M than the real one (Terré 1984). Apart from applying Pauly's method, we used the production model of Csirke and Caddy (1983) as described in Espino and Wosnitza-Mendo (1984) in order to determine M values that are independent from growth parameters. Because in the first two years of investigation (1971 and 1972) only the coastal fishery and no open-sea fishery existed, we assumed that the Z values for these years approached natural mortality (M). M for these years was about 0.3, indicating that our former estimate of M is realistic. Another source of potential error would be a difference in age composition of the foreign high-seas catch and the coastal demersal catches; however, from bottom trawl surveys, we believe that little difference exists.

Our results indicate that the previous estimates of hake abundance based on swept-area methods are very likely too high. The last surveys resulted in estimates of 1-2 million MT (except for "Humboldt" cruise 8103-04 which resulted in an estimate of 600,000 to 800,000 MT using a catchability coefficient for the net of 0.75). The former estimates did not determine confidence limits, did not employ stratification for the area, and used extremely low catchability coefficients of 0.25. From these results it is apparent that FAO's (1978) proposed potential production of 200,000 to 250,000 MT of Peruvian hake cannot be attained. With the expected recovery of the hake stock after the 1982-83 El Niño, we recommend a yearly catch of 100,000 MT assuming "normal" conditions. This could be slightly raised later on and will unavoidably diminish during other El Niño events.

ACKNOWLEDGMENTS

We want to thank Kevin Bailey for review of the biological aspects of this manuscript, and an anonymous scientist for review of the cohort analysis.

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RELATIVE ABUNDANCE OF FOUR SPECIES OF *SEBASTES* OFF CALIFORNIA AND BAJA CALIFORNIA

JOHN S. MacGREGOR
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Estimates of relative abundance of rockfish larvae were made for the area from San Francisco to southern Baja California. Over the 14 years studied, 30% of spawning occurred in February, 18% in January, 17% in March, and 12% in April. For the four identified species of rockfish larvae, peak spawning occurred in February (65%) for *S. jordani*; in January (45% and 40%, respectively) for *S. levis* and *S. paucispinis*; and in April (32%) for *S. macdonaldi*.

Half of the *S. jordani* larvae were taken within 10 nautical miles of land. About half of the other three species were taken within 20 nautical miles of land. *Sebastes* larvae were most abundant off San Francisco and Monterey and in the area of the Channel Islands off southern California, with the former area accounting for 53% of all larvae and the latter for 35%.

RESUMEN

Se estimó la abundancia relativa de larvas de *Sebastes* en el área entre San Francisco y el Sur de Baja California. Durante los 14 años de estudio, un 30% del desove ocurrió en febrero, un 18% en enero, un 17% en marzo, y un 12% en abril. Para las cuatro especies de larvas de *Sebastes* identificadas, el desove máximo se presentó en febrero (65%) para *S. jordani*, en enero (45% y 40%, respectivamente) para *S. levis* y *S. paucispinis*, y en abril (32%) para *S. macdonaldi*.

La mitad del número de larvas de *S. jordani* fue colectada dentro de las 10 millas náuticas desde la costa. Alrededor de un 50% de las otras tres especies fue colectado dentro de las 20 millas náuticas desde la costa. Las larvas de *Sebastes* fueron más abundantes frente a San Francisco y Monterey (53% del total de larvas), y en el área de las "Channel Islands" al Sur de California (35%).

INTRODUCTION

Hubbs et al. (1979) list 62 species of rockfish of the genus *Sebastes* occurring in the coastal waters of California. Some rockfishes are important to sport and commercial fisheries; others are too infrequently taken or do not grow large enough to significantly contribute to the fisheries.

Since 1950, CalCOFI members the National Marine Fisheries Service (U.S. Department of Commerce), its predecessor agency the Bureau of Commercial Fisheries, and Scripps Institution of Oceanography have furnished vessels to obtain biological, physical, and chemical samples over a pattern of stations off the coasts of California and Baja California (see inside back cover). The pattern was sampled monthly for the ten years from 1950 through 1959 and has been sampled intermittently since then.

Plankton are sampled at each station with a 1-m net. The larval fish taken in each net tow are identified and enumerated. In past years rockfish were identified to genus only. More recently (1977) Moser et al. described the larvae of 4 of the 62 species—*S. paucispinis* (bocaccio), *S. jordani* (shortbelly rockfish), *S. levis* (cow rockfish), and *S. macdonaldi* (Mexican rockfish).

Ahlstrom (1959) obtained information on the temperature and depth distribution of larval rockfish from a series of 17 vertical distribution net tows at 12 depths from 2 to 285 m. *Sebastes* larvae were taken at temperatures between 9.0° and 17.2°C, with the larger concentrations occurring at temperatures between 10.2° and 16.1°. Ahlstrom found that only nine rockfish larvae were taken below 100 meters (actually in the 122-89-m haul). The depth distribution follows a normal distribution (Figure 1), with a peak at about 40 m and a standard deviation of 21.6 m. However, distribution is probably determined to a considerable extent by the position of the thermocline. Ahlstrom also decided that there was no significant difference between the numbers of rockfish larvae taken in night and day net hauls. (For some species of fishes more larvae are taken in night hauls.)

This paper presents data based on the identification and enumeration of the larvae of four species of rockfish for 5 CalCOFI survey years and for all *Sebastes* larvae for 14 years. Although it is not yet possible to identify all sizes of larvae of most rockfish species, the results of this study provide a background for evaluating the potential use of larval surveys to study distribution and abundance. The larval data were provided by H. Geoffrey Moser, under whose direction

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[Manuscript received February 11, 1986.]

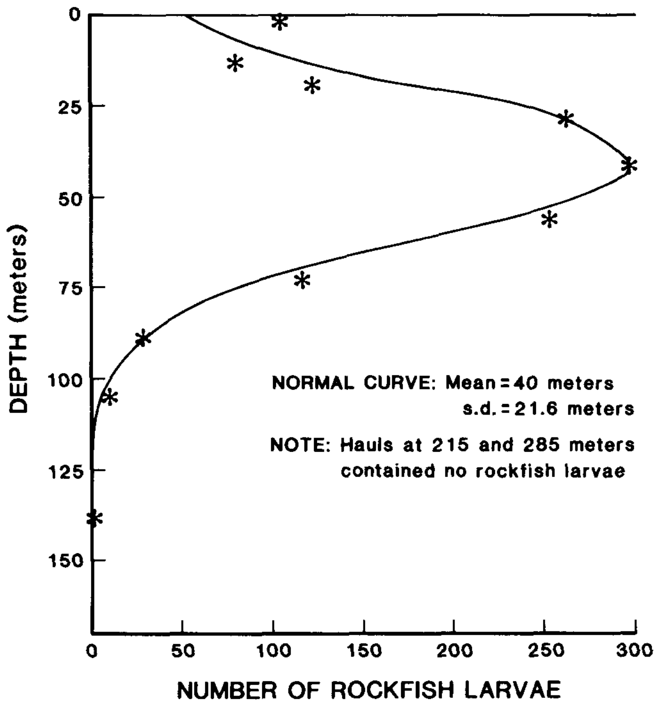

Figure 1. Depth distribution of rockfish larvae.

the four species of larval rockfishes were identified, counted, and measured by Elaine Sandknop with the assistance of Connie Fey and Susan D'Vincent.

MATERIALS AND METHODS

Sebastes larvae taken at each CalCOFI station for each survey cruise have been enumerated routinely each year. For this study, larvae of *S. paucispinis*, *S. jordani*, *S. levis*, and *S. macdonaldi* were identified, counted, and measured for each monthly survey for the years 1956, 1969, 1972, 1975; for *S. jordani* and *S. macdonaldi* 1966 was also included.

Routine CalCOFI plankton sampling methods and equipment have been described in detail by Ahlstrom (1948, 1953). The amount of water strained by the plankton net is measured so that the data may be converted to the numbers of organisms under one square meter of sea surface and therefore be comparable between stations.

The area included in this survey extended from the strip of ocean represented by CalCOFI line 60, just north of San Francisco Bay, to the strip represented by line 157, off the southern tip of Baja California (inside back cover). Coverage of the area north of line 60 was too spotty to be usable. The number of rockfish larvae taken at each station was expanded to give an abundance estimate for the area represented by that station. These estimates were combined to estimate the larval population present in the 40-nautical-mile-wide strip of ocean represented by each CalCOFI line. In some months no cruise was made, or some lines were omitted from the pattern. Estimates were calculated for these omissions based on the average percentages of larvae taken in those months or on those lines in the other years when they were sampled; i.e., if *X*% of the larvae were taken on a line or in a month when they were sampled, I assume that *X*% were present at similar times when they were not sampled. However, these omitted lines or months were generally outside the main spawning season and did not affect the estimates significantly. The estimates obtained are for the numbers of larvae in the area at the time of the cruise. No data are available that would allow us to interpolate between months in order to obtain more representative estimates of annual spawning.

Although the stations on some lines were sampled much farther to sea than on others, I believe that most of the offshore distribution was sampled adequately. Half of the *S. paucispinis* and *S. macdonaldi* larvae were taken within 20 nautical miles of land, and half of the *S. jordani* larvae within 10 nautical miles of land (Table 1). *S. paucispinis* appears to have a somewhat more offshore distribution than the other larvae, while the distribution of *S. jordani* is more inshore. There were too few data to determine the offshore distribution of *S. levis*, but it appears to be similar to the other *Sebastes* larvae.

The numbers and percentages in the tables include several degrees of magnitude. Digits are retained in the larger numbers for purposes of alignment and do not imply great accuracy of these numbers.

RESULTS AND DISCUSSION

Estimates of larval rockfish abundance in the area represented by lines 60 through 137 (Table 2) range from 38×10^{12} in 1959 to 219×10^{12} in 1969 for the 14 years 1950-59, 1966, 1969, 1972, and 1975. The 14-year average abundance is 135×10^{12} larvae.

Because rockfishes are live bearers whose larvae develop within the ovaries and hatch at the time of spawning, and because most of the larvae taken were close to the hatching size, the occurrence of larvae should delimit the spawning season fairly well. For the 14 years 18% of the spawning occurred in January, 30% in February, 17% in March, and 12% in April.

In any given year, if the spawning was low in one of these four months, it tended to be low in the other three months, and, if high, it tended to be high in the other three months. Rank correlation of the amount of spawning in January, February, and March yielded correlation coefficients of 0.65 (January/February), 0.70 (January/March), and 0.78 (February/March). The correlation coefficient for a probability of 0.01 is 0.66. Correlations with April were less significant.

TABLE 1
Cumulative Percentage Distribution of Rockfish Larvae (Five-Year Average) Relative to Distance from Nearest Land for Each of Three Species Compared to Percent Distribution of All Species of Rockfish Larvae Less the Species Compared

Nautical miles from land	*Sebastes paucispinis*	All other rockfish	*Sebastes jordani*	All other rockfish	*Sebastes macdonaldi*	All other rockfish
0-10	29.3	63.7	56.9	65.6	43.9	46.5
0-20	50.4	76.6	68.2	76.7	56.5	65.6
0-30	56.9	85.4	93.3	83.1	69.7	85.0
0-40	74.4	90.1	97.0	88.5	81.2	89.2
0-50	85.8	95.2	99.1	94.2	83.3	92.9
0-100	97.6	98.5	99.9	98.2	100.0	96.4
0-150	99.1	99.2	100.0	99.2		98.1
0-200	100.0	99.8		99.7		100.0
0-250		100.0		100.0		

Total rockfish larvae include only larvae occurring in the same areas as species with which compared; i.e., no *S. paucispinis* larvae were taken south of line 113, no *S. jordani* south of line 120, no *S. macdonaldi* north of line 83. Also *S. paucispinis* was not identified in the 1966 samples.

The high correlations among the first three months indicate that the sampling program provided representative estimates of larval abundance, and that short-term random changes in larval abundance do not mask annual changes during the major spawning season. Years of low abundance estimates probably indicate low spawning effort and/or high early larval mortality, whereas years of high abundance estimates indicate

TABLE 2
Estimated Rockfish Larvae (Billions) for 14 Years

	Year							
Month	1950	1951	1952	1953	1954	1955	1956	1957
Jan.	14,622	12,109	9,707	17,284	26,355	29,950	24,018	36,519
Feb.	16,118	18,715	35,049	47,529	55,980	50,871	63,875	72,650
Mar.	12,999	15,931	23,730	19,506	22,583	15,951	37,967	31,048
Apr.	16,716	25,438	14,820	8,401	16,943	16,578	9,886	30,031
May	4,593	11,414	7,575	4,496	9,447	5,810	5,763	13,457
June	4.445	9,367	9,285	4,576	7,453	5,404	4,264	8,232
July	2,969	2,580	4,652	3,467	4,858	10,993	4,295	4,591
Aug.	3,149	3,418	1,600	2,768	2,791	2,698	5,683	490
Sept.	1,433	904	1,119	2,141	1,316	987	0	701
Oct.	1,093	781	2,086	6,098	1,536	1,709	2,121	1,185
Nov.	1,109	2,462	1,801	1,486	2,110	5,192	1,376	2,083
Dec.	2,310	1,853	3,248	5,115	3,708	2,766	8,929	8,954
Totals	81,556	104,972	114,672	122,867	155,080	148,909	168,177	209,941

	Year							
Month	1958	1959	1966	1969	1972	1975	Mean	Percent
Jan.	17,424	5,777	24,736	38,560	48,378	28,617	23,861	17.68
Feb.	21,297	8,863	27,401	77,687	30,567	46,245	40,918	30.32
Mar.	15,370	4,572	23,878	40,409	30,382	28,165	23,035	17.07
Apr.	7,235	6,569	20,845	25,792	16,617	16,573	16,603	12.30
May	9,583	4,226	8,812	9,156	12,110	5,129	7,969	5.90
June	4,161	2,274	8,003	7,578	5,484	5,469	6,143	4.55
July	3,765	2,205	6,075	6,363	4,886	3,252	4,639	3.44
Aug.	113	623	1,438	3,102	2,681	2,675	2,374	1.76
Sept.	477	554	2,196	2,809	1,966	1,961	1,326	0.98
Oct.	1,300	420	1,989	1,693	2,208	1,805	1,859	1.38
Nov.	376	542	474	3,755	2,620	3,241	2,045	1.51
Dec.	1,320	1,242	3,420	2,074	4,878	8,939	4,197	3.11
Totals	82,421	37,867	129,267	218,978	162,777	152,071	134,969	100.00

Estimates are for the area represented by CalCOFI lines 60 through 137 at the time the samples were taken.

TABLE 3
Rockfish Larvae 14-Year Annual Averages

CalCOFI line	Number (billions)	Percent
60	16,044	11.841
63	15,779	11.646
67	12,685	9.362
70	5,329	3.933
73	4,201	3.101
77	6,159	4.546
Total (60-77)	60,197	44.429
80	7,476	5.518
83	12,896	9.518
87	16,326	12.049
90	9,791	7.226
93	5,094	3.760
Total (80-93)	51,583	38.071
97	3,275	2.417
100	2,973	2.194
103	1,775	1.310
107	1,419	1.048
Total (97-107)	9,442	6.969
110	1,448	1.069
113	2,014	1.486
117	3,944	2.911
120	2,182	1.610
Total (110-120)	9,588	7.076
123	1,336	0.986
127	881	0.650
130	579	0.428
133	824	0.608
137	539	0.398
Total (123-137)	4,159	3.070
140	128	0.094
143	64	0.047
147	237	0.175
150	68	0.050
153	8	0.006
157	17	0.013
Total (140-157)	522	0.385
Total (60-157)	135,491	100.000

high spawning effort and/or low early mortality rather than random fluctuations resulting from inadequate sampling.

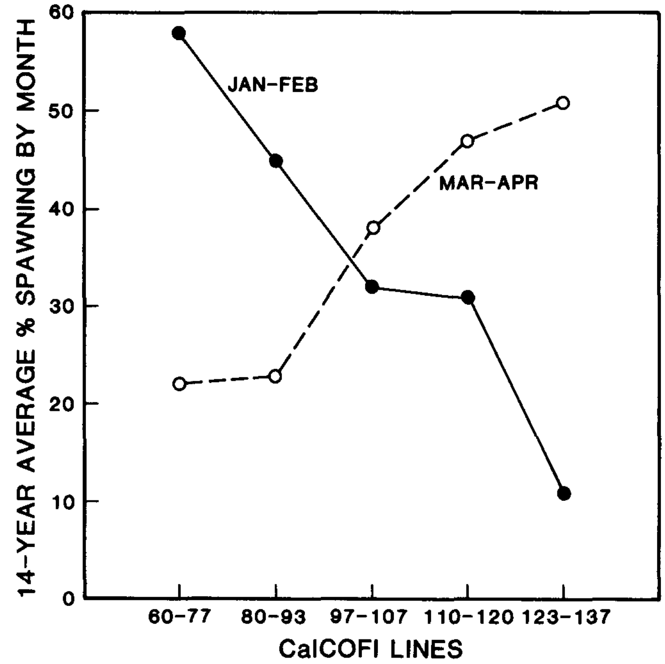

Figure 2. Percent of total year's rockfish spawning occurring in January/February and March/April for five areas as measured by larvae (14-year average).

The 14-year average number of larvae by CalCOFI line (Table 3) shows high abundance levels in the San Francisco-Monterey area (lines 60-67). These lines account for 33% of the larvae found in the main survey area (30 lines, 60-157). Sparse data for the six lines north of line 60 (lines 40-57) indicate a population equal to about 75% of the population in the area represented by the six lines 60-77, with about a third of these larvae found on line 57. Along the exposed coast south of Monterey (line 70) the larval abundance decreases to Point Conception (line 80). In the Channel Islands area (lines 83-90) larval abundance again increases. These three lines account for 29% of the larvae found in the main survey area. The number of larvae continues to decrease southward to line 157 with one smaller increase in the area around and north of Punta Eugenia and Cedros Island (lines 113-120).

The spawning season appears to be later farther south (Figure 2). April is the peak spawning month off Mexico (lines 97-137). This area accounts for only 17½% of the total average yearly production of rockfish larvae, in contrast to 82½% for U.S. waters (lines 60-93), which tends to mask this seasonal phenomenon (Table 3). The increase in late spawning in the more southern areas is probably due to increased proportions of late-spawning species of rockfishes like the Mexican rockfish and the subgenus *Sebastomus* (Chen 1971), which become relatively more abundant in the rockfishes' southern range.

Estimates of the numbers of all rockfishes, *S. jordani*, and *S. macdonaldi* were calculated by month and line for 1956, 1966, 1972, and 1975, and of *S. paucispinis* and *S. levis* for 1956, 1969, 1972, and 1975[1]. A summary of the estimated larval abundance by year and month (Table 4) shows that the seasonal distribution of all rockfish larvae for the 5 selected

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[1] Tables to be issued as an administrative report of the Southwest Fisheries Center.

TABLE 4
Estimated Larvae (Billions) from CalCOFI Lines 60-137 (60-157 for *Sebastes macdonaldi*) for All Rockfish, and Four Species of Rockfish

Month	Year						
All RF	1956	1966	1969	1972	1975	Mean	Percent
Jan.	24,018	24,736	38,560	48,378	28,617	32,862	19.766
Feb.	63,875	27,401	77,687	30,567	46,245	49,155	29.566
Mar.	37,967	23,878	40,409	30,382	28,165	32,160	19.344
Apr.	9,886	20,845	25,792	16,617	16,573	17,943	10.792
May	5,763	8,812	9,156	12,110	5,129	8,194	4.929
June	4,264	8,003	7,578	5,484	5,469	6,160	3.705
July	4,295	6,075	6,363	4,886	3,252	4,974	2.992
Aug.	5,683	1,438	3,102	2,681	2,675	3,116	1.874
Sept.	0	2,196	2,809	1,966	1,961	1,786	1.075
Oct.	2,121	1,989	1,693	2,208	1,805	1,963	1.181
Nov.	1,376	474	3,755	2,620	3,241	2,298	1.379
Dec.	8,929	3,420	2,074	4,878	8,939	5,648	3.397
Totals	168,177	129,267	218,978	162,777	152,071	166,254	100.000
S. paucispinis							
Jan.	548		2,651	3,966	2,050	2,304	40.131
Feb.	351		2,934	1,615	1,693	1,648	28.713
Mar.	514		1,374	1,388	952	1,057	18.413
Apr.	65		462	333	235	274	4.769
May	17		170	304	82	143	2.495
June	17		20	17	24	20	0.340
July	0		0	0	0	0	0.000
Aug.	0		0	0	0	0	0.000
Sept.	0		0	0	0	0	0.000
Oct.	0		0	13	6	5	0.083
Nov.	0		12	12	19	11	0.187
Dec.	133		168	341	476	280	4.869
Totals	1,645		7,791	7,989	5,537	5,742	100.000
S. jordani							
Jan.	1,611	2,761	1,611	3,551	2,160	2,339	13.564
Feb.	14,300	8,118	20,932	2,426	10,590	11,273	65.378
Mar.	2,962	2,017	4,186	2,541	2,419	2,825	16.383
Apr.	492	667	1,183	364	666	674	3.911
May	23	0	113	310	46	98	0.571
June	0	0	9	1	3	3	0.015
July	0	0	4	0	0	1	0.005
Aug.	0	0	23	11	21	11	0.064
Sept.	0	0	0	0	0	0	0.000
Oct.	0	0	0	0	0	0	0.000
Nov.	0	0	17	11	66	19	0.109
Dec.	0	0	0	0	0	0	0.000
Totals	19,388	13,563	28,078	9,215	15,971	17,243	100.000
S. levis							
Jan.	40		56	214	574	221	45.473
Feb.	0		170	53	164	97	19.908
Mar.	0		93	118	144	89	18.261
Apr.	8		119	7	139	68	14.043
May	0		15	7	0	6	1.132
June	0		0	0	0	0	0.000
July	0		23	0	0	6	1.183
Aug.	0		0	0	0	0	0.000
Sept.	0	0		0	0	0	0.000
Oct.	0	0		0	0	0	0.000
Nov.	0		0	0	0	0	0.000
Dec.	0	0		0	0	0	0.000
Totals	48		476	399	1,021	487	100.000

(Table 4 continued on next page)

TABLE 4 (continued)

Month	Year						
	1956	1966	1969	1972	1975	Mean	Percent
S. macdonaldi							
Jan.	268	36	86	35	167	118	10.432
Feb.	279	437	637	125	153	326	28.740
Mar.	67	473	298	750	7	319	28.106
Apr.	17	979	172	459	162	358	31.524
May	17	0	6	7	2	6	0.564
June	0	0	0	0	0	0	0.000
July	0	0	0	0	0	0	0.000
Aug.	0	0	0	0	0	0	0.000
Sept.	0	0	0	0	0	0	0.000
Oct.	0	0	0	0	0	0	0.000
Nov.	0	10	0	3	0	3	0.299
Dec.	0	0	18	5	0	5	0.405
Totals	648	1,935	1,217	1,384	491	1,135	100.000

years is not much different from the 14-year average of which it is a part (Table 2). However, the 5 years were among the years of higher abundance estimates. The mean abundance index was 166×10^{12} compared to 135×10^{12} for the 14-year average.

For the 5 years in which individual species were enumerated, 30% of all rockfish larvae were taken in February, 20% in January, 19% in March, and 11% in April (Figure 3). *S. jordani*, which accounted for 10.4% of all rockfish larvae, was most abundant in February in 4 of 5 years; an average of 65% of the larvae was taken in this month. January, February, and March accounted for 95% of the larvae of this species. The larvae of *S. paucispinis* were most abundant in January, when 40% of the estimated annual number was found. In January, February, and March—the months of heaviest spawning—87% of the annual larval population of this species was present. *S. paucispinis* was about one-third as abundant as *S. jordani*. *S. levis* also appears to be an earlier-spawning species, with 45% of the spawning taking place in January. In January, February, and March 84% of the larvae were taken. *S. levis* larvae were only 1/35 as abundant as *S. jordani* larvae. *S. macdonaldi* appeared to be a later-spawning species, with 32% of the spawning occurring in April. About 89% of the total larvae were taken in February, March, and April. *S. macdonaldi* larvae were about 1/15 as abundant as *S. jordani* larvae.

The distribution of all rockfish larvae by line for the 5 years (Table 5; Figure 4) is not much different from the distribution for the 14 years (Table 3).

The distribution of *S. jordani* larvae by line and year (Table 6) indicates concentrations in the San Francisco-Monterey area (lines 60-67), where 53% of the 5-year mean of the number of larvae occurred, and in the Channel Islands area (lines 83-90), where 35% of the larvae were found. No larvae were taken south of line 120 (Cedros Island). No data are available for the area north of line 60.

S. paucispinis larvae appear to follow all rockfish larvae in distribution by line within their range (Table 7). They were most abundant in the Channel Islands

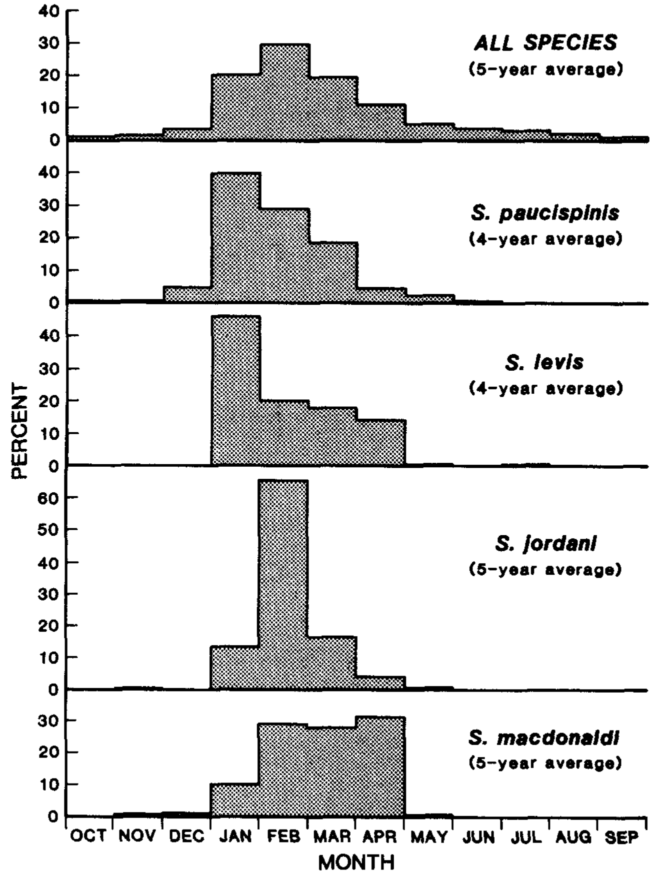

Figure 3. Percent spawning by month as indicated by larval rockfish taken in net tows.

TABLE 5
Percent Distribution of Rockfish Larvae by CalCOFI Line

	Year					
Line	1956	1966	1969	1972	1975	Average
60	13.240	12.455	14.933	11.926	10.560	12.816
63	11.490	12.303	14.494	6.569	11.926	11.524
67	9.944	12.232	10.361	6.752	8.439	9.509
70	4.065	5.449	4.660	4.840	4.496	4.668
73	2.879	3.170	3.098	2,869	4.421	3.262
77	4.369	5.615	4.543	8.468	3.481	5.249
60-77	45.987	51.224	52.089	41.424	43.323	47.028
80	3.213	4.578	4.710	10.494	4.644	5.507
83	7.070	10.832	11.112	14.634	13.469	11.372
87	11.556	11.068	11.713	10.566	15.135	11.983
90	8.945	5.354	8.845	9.741	7.834	8.312
93	1.978	3.027	2.502	3.441	2.976	2.748
80-93	32.762	34.859	38.882	48.876	44.058	39.922
97	0.824	1.901	0.966	2.118	1.603	1.425
100	2.520	2.849	1.226	1.352	1.631	1.839
103	1.738	0.673	0.649	0.750	1.365	1.024
107	1.993	0.952	0.832	0.419	0.775	0.994
97-107	7.075	6.375	3.673	4.639	5.374	5.282
110	1.486	1.176	0.992	0.515	0.975	1.024
113	1.148	1.036	0.778	0.549	0.874	0.866
117	4.479	2.321	1.283	1.240	2.123	2.236
120	3.689	0.860	0.844	0.800	1.500	1.533
110-120	10.802	5.393	3.897	3.104	5.472	5.659
123	1.013	1.137	0.636	0.937	0.545	0.833
127	0.930	0.383	0.255	0.413	0.537	0.494
130	0.228	0.112	0.093	0.077	0.179	0.136
133	0.568	0.230	0.226	0.270	0.187	0.297
137	0.501	0.142	0.156	0.143	0.189	0.227
123-137	3.240	2.004	1.366	1.840	1.637	1.987
140	0.065	0.073	0.045	0.055	0.069	0.060
143	0.041	0.041	0.028	0.033	0.045	0.036
147	0.000	0.000	0.000	0.000	0.000	0.000
150	0.009	0.009	0.006	0.010	0.006	0.008
153	0.008	0.011	0.006	0.007	0.008	0.008
157	0.011	0.011	0.008	0.012	0.008	0.010
140-157	0.134	0.145	0.093	0.117	0.136	0.122
60-157	100.000	100.000	100.000	100.000	100.000	100.000

area off southern California, and north to Point Conception. Nineteen percent of the larvae occurred in the area represented by line 83, and 53% in the area represented by lines 80-90. The peak on lines 60-67 is less marked than for all rockfish, and there are no data for the area to the north.

The distribution of *S. levis* (Table 8) appears to be restricted primarily to southern California. Miller and Lea (1972) give the range of this species as from Mendocino County (line 50) to Ranger Bank (line 117). Most larvae—86%—were taken on lines 83-90. Only 7% occurred in the area represented by the six lines north of Point Conception.

S. macdonaldi (Table 9) has the most southerly distribution of the four species. No larvae were taken from Point Conception (line 80) north. Ninety-seven percent of the larvae were spread over the area represented by the 10 lines 110-140, with 37% occurring along line 117. A second apparent peak was found south of Point Eugenia along line 123. The population decreased to line 143 (Magdalena Bay area), and no larvae were taken to the south.

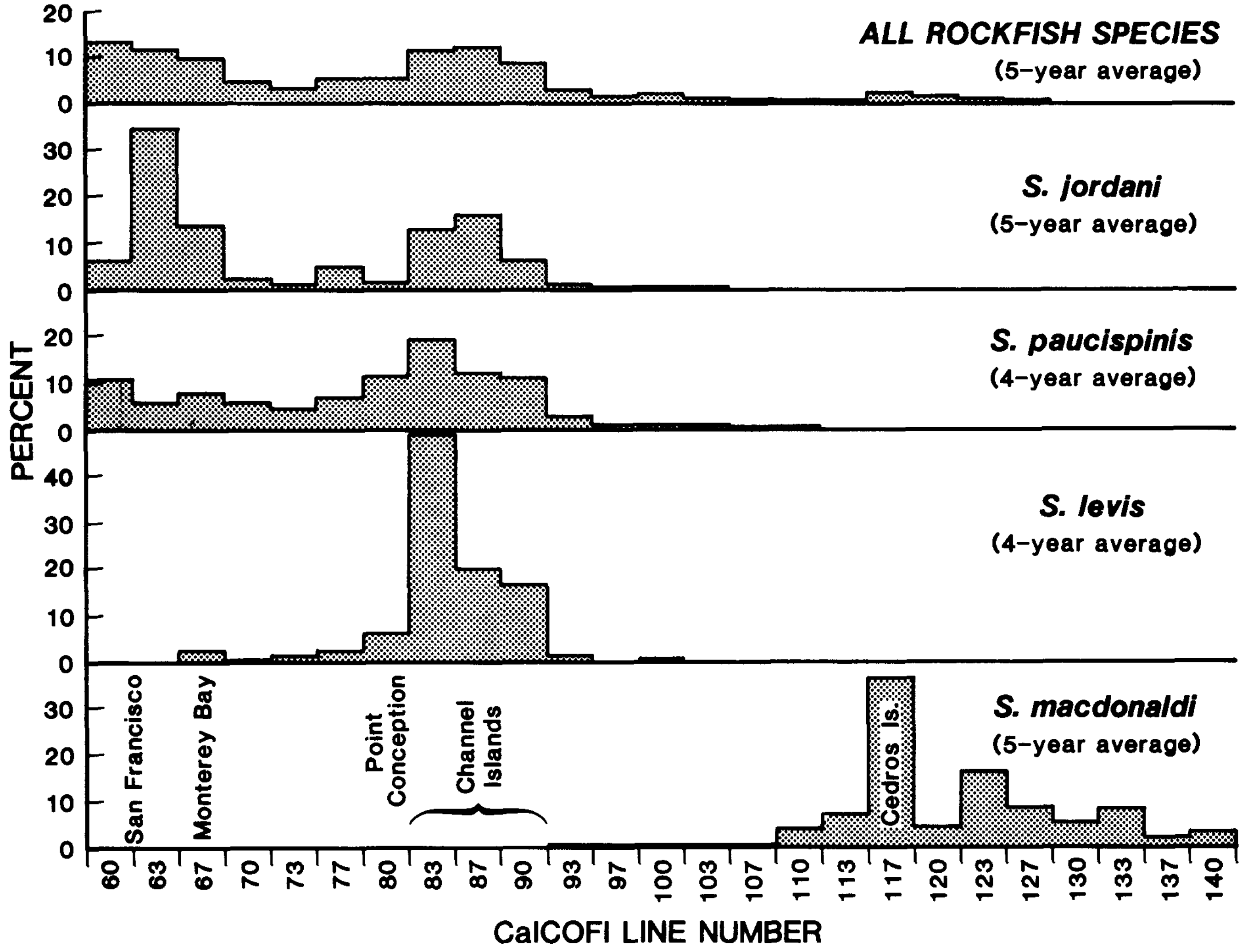

Figure 4. Larval rockfish percent distribution by CalCOFI line.

S. jordani, the most abundant of the four identified species, accounted for 10.4% of all rockfish larvae taken on lines 60-137 (Table 10). It was most abundant between San Francisco and Monterey (lines 63 and 67), where *S. jordani* was 23.4% of all rockfish larvae, and in the Channel Islands (lines 83 and 87), where it was 12.9% of all larvae. *S. paucispinis* accounted for 3.27% of all rockfish larvae. Its distribution was disproportionately high between the abundance peaks of all rockfish larvae. In this area (lines 70-80) it accounted for 5.0% of all rockfish larvae. *S. levis* was the least abundant of the four species, constituting only 0.28% of all rockfishes. It was most abundant in the Channel Islands area, where it accounted for 0.73% of the larvae on the three lines 83-90. *S. macdonaldi* larvae amounted to 0.68% of the total rockfish larvae. They were most abundant on line 117, where they equalled 11.14% of all rockfish larvae. However, smaller numbers of *S. macdonaldi* to the south of this area constituted a larger portion of the population (up to 27.8% on line 130) as numbers of other species decreased rapidly.

Length compositions (Tables 11-14) for *S. jordani* and *S. paucispinis* show an apparent increase in the percent of larger larvae as the season progresses; this is not apparent for the two less-abundant species. However, most of the larvae for all four species are smaller, more recently hatched larvae.

Moser et al. (1977) give the size of newly hatched *S. paucispinis* and *S. macdonaldi* as 4.5 mm, *S. levis* as 5.0 mm, and *S. jordani* as 5.4 mm. About 87% of *S. jordani*, 78% of *S. paucispinis*, 83% of *S. macdonaldi*, and 70% of *S. levis* were within 1 mm of the size of newly hatched larvae (Figure 5). This indicates that, unless rockfish larvae have exceptionally slow growth, a large portion of captured larvae were spawned during the month of capture. The decrease in numbers of longer larvae indicates a very high mortality combined

TABLE 6
Percent Distribution of *Sebastes jordani* Larvae by CalCOFI Line

	Year					
Line	1956	1966	1969	1972	1975	Average
60	5.875	5.190	5.805	6.989	6.906	6.055
63	35.976	30.229	38.977	22.398	36.535	34.701
67	12.554	16.560	12.925	6.424	12.949	12.723
70	1.547	2.625	2.148	3.039	1.703	2.100
73	0.928	0.509	1.079	0.846	2.285	1.154
77	4.513	5.766	4.861	4.775	3.995	4.756
60-77	61.393	60.879	65.795	44.471	64.373	61.489
80	0.423	0.819	2.799	1.357	1.903	1.633
83	12.111	15.483	8.594	26.088	12.316	13.028
87	18.207	17.105	15.468	11.915	15.879	16.038
90	5.555	4.394	6.336	14.704	3.970	6.311
93	0.753	0.605	0.641	1.020	0.488	0.673
80-93	37.049	38.406	33.838	55.084	34.556	37.683
97	0.031	0.288	0.103	0.141	0.507	0.195
100	0.676	0.383	0.185	0.108	0.338	0.347
103	0.660	0.015	0.018	0.000	0.163	0.187
107	0.000	0.000	0.025	0.011	0.013	0.011
97-107	1.367	0.686	0.331	0.260	1.021	0.740
110	0.191	0.000	0.000	0.000	0.050	0.052
113	0.000	0.000	0.000	0.000	0.000	0.000
117	0.000	0.029	0.032	0.185	0.000	0.035
120	0.000	0.000	0.004	0.000	0.000	0.001
110-120	0.191	0.029	0.036	0.185	0.050	0.088
123-157	0.000	0.000	0.000	0.000	0.000	0.000
60-157	100.000	100.000	100.000	100.000	100.000	100.000

with increasing ability to dodge the net as the larvae develop and grow. The decrease also may be affected by differences in growth rates among the species.

Exponential equations fitted to the data by transforming catches to logarithms and then using standard least squares regression techniques indicate a 61%

TABLE 7
Percent Distribution of *Sebastes paucispinis* Larvae by CalCOFI Line

	Year				
Line	1956	1969	1972	1975	Average
60	12.462	9.703	15.296	5.261	10.774
63	6.079	8.895	1.940	6.003	5.575
67	7.355	12.091	3.980	5.985	7.456
70	5.836	4.698	5.232	7.304	5.618
73	4.924	4.646	2.616	7.431	4.629
77	6.809	5.776	8.512	5.496	6.733
60-77	43.465	45.809	37.576	37.480	40.785
80	8.632	9.986	12.467	13.560	11.611
83	12.644	19.073	21.430	17.158	18.966
87	14.347	11.693	9.751	14.211	11.811
90	14.225	9.126	10.802	12.746	10.944
93	1.824	2.978	3.655	1.356	2.739
80-93	51.672	52.856	58.105	59.031	56.071
97	1.155	0.500	2.028	0.958	1.189
100	2.371	0.488	1.027	0.651	0.849
103	0.425	0.257	0.851	1.537	0.784
107	0.000	0.051	0.225	0.036	0.104
97-107	3.951	1.296	4.131	3.182	2.926
110	0.182	0.039	0.188	0.307	0.166
113	0.730	0.000	0.000	0.000	0.052
117	0.000	0.000	0.000	0.000	0.000
120	0.000	0.000	0.000	0.000	0.000
110-120	0.912	0.039	0.188	0.307	0.218
123-157	0.000	0.000	0.000	0.000	0.000
60-157	100.000	100.000	100.000	100.000	100.000

TABLE 8
Percent Distribution of *Sebastes levis* Larvae by CalCOFI Line

	Year				
Line	1956	1969	1972	1975	Average
60	0.000	0.000	0.000	0.000	0.000
63	0.000	0.000	0.000	0.000	0.000
67	2.083	6.513	0.000	1.371	2.377
70	2.083	1.681	0.000	0.000	0.465
73	2.083	0.630	0.000	2.057	1.292
77	2.084	5.252	6.154	0.000	2.584
60-77	8.333	14.076	6.154	3.428	6.718
80	0.000	8.824	7.436	4.799	6.202
83	0.000	22.689	40.769	66.993	49.147
87	39.583	27.731	31.282	11.460	20.155
90	52.084	21.639	14.359	13.320	16.538
93	0.000	3.151	0.000	0.000	0.775
80-93	91.667	84.034	93.846	96.572	92.817
97	0.000	0.000	0.000	0.000	0.000
100	0.000	1.260	0.000	0.000	0.310
103	0.000	0.000	0.000	0.000	0.000
107	0.000	0.000	0.000	0.000	0.000
97-107	0.000	1.260	0.000	0.000	0.310
110	0.000	0.000	0.000	0.000	0.000
113	0.000	0.000	0.000	0.000	0.000
117	0.000	0.630	0.000	0.000	0.155
120	0.000	0.000	0.000	0.000	0.000
110-120	0.000	0.630	0.000	0.000	0.155
123-152	0.000	0.000	0.000	0.000	0.000
60-157	100.000	100.000	100.000	100.000	100.000

TABLE 9
Percent Distribution of *Sebastes macdonaldi* Larvae by CalCOFI Line

	Year					
Line	1956	1966	1969	1972	1975	Average
60-77	0.000	0.000	0.000	0.000	0.000	0.000
80	0.000	0.000	0.000	0.000	0.000	0.000
83	0.000	0.000	1.479	0.361	0.000	0.405
87	0.000	0.000	0.000	0.000	0.000	0.000
90	0.000	0.000	0.000	0.000	0.000	0.000
93	0.000	0.413	0.000	0.000	0.000	0.141
80-93	0.000	0.413	1.479	0.361	0.000	0.5464
97	0.000	0.310	0.000	0.145	0.204	0.159
100	0.000	0.052	0.740	0.361	0.204	0.282
103	2.932	0.000	0.000	0.000	0.407	0.370
107	0.000	0.000	2.136	0.289	0.611	0.581
97-107	2.932	0.362	2.876	0.795	1.426	1.392
110	9.722	2.791	4.601	1.300	7.943	4.053
113	2.469	5.530	7.560	6.142	24.236	7.384
117	12.191	50.749	25.301	40.607	27.902	36.546
120	6.019	2.635	5.423	5.997	1.222	4.317
110-120	30.401	61.705	43.385	54.046	61.303	52.300
123	35.494	11.576	19.392	13.512	10.998	16.405
127	4.938	7.804	15.366	4.552	12.831	8.740
130	17.901	4.238	2.711	4.046	5.499	5.533
133	0.000	7.338	7.231	16.257	2.037	8.194
137	2.624	2.016	3.205	2.023	1.629	2.309
123-137	60.957	32.972	47.905	40.390	32.994	41.181
140	4.321	3.876	3.287	3.396	3.055	3.612
143	1.389	0.672	1.068	1.012	1.222	0.969
147	0.000	0.000	0.000	0.000	0.000	0.000
150	0.000	0.000	0.000	0.000	0.000	0.000
153	0.000	0.000	0.000	0.000	0.000	0.000
157	0.000	0.000	0.000	0.000	0.000	0.000
140-157	5.710	4.548	4.355	4.408	4.277	4.581
60-157	100.000	100.000	100.000	100.000	100.000	100.000

TABLE 10
Estimated Mean Numbers of Rockfish (for 1956, 1966, 1969, 1972, 1975) and Percent Each Species Is of All Rockfish

	5-year average					4-year average				
Line	All rockfish	*S. jordani*		*S. macdonaldi*		All rockfish	*S. paucispinis*		*S. levis*	
	No.	No.	%	No.	%	No.	No.	%	No.	%
60	21,333	1,004	4.89	0	0.00	22,636	619	2.73	0	0.00
63	19,182	5,984	31.19	0	0.00	19,996	320	1.60	0	0.00
67	15,829	2,194	13.86	0	0.00	15,827	428	2.70	12	0.07
70	7,770	362	4.66	0	0.00	7,948	322	4.06	2	0.03
73	5,430	199	3.67	0	0.00	5,762	266	4.61	6	0.11
77	8,737	820	9.39	0	0.00	9,104	386	4.25	13	0.14
Total	78,281	10,603	13.54	0	0.00	81,273	2,341	2.88	33	0.04
80	9,167	282	3.07	0	0.00	9,977	667	6.68	30	0.30
83	18,929	2,247	11.87	5	0.02	20,155	1,089	5.40	238	1.18
87	19,945	2,765	13.87	0	0.00	21,350	678	3.18	98	0.46
90	13,836	1,088	7.87	0	0.00	15,563	628	3.39	80	0.51
93	4,575	116	2.54	2	0.04	4,739	157	3.32	4	0.08
Total	66,452	6,498	9.78	7	0.01	71,784	3,219	4.48	449	0.63
97	2,372	34	1.42	2	0.08	2,349	68	2.91	0	0.00
100	3,061	60	1.95	3	0.11	2,905	49	1.68	2	0.05
103	1,704	32	1.89	4	0.25	1,912	45	2.35	0	0.00
107	1,655	2	0.12	7	0.40	1,761	6	0.34	0	0.00
Total	8,792	128	1.45	16	0.18	8,927	168	1.88	2	0.02
110	1,704	9	0.53	46	2.70	1,750	10	0.54	0	0.00
113	1,441	0	0.00	84	5.82	1,466	3	0.21	0	0.00
117	3,723	6	0.16	415	11.14	3,902	0	0.00	3	0.08
120	2,553	+	0.01	49	1.92	2,913	0	0.00	0	0.00
Total	9,421	15	0.16	594	6.30	10,031	13	0.13	3	0.03
123	1,386	0	0.00	186	13.44	1,365	0	0.00	0	0.00
127	822	0	0.00	99	12.06	904	0	0.00	0	0.00
130	226	0	0.00	63	27.79	246	0	0.00	0	0.00
133	495	0	0.00	93	18.80	544	0	0.00	0	0.00
137	378	0	0.00	26	6.93	427	0	0.00	0	0.00
Total	3,307	0	0.00	467	14.13	3,486	0	0.00	0	0.00
140-157	203	0	0.00	52	25.59	207	0	0.00	0	0.00
All lines	166,457	17,243	10.36	1,135	0.68	175,708	5,740	3.27	486	0.28

decrease in numbers with each mm of length growth for *S. jordani*. The decrease is 58% for *S. macdonaldi*, 54% for *S. levis*, and 43% for *S. paucispinis*. *S. jordani* is a small species and may have slower-growing larvae. *S. paucispinis* grows more rapidly than other rockfish later in life and may also have faster-growing larvae. The differences in decrease in numbers of larvae may reflect these growth differences rather than temporal mortality.

The larval abundance estimates yield interesting data on relative numbers of larvae by year, month, and area of the four species in relation to all larvae and to each other. But we need additional data in order to estimate the total numbers of larvae produced each year and, from that, the biomass of the spawning population. The two most important missing elements are the growth of larvae with time and temperature, and larval mortality. With these data we could interpolate for between-cruise estimates and obtain a rough estimate of the total annual production for each identified species. In order to convert larval data to adult biomass we need data on species size at maturity, ratio of adult females to males, number of larvae produced per unit weight of females per spawning, and number of spawnings per year. According to Phillips (1964), a few *S. jordani* mature at 6″ total length (152 mm, 31 g), age 2; 50% at 6½″ (165 mm, 30 g), age 3. They attain a maximum size of 12″ (306 mm, 275 g) and age of 10 years. A few *S. paucispinis* spawn at 14″ TL (356 mm, 456 g), age 3; 50% mature at 16¼″ (413 mm, 723 g),

TABLE 11
Number and Percent of *Sebastes paucispinis* by Size and Month*

Length	Number (billions)										
(mm)	Jan.	Feb.	Mar.	Apr.	May	June	Oct.	Nov.	Dec.	Total	Percent
2.0	10.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.7	0.19
2.5	40.2	20.5	0.0	0.0	0.0	0.0	0.0	0.0	13.4	74.1	1.30
3.0	96.3	5.8	5.4	14.6	4.3	0.0	0.0	0.0	49.2	175.6	3.08
3.5	291.7	38.1	21.9	19.4	8.6	0.0	0.0	0.0	35.8	415.5	7.28
4.0	696.0	278.3	137.0	43.7	4.3	5.9	3.1	0.0	53.7	1,222.0	21.40
4.5	422.9	389.8	230.1	48.6	8.6	0.0	3.1	4.3	49.2	1,156.6	20.26
5.0	275.7	383.8	246.6	29.1	8.6	5.9	0.0	4.3	17.9	971.9	17.02
5.5	165.9	140.7	71.3	19.4	0.0	0.0	0.0	0.0	8.9	406.2	7.11
6.0	101.7	149.4	60.3	9.7	17.2	0.0	0.0	0.0	8.9	347.2	6.08
6.5	45.5	43.9	60.3	4.9	12.9	0.0	0.0	0.0	0.0	167.5	2.93
7.0	56.2	88.0	43.9	9.7	4.3	0.0	0.0	0.0	0.0	202.1	3.54
7.5	34.8	26.4	21.9	4.9	8.6	0.0	0.0	0.0	0.0	96.6	1.69
8.0	16.0	79.1	27.4	4.9	0.0	0.0	0.0	0.0	0.0	127.4	2.23
8.5	21.4	35.2	21.9	14.6	8.6	0.0	0.0	0.0	4.5	106.2	1.86
9.0	13.5	29.4	16.4	4.9	4.3	0.0	0.0	0.0	4.5	73.0	1.28
9.5	5.3	8.7	5.4	0.0	0.0	0.0	0.0	0.0	0.0	19.4	0.34
10.0	16.0	11.7	5.4	0.0	4.3	0.0	0.0	0.0	4.5	41.9	0.73
10.5	0.0	3.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	8.4	0.15
11.0	5.3	3.0	11.0	0.0	4.3	0.0	0.0	0.0	0.0	23.6	0.41
11.5	2.8	5.8	5.4	0.0	4.3	0.0	0.0	0.0	0.0	18.3	0.32
12.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.05
12.5	0.0	0.0	0.0	4.9	4.3	0.0	0.0	0.0	0.0	9.2	0.16
13.0	0.0	0.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	5.4	0.10
13.5	0.0	3.0	0.0	9.7	0.0	0.0	0.0	0.0	0.0	12.7	0.22
14.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.05
14.5	0.0	0.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	5.4	0.10
—											
16.0	0.0	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	4.3	0.07
—											
18.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.05
Total	2,320.7	1,749.6	1,007.8	243.0	111.8	11.8	6.2	8.6	250.5	5,710.0	100.00
Percent	40.645	30.637	17.654	4.253	1.958	0.206	0.108	0.152	4/387		100.00

*Average data for all years.

TABLE 12
Number and Percent of *Sebastes levis* by Size and Month*

Length	Number (billions)								
(mm)	Jan.	Feb.	Mar.	Apr.	May	July	Dec.	Total	Percent
4.0	45.7	0.0	5.5	0.0	0.0	0.0	4.0	55.2	11.19
4.5	35.5	3.2	13.8	21.8	0.6	0.0	0.0	75.0	15.21
5.0	35.5	9.6	30.4	10.9	0.0	0.0	3.9	90.5	18.35
5.5	20.3	6.4	16.6	5.5	0.0	0.0	0.0	48.8	9.90
6.0	25.4	16.1	13.8	16.4	0.0	5.9	0.0	77.6	15.73
6.5	20.3	28.9	8.3	0.0	0.0	0.0	3.9	61.5	12.46
7.0	10.2	6.4	2.8	0.0	0.6	0.0	0.0	19.9	4.04
7.5	20.3	3.2	5.5	10.9	0.0	0.0	0.0	40.0	8.11
8.0	15.2	3.2	0.0	0.0	0.6	0.0	0.0	19.0	3.86
8.5	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.6	0.12
—									
10.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0	5.1	1.03
Total	233.5	77.1	96.8	65.5	2.3	5.9	11.8	493.1	100.00
Percent	47.36	15.64	19.64	13.29	0.47	1.20	2.40		100.00

*Average data for all years.

TABLE 13
Number and Percent of *Sebastes macdonaldi* by Size and Month*

Length (mm)	Number (billions) Jan.	Feb.	Mar.	Apr.	May	Nov.	Dec.	Total	Percent
3.5	0.0	0.0	0.0	8.6	0.0	0.0	0.0	8.6	0.74
4.0	22.5	22.1	68.6	86.4	1.1	0.0	0.0	200.7	17.19
4.5	28.9	119.3	103.0	83.5	2.7	2.4	0.0	339.8	29.11
5.0	33.7	68.5	76.6	103.6	0.2	2.4	0.0	285.0	24.42
5.5	20.9	68.5	10.6	31.7	0.2	0.0	0.0	131.9	11.29
6.0	4.8	37.6	7.9	40.3	0.4	0.0	0.0	91.0	7.79
6.5	0.0	8.8	13.2	2.9	0.0	0.0	0.0	24.9	2.14
7.0	6.4	6.6	5.3	2.9	0.0	0.0	0.0	21.2	1.82
7.5	0.0	13.3	0.0	2.9	0.0	0.0	0.0	16.2	1.38
8.0	1.6	6.6	0.0	5.7	0.5	0.0	0.0	14.4	1.24
8.5	0.0	2.2	0.0	5.7	0.0	0.0	0.0	7.9	0.68
9.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	2.2	0.19
9.5	0.0	4.4	0.0	5.7	0.0	0.0	4.5	14.6	1.26
10.0	0.0	2.2	0.0	0.0	0.5	0.0	0.0	2.7	0.23
10.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00
11.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0	2.9	0.25
12.5	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.01
14.5	0.0	0.0	0.0	2.9	0.0	0.0	0.0	2.9	0.25
15.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.01
Total	118.8	362.3	285.2	385.7	6.0	4.8	4.5	1,167.3	100.00
Percent	10.18	31.03	24.44	33.04	0.50	0.42	0.39		100.00

TABLE 14
Number and Percent of *Sebastes jordani* by Size and Month*

Length (mm)	Number (billions) Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Nov.	Total	Percent
4.0	28.8	0.0	3.6	0.0	4.3	0.0	0.0	0.0	7.3	44.0	0.25
4.5	558.9	210.7	114.7	13.0	0.0	0.0	0.0	0.0	2.5	899.8	5.18
5.0	862.6	2,935.5	696.0	123.3	12.9	0.0	0.4	11.2	7.3	4,649.2	26.77
5.5	592.7	3,080.6	721.3	100.6	21.4	0.0	0.4	11.2	2.4	4,530.6	26.09
6.0	222.5	2,177.7	351.6	220.7	12.9	0.0	0.0	0.0	2.4	2,987.8	17.20
6.5	73.0	1,846.0	157.8	58.4	8.6	0.0	0.0	0.0	0.0	2,143.8	12.35
7.0	45.9	738.2	136.4	42.2	0.0	0.0	0.0	0.0	0.0	962.7	5.54
7.5	20.3	322.5	86.0	42.2	0.0	0.0	0.0	0.0	0.0	471.0	2.71
8.0	8.5	115.2	75.4	32.5	8.6	0.0	0.0	0.0	0.0	240.2	1.38
8.5	5.1	49.5	43.1	22.7	0.0	0.0	0.0	0.0	0.0	120.4	0.69
9.0	0.0	28.8	64.6	19.5	4.3	0.0	0.0	0.0	0.0	117.2	0.67
9.5	0.0	2.9	43.1	13.0	0.0	0.0	0.0	0.0	0.0	59.0	0.34
10.0	0.0	2.9	43.1	16.2	0.0	0.0	0.0	0.0	0.0	62.2	0.36
10.5	0.0	0.0	25.1	3.3	0.0	0.0	0.0	0.0	0.0	28.4	0.16
11.0	0.0	2.9	17.8	3.3	0.0	0.0	0.0	0.0	0.0	24.0	0.14
11.5	0.0	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	4.3	0.03
12.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.02
12.5	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	3.3	0.02
13.0	0.0	2.9	0.0	3.3	0.0	0.0	0.0	0.0	0.0	6.2	0.04
13.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	3.0	0.02
21.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	3.3	0.02
24.5	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	3.3	0.02
Total	2,418.3	11,516.3	2,583.2	724.1	77.3	3.0	0.8	22.4	21.9	17,367.3	100.00
Percent	13.925	66.310	14.875	4.168	0.444	0.017	0.005	0.129	0.127		100.00

*Average data for all years.

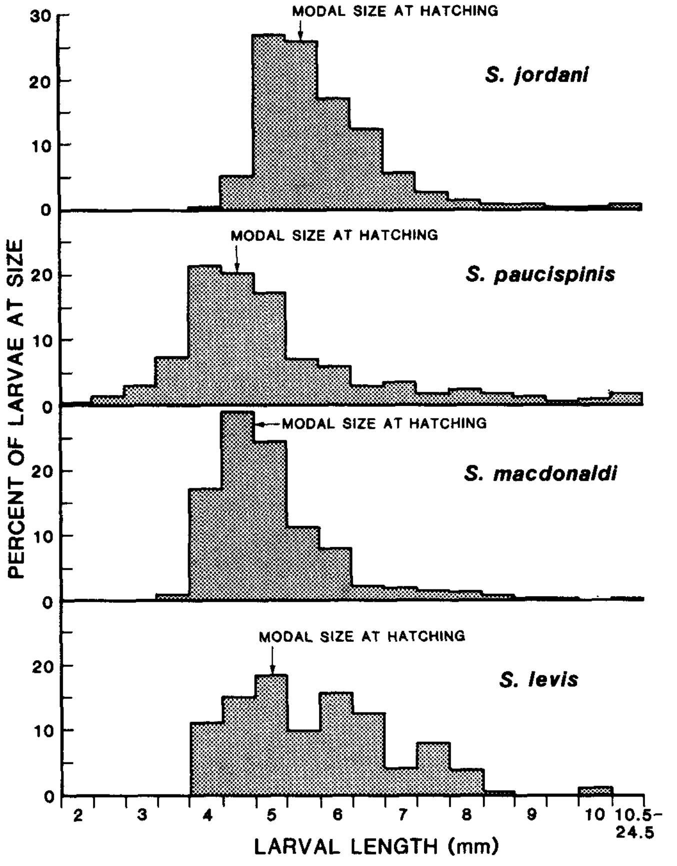

Figure 5. Percent length distribution of larval rockfish.

age 4. They live to a maximum age of 30 years and attain a maximum size of 34″ (864 mm, 7096 g).

Phillips (1964) also gives fecundity data for these two species. Both show an increase in relative as well as absolute fecundity with increasing size of fish. Based on ten specimens of *S. jordani* weighing 46 to 275 g, a 50-g fish should produce an average of 115 eggs (larvae) per gram of spawning female fish, while a 275-g fish should produce 139 eggs/g. For *S. paucispinis* (based on 24 specimens weighing 560 to 5000 g) the relative fecundity was 200 eggs/g for a 550-g fish and 434 eggs/g for a 5000-g fish.

The average fecundity for Phillips' *S. Jordani* sample was 134 eggs/g, and for his *S. paucispinis* sample 339 eggs/g. A sample of 13 *S. paucispinis* from Fortymile Bank off southern California (MacGregor 1970) had an average fecundity of 211 eggs/g. These fish were smaller than Phillips' sample from the Monterey area.

We believe that rockfish spawn twice a year (Moser 1967; MacGregor 1970). Based on the ten specimens of *S. jordani*, this would mean that 268 larvae represent one gram of spawning female (if we discount larval mortality for present purposes); 610 larvae represent one gram of spawning female *S. paucispinis* (based on the combined total of 37 fish). The average number of *S. paucispinis* larvae found in the survey area for the four years was 5.7 trillion, with about three times as many *S. jordani*, 17.2 trillion. Based on the difference in relative fecundity, and assuming equal larval mortality rates, the spawning biomass of *S. jordani* should be about seven times larger than that of *S. paucispinis*.

In estimating the population of larvae present in the survey area, I have used a very small sampled area expanded to a population estimate for a very large area. I do not know how accurate this expansion is. However, the larval data are more consistent within years and among years than for egg and larval data of other species that have been studied in the CalCOFI area. As mentioned earlier, in years when rockfish larvae are more abundant, they tend to be abundant throughout the area and spawning season; when less abundant, they are consistently less abundant throughout the area and season. This would indicate that years of low larval abundance are truly years of scarcity, and years of high larval abundance are truly years of greater spawning success, and that these changes in abundance are not the result of erratic distribution.

Although the total production of *Sebastes* larvae varies from year to year, the numbers of larvae taken on each line remain proportionally similar both for all larvae and for the more abundant identified species. Both the season and area of spawning remained remarkably stable for the four species for the 4 or 5 years of the survey and for all species for the 14 years of data. However, all species do not have good spawning years at the same time. The second best year for *S. jordani* (1956) produced the smallest number of larvae for the other three species, and the year of smallest *S. jordani* larval production (1972) was the best or second best for the other three species.

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LARGE FLUCTUATIONS IN THE SARDINE FISHERY IN THE GULF OF CALIFORNIA: POSSIBLE CAUSES

DANIEL LLUCH-BELDA, FRANCISCO J. MAGALLON
Centro de Investigaciones Biológicas de Baja California Sur
Ocampo No. 312
23000 La Paz, Baja California Sur
México

RICHARD A. SCHWARTZLOSE
Centro de Investigaciones Biológicas de Baja California Sur and
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093

ABSTRACT

The sardine fishery in the Gulf of California has fluctuated widely since its beginning in the late 1960s, causing management problems. This fishery comprises the Monterrey sardine (*Sardinops caerulea*)—the same temperate species that appears on the west coast of North America—and the crinuda sardine (Mexican name for thread herring, genus *Opisthonema*)—a tropical species. The sardine fishery moves south and north as these fish populations migrate south in the winter and spring and north in the later spring and summer. Most fishing takes place along the east side of the central gulf when the Monterrey sardines are spawning. Upwelling and cold water correlate with higher catches and catch per unit of effort (CPUE) for the Monterrey sardine, whereas warmer water produces lower catch and CPUE, especially during an El Niño event. These climatic conditions produce the opposite effect on the crinuda sardine fishery. Larger, more numerous vessels have increased the catch with time, but these changes have not masked the environmental effects on the catch.

RESUMEN

La pesquería de sardina en el Golfo de California ha presentado grandes fluctaciones desde sus inicios a fines de le década de 1960, creando problemas administrativos. Esta pesquería está compuesta por dos especies: la sardina Monterrey (*Sardinops caerulea*), que es la misma especie templada presente en la costa Oeste de Norteamérica, y la sardina crinuda (género *Opisthonema*), que incluye a varias especies tropicales. La pesquería de sardina se desplaza siguiendo las migraciones de las poblaciones de sardina hacia el Sur en el invierno y primavera, y después hacia el Norte a fines de la primavera y el verano. La mayor parte de la pesca se realiza a lo largo de la costa oriental en la parte central del golfo, durante el período de desove de la sardina Monterrey. La surgencias y las aguas frías se correlacionan con las capturas y capturas por unidad de esfuerzo (CPUE) más altas para la sardina Monterrey, mientras que las aguas cálidas están relacionadas con las capturas y CPUE más bajas especialmente durante el evento "El Niño." Estas condiciones climáticas producen el efecto opuesto en la pesquería de la sardina crinuda. La incorporación de embarcaciones mayores y el aumento en el número de barcos han incrementado la captura, pero dichos cambios no han ocultado los efectos ambientales sobre la captura.

INTRODUCTION

There is an important fishery in the Gulf of California for two species of sardines, locally known as Monterrey sardine (*Sardinops caerulea*) and crinuda sardine (genus *Opisthonema*). They are presently caught in the central gulf and, to a much smaller extent, along the west coast of southern Baja California. The Monterrey sardine is a temperate species generally considered to be isolated in the gulf from other subpopulations, which range off the west coast of North America. The crinuda sardine is a component of the tropical fauna, and ranges from the Gulf of Panama to the west coast of southern Baja California and into the Gulf of California.

Catch records are available for *S. caerulea* from British Columbia to California starting in 1916 (Radovich 1982). For the west coast of Baja California, catch data are available from 1929 (Pedrin-Osuna and Ancheita-Avalos 1976). This fishery off the west coast of North America increased to a peak catch in the 1940s, then declined rapidly; by the mid-1960s it had disappeared except off southern Baja California. Because of the small catches on Baja California's west coast, a few boats in the sardine fleet moved to the central Gulf of California, establishing a new fishery (Pedrin-Osuna and Ancheita-Avalos 1976). The catch in the 1967-68 season was estimated at 126 metric tons (MT).

Large fluctuations in annual catch have caused considerable management problems. We will discuss these fluctuations and a hypothesis concerning their causes, which appear partly to be interannual changes in the ocean climate. Our study involves only the sardine fishery for the port of Guaymas in the Gulf of California.

MIGRATION AND SPAWNING

Sokolov (1974) hypothesized a general migratory circuit for the Monterrey sardine. He described a north-to-south migration from winter to spring along the east-

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ern coast of the Gulf of California from just north of Guaymas to Topolobampo. During the 1970-71 fishing season the southward migration may have reached Mazatlan, but this is not usual. The migration begins in October-November, with the start of the northerly winds that induce upwelling along the gulf's east coast. By summer the winds shift from northerly to southerly, and the Monterrey sardines migrate back north.

January to April is the spawning period for the Monterrey sardine. Sokolov (1974) says that the eggs and larvae drift towards the gulf's western coast, where the larvae grow until they attain sexual maturity in their second year. They then move north and join the adult population around Angel de la Guarda Island.

At the same time that the Monterrey sardines are migrating south (winter to spring), crinuda sardines also move south as the water cools (as indicated by unpublished data from the Instituto Nacional de Pesca). Crinuda sardines begin returning north during late spring-early summer when the water warms, upwelling stops, and winds become southerly. Crinuda sardines spawn over much of the gulf during the summer months—the warmest period of the year (Moser et al. 1974).

There are no recent estimates of the biomass of these species in the gulf. Moser et al. (1974), using egg abundance data, calculated the spawning stock for the Monterrey sardine to be 48,000 MT in February 1956, 505,000 MT in April 1956, and 74,000 MT in February 1957. Sokolov (1974) estimated the Monterrey sardine population to be about 200,000 MT. He said that the catch should not be more than 25 percent of the resource and that 50,000 MT could be caught in 1972. There are no population estimates for the crinuda sardine.

THE FISHERY

The fishery exploits the Monterrey sardine and crinuda sardine, depending on their availability, for use as canned fish and fish meal. The fishery began in about 1967 with a very few boats. The catch data and number of boats in the fishery are not reliable until the 1969-70 fishing season. For the first 11 years the boats fished from October-November through May-June along the east coast of the gulf close to the ports of Guaymas, Sonora, and Yavaros, Sinaloa. All the boats had a small capacity and no ice for preservation. Starting in 1978 the fleet added the summer months to its fishing season and fished in the zone between the northern and central gulf, near the large islands of Tiburón and Angel de la Guarda (Figure 1).

In the second period, from 1977 to 1983, 30 boats were added to the fleet (Figure 2). This was a 75 percent increase in number, but a much greater increase in fishing capacity because the boats were larger and able to preserve the fish for a number of days before having to go to port to unload. The new boats came from the west coast of Baja California, where fishing was becoming less profitable. The additional boats enabled the fishing area to be increased and fishing activity to continue throughout the year. As a result, the 1979-80 Monterrey sardine catch increased by 169 percent from the previous year (Figure 3).

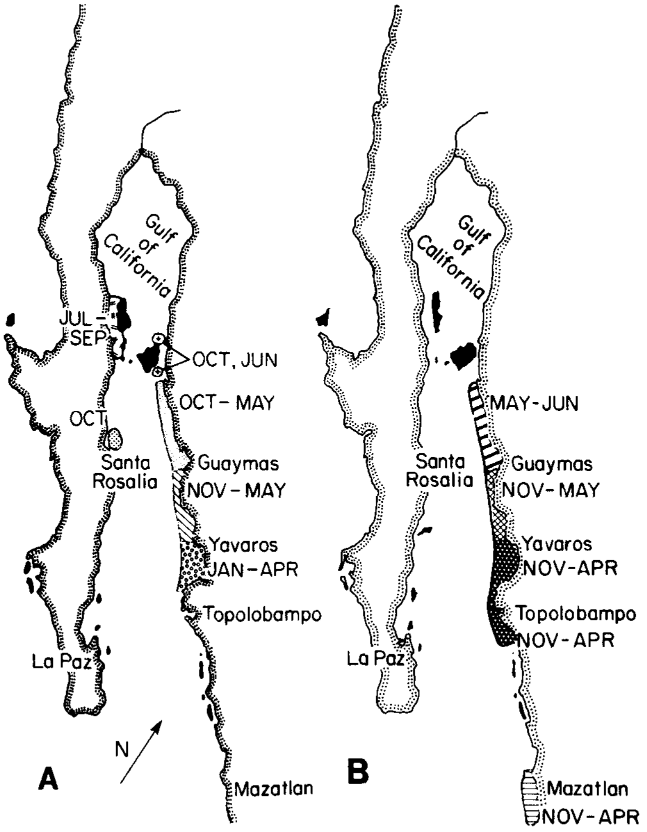

Figure 1. *A*, generalized Monterrey sardine fishery areas and months in the Gulf of California. *B*, generalized crinuda sardine fishery areas and months.

The catch of Monterrey and crinuda sardines for the November-May period of each fishing season has fluctuated widely (Figure 3). The 1975-76 season showed a Monterrey sardine catch of 51,000 MT, whereas the next season it was about 8,000 MT. By 1978-79 the catch was about 23,000 MT; the next season it increased to 62,000 MT. The crinuda sardine catch has also fluctuated, but not nearly as dramatically as the Monterrey sardine catch until the 1982-83 season, when the crinuda catch increased from the previous year by 42,000 MT. The largest catch for Monterrey sardine was in the 1980-81 season, when approximately 88,000 MT were caught. The largest crinuda sardine catch was in 1982-83, when approximately 68,000 MT were caught.

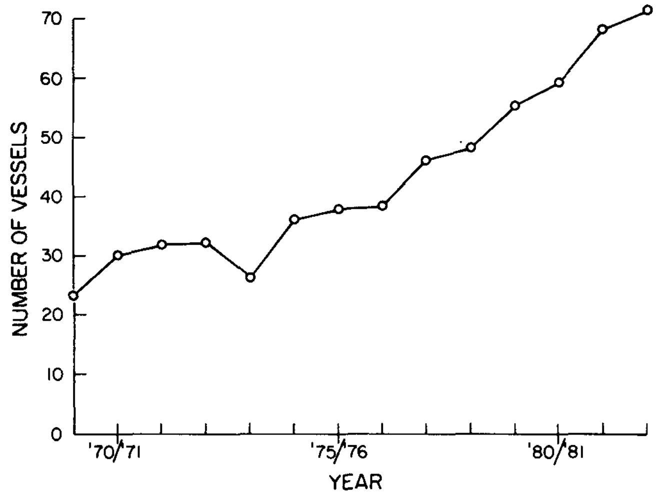

Figure 2. Number of sardine fishing vessels, Guaymas, Sonora.

THE DATA

Catch and effort data for the sardine fishery have been obtained from published reports (Pedrin-Osuna and Ancheita-Avalos 1976) as well as unpublished internal reports from government fisheries offices (Molina et al. 1984). For comparison purposes, we have used data from all catches registered in the Gulf of California wherever available, but our analysis is mostly based on port of Guaymas data for the November-May season. This port accounted for 81 percent of the total registered catch in the gulf in 1980 and a higher percentage in earlier years.

Catch per unit of effort (CPUE) has been used as an index of availability (either abundance, accessibility, or both combined). It is obtained by simply dividing the total catch per species for the fishing season by the corresponding total number of registered trips. The use of CPUE as an index of abundance of small pelagic species has been severely questioned by various authors, for example, Radovich (1982). Two considerations are in order in this respect: first, CPUE is the best possible index available at the present time; second, we are not attempting to estimate the parameters of the sardine's population dynamics, but only to obtain a gross relative estimate of the availability of either species on the fishing grounds accessible to the Guaymas-based fleet.

Yearly mean sea-level and sea-surface temperature data for Guaymas and Manzanillo from October through September were compared with the seasonality of CPUE for each fishery (Figure 4). Because of missing data for each station, we constructed composite series of yearly mean sea level and yearly mean sea-surface temperature data by averaging the two

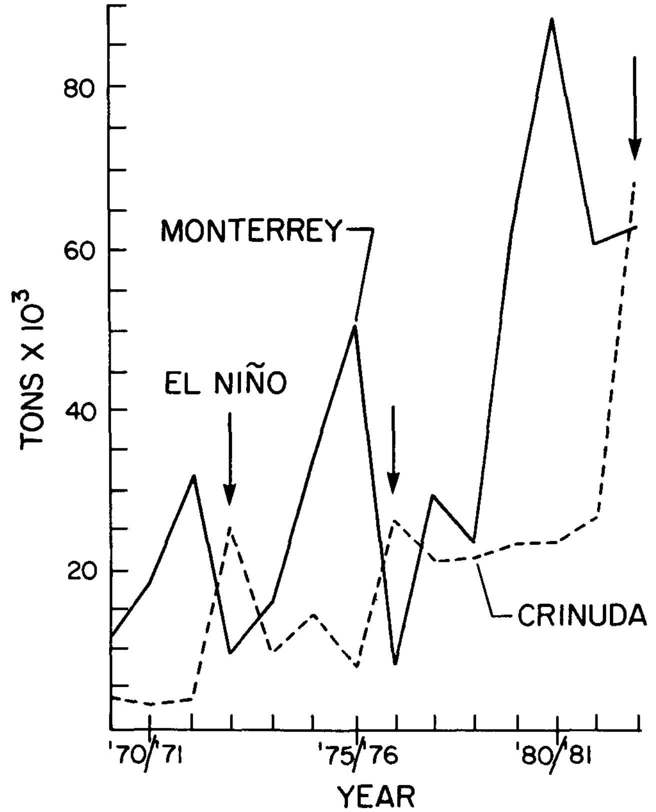

Figure 3. Guaymas, Sonora, sardine catch for the months from November through May. Arrows indicate El Niño events.

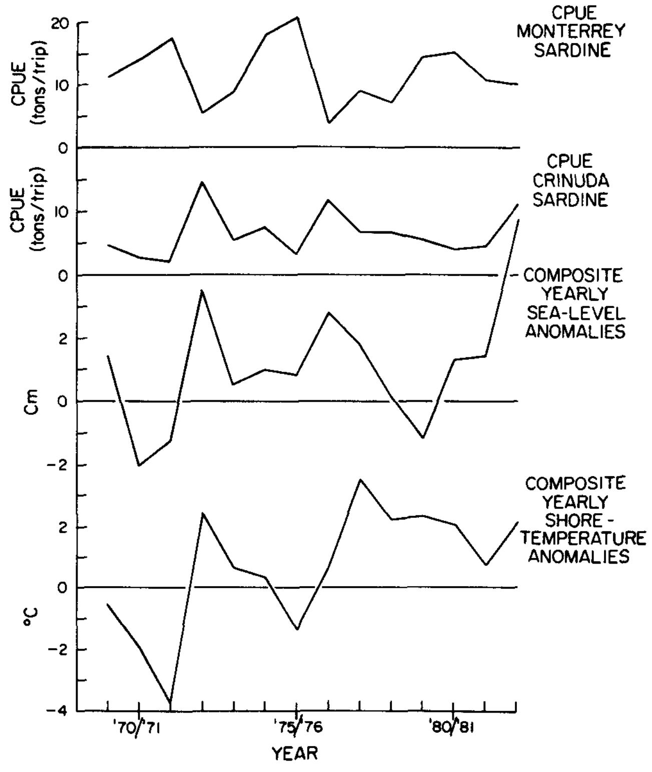

Figure 4. Anomalies of catch per unit of effort for Monterrey and crinuda sardines, and a composite of Guaymas and Manzanillo sea level and sea-surface temperature.

stations' data. Whenever gaps were present for one of the series, we used the value for the other station. Our aim was to construct a series that could be used to indicate extensive geographical conditions.

DISCUSSION

The causes for the large fluctuations in catch, particularly for the Monterrey sardine, have been discussed by several authors. Holtschmit (1977) analyzed the catches and CPUE of Monterrey and Crinuda sardines unloaded at Guaymas as related to environmental parameters such as atmospheric and water temperatures, rainfall, and prevailing winds. He found that the most significant correlations were an inverse relationship between Monterrey sardine catch and water temperature for December of the same season, whereas crinuda sardine catches were inversely related to the average atmospheric temperature of the preceding year.

Molina et al. (1984) assumed that sardine catches were strongly influenced by their availability to the fleet, particularly during 1969-77, when the boats operated almost exclusively on a one-night-per-trip basis, mostly because of their restricted carrying capacity and lack of refrigeration. When more, larger boats began to enter the fleet in 1978, the fishing area and season were increased. Molina et al. further concluded that the intensity of the north-south migration was the main factor affecting the size of catches, as well as the composition of species during 1969-77. Since that time, Molina et al. believe, this factor has mainly affected the smaller boats; the larger boats have moved wherever sardines are available.

The data are sparse concerning these species' movements and location at different times of the year. It is apparent, however, that Monterrey sardine can be found in most regions of the gulf during some years. (Sokolov 1974; Moser et al. 1974; de la Campa de Guzman and Gutierrez 1974; de la Campa de Guzman and Ortiz 1975). This appears to be true also for the crinuda sardine, but each species is restricted by the environment during different seasons of the year. The spawning Monterrey sardine is concentrated in the east side of the central gulf, with outlying patches to the north and south during the winter and spring. The spawning crinuda sardine dominates the gulf in the summer, particularly concentrating in the coastal zones of the central and northern regions.

We incorporate some of the observations of Sokolov (1974), Molina et al. (1984), and Holtschmit (1977), but we believe our hypothesis is more complete concerning the large fluctuations of the sardine fishery in the gulf.

In October-November, northerly winds begin to sweep the gulf because of the changing atmospheric pattern toward a winter circulation (Granados and Schwartzlose 1977; Hubbs and Roden 1964). These winds, plus the normal seasonal cooling of the gulf waters, cause a more temperate ocean climate. There is upwelling along the east coast of the gulf. These conditions along the eastern shore coincide with the Monterrey sardine's annual southward spawning migration and the beginning of the fishing season. The crinuda sardine is also migrating southward because of the cooling water. The fish, especially the preferred Monterrey sardine, thus become available to fishermen from the port of Guaymas.

The southernmost movement of the fish depends on the intensity of the upwelling, the seasonal cooling of the surface water, and southern flow of the surface waters. Thus in cool years fish should be available to the fishermen over a longer period and over a greater geographic region along the east coast of the central gulf. Conversely, the warmer the season the less available are Monterrey sardines, because of a shorter migratory season and a smaller geographic region. From Figures 2, 3, and 4 we see that 1971-72 and 1975-76 were clearly colder years; they were also years of much higher catch, and the CPUE was up, even with only a small change in the number of fishing vessels. The cold year of 1971-72 was one of the few seasons when Monterrey sardines were caught as far south as Mazatlan. From these same figures, we see that the catch and CPUE is down for Monterrey sardines and up for crinuda sardines in the warm years while the water temperature is increased from the previous year. The El Niño events, as shown by Baumgartner et al. (1985), Wooster (1983), and Baumgartner and Christensen (1985), among others, are marked by arrows on Figure 3 and coincide with dramatically lower Monterrey sardine catches and higher crinuda sardine catches. Thus the availability of the species is clearly shown in Figure 4 in the relationships for each species with sea level and water temperature. The cross-correlation coefficients of these parameters are all significant at either the 95 or 99 percent level (Table 1).

Cold years may also result in successful spawning for the Monterrey sardine, since there is a larger area for spawning and the growth of recruits. This might be reflected by the relative dominance of year classes. Although we do not present evidence of this, unpublished material by Leonardo Huato Soberanes of CICIMAR seems to confirm the assumption.

Seasonal warming of the water and reduced upwelling cause adult Monterrey sardines to end their spawning and return north to the vicinity of the large islands of Angel de la Guarda and Tiburón. This region has strong tidal mixing and upwelling most of the year, and surface temperatures are lower than in the remainder

TABLE 1
Coefficients of Cross-Correlation

	Manzanillo		Composite		Monterrey sardine	Crinuda sardine
	MSL	MST	MSL	MST	CPUE	CPUE
Guaymas						
MSL	.89**	—	—	—	−.62*	.69**
MST	—	.55*	—	—	—	—
Composite						
MSL	—	—	—	.56*	−.57*	.79**
MST	—	—	—	—	−.53*	.57*

MSL = yearly mean sea level
MST = yearly mean sea-surface temperature
Composite = Guaymas and Manzanillo
* Significance at the 95% level
**Significance at the 99% level

of the gulf even during summer (Hubbs and Roden 1964; Badan-Dangon et al. 1985, among others). It is quite possible that there is a resident population in this region year-round. Summer catches of Monterrey sardine are made in this region, particularly in the southern portions of the upwelling area of the Ballenas Channel. This additional fishing area and season added about 22 percent to the total annual catch of Monterrey sardine. In 1985 the area around the islands of Tiburón and Angel de la Guarda was closed to Monterrey sardine fishing in July, August, and September because juveniles constituted the largest part of the catch in the near-surface layer.

We conclude that the large fluctuations of the November-May catch of both the Monterey and crinuda sardines are due to their availability to the fishing fleet, and that availability is largely influenced by the ocean climate in the Gulf of California—for example, a cool year of upwelling and northerly winds, or a warm year that might result from an El Niño event. A cold year increases the area of availability for the Monterrey sardine; there is an opposite effect on the crinuda sardine. A warm year supports the crinuda sardine's availability and depresses the Monterrey sardine. The large, sustained increases in the catch from 1979 through 1983 were due to the growing number of larger-capacity vessels and their ability to preserve the catch for several days.

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MODELO POLINOMIAL PARA CRECIMIENTO INDIVIDUAL DE LARVAS DE LA ANCHOVETA NORTEÑA, *ENGRAULIS MORDAX*

CASIMIRO QUIÑONEZ-VELAZQUEZ Y VICTOR MANUEL GOMEZ-MUÑOZ
Centro Interdisciplinario de Ciencias Marinas
Playa El Conchalito S/N
Apartado Postal 592
La Paz, B.C.S., México

RESUMEN

En base a la tendencia observada en el crecimiento individual de *Engraulis mordax* durante los primeros estadíos de su desarrollo bajo diferentes fuentes de alimentación, se propone un modelo polinomial de tercer grado para describirlo. Este modelo permite detectar el agotamiento del saco vitelino, el "período crítico" y su duración (cuando se presenta) y el inicio del crecimiento acelerado.

ABSTRACT

Based on individual growth patterns of *Engraulis mordax* during early life stages under different food sources, a third-degree polynomial model of this growth is proposed. It describes when the yolk sac is consumed, the critical period (its timing and length), and the onset of accelerated growth.

INTRODUCCION

El crecimiento durante los primeros estadíos de desarrollo de larvas de peces marinos es influenciado por la disponibilidad de alimento adecuado posterior al agotamiento del vitelo (Lasker 1965).

La secuencia de los incrementos en crecimiento durante las etapas más tempranas del desarrollo de peces marinos se ha representado utilizando normalmente el modelo de Gompertz (Kramer y Zweifel 1970; Stevens y Moser 1982), o el de tipo exponencial (Bolz y Lough 1983). Dichos modelos obscurecen eventos biológicos importantes durante el lapso de prolarva y postlarva. Estos eventos pueden manifestar deficiencias en alimentación provocando la presencia de un período crítico (Marr 1956).

El objetivo del presente trabajo es presentar un modelo polinomial de tercer grado para describir el crecimiento individual durante los primeros estadíos de desarrollo de larvas de *Engraulis mordax* bajo diferentes regímenes de alimentación.

PRESENTACION Y USO DEL MODELO

Se describe la longitud Lt a la edad t durante los primeros estadíos de vida de la anchoveta norteña *E. mordax* mediante un modelo polinomial de tercer grado, cuya expresión general es la siguiente:

$$Lt = a + bt + ct^2 + dt^3 \qquad (1)$$

Para este tipo de aplicación, el modelo puede representar el crecimiento de larvas como el que se muestra en la Figura 1, en donde se aprecia que la curva alcanza un máximo local a la edad E_1 y un mínimo local a la edad E_2 quedando definidos tres períodos en los que ocurren los siguientes eventos biológicos:

$0 \leq t \leq E_1$: Consumo del saco vitelino que permite el crecimiento de la larva desde la eclosión hasta que alcanza la edad E_1.
$E_1 \leq t \leq E_2$: Período crítico (Marr 1956) durante el cual la larva, al no alimentarse y no disponer de vitelo, queda en condiciones de inanición (Lasker 1965).
$t \geq E_2$: Inicio del crecimiento acelerado de la larva en base al suministro adecuado de alimento (Kramer y Zweifel 1970).

Es posible que no exista período crítico, en cuyo caso el modelo (1) no tiene ni máximo ni mínimo

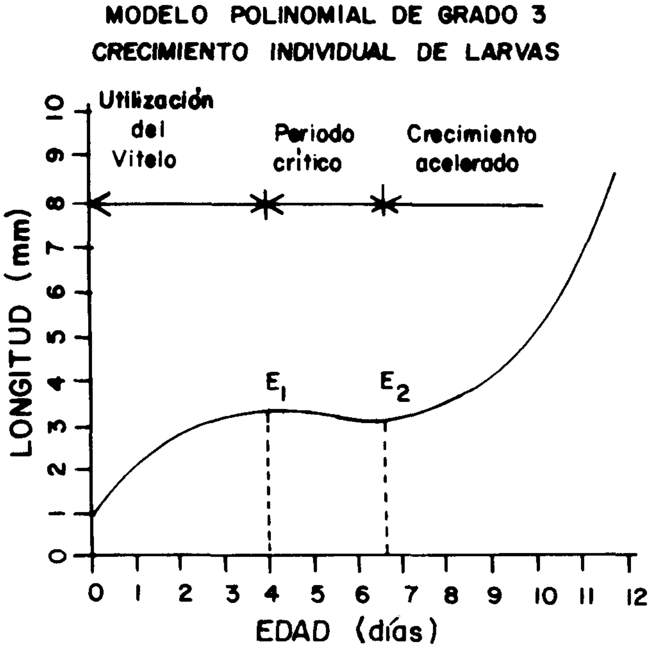

Figura 1. Curva teórica de crecimiento individual durante los primeros estadíos de desarrollo para *Engraulis mordax*.

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locales, sino solamente un punto de inflexión que representa simultáneamente el agotamiento del vitelo y el inicio del crecimiento acelerado los cuales, en tal caso, quedan perfectamente sincronizados.

La identificación de los eventos mencionados se formaliza en base al cálculo diferencial como sigue. Si el modelo (1) presenta máximo y mínimo locales se debe tener que en tales puntos la derivada se anula, es decir:

$$L't = b + 2ct + 3dt^2 = 0$$

Para que esta ecuación de segundo grado tenga soluciones reales es necesario que el discriminante sea no-negativo, esto es:

$$c^2 - 3bd \geqslant 0$$

En tales casos las edades en que se alcanza un máximo y un mínimo en crecimiento estarán dadas por:

$$E_1 = \frac{-c - \sqrt{c^2 - 3bd}}{3d}$$

$$E_2 = \frac{-c + \sqrt{c^2 - 3bd}}{3d}$$

Si se tiene:

$$c^2 - 3bd < 0 \text{ y } d \neq 0$$

la curva tiene un punto de inflexión a la edad:

$$E = -\frac{c}{3d}$$

en el cual la derivada se anula.

APLICACION DEL MODELO

El modelo (1) se ajusta a datos de crecimiento diario de larvas de la anchoveta *E. mordax* mantenidas en diferentes combinaciones de alimentación en condiciones controladas de laboratorio.

Como fuente de alimento se utilizaron espuma orgánica (MOP), el nanoflagelado *Tetraselmis* sp, y microzooplancton. Las concentraciones diarias de cada elemento alimenticio fueron 150 ml de MOP, 50,000 cels./ml de *Tetraselmis* sp, y 2 orgs./ml de microzooplancton.

A diario y hasta el final del experimento se extrajeron al azar tres larvas vivas de cada tratamiento y su réplica para determinar el crecimiento. Todos los tratamientos fueron concluídos al duodécimo día después de la eclosión de las larvas, con excepción de aquellos concluídos antes debido a la mortalidad total de los organismos. Al final de cada tratamiento los recipientes se vaciaron, se contaron y midieron todas las larvas sobrevivientes cuando éstas eran menos que diez; en caso contrario se midieron sólo diez del total de sobrevivientes.

La Tabla 1 presenta los parámetros del modelo (1) para cada tratamiento así como su duración que varió desde ocho días para condiciones de inanición a doce días en los tratamientos con microzooplancton.

Los valores del punto de inflexión se muestran en la Tabla 2 (para el caso en que no se presentan máximo ni mínimo de crecimiento) y las edades E_1 y E_2 a las que ocurren el máximo y mínimo local de crecimiento. El período crítico no apareció en ninguno de los dos tratamientos que incluyen microzooplancton (Figura 2a y 2c). El período crítico duró 2.27 días en el tratamiento MOP-*Tetraselmis* sp (Figura 2b) y 2.81 días en condiciones de inanición (Figura 2d); este último tratamiento se inició ligeramente antes que el anterior.

Se concluye que cuando se presenta un período crítico, éste se inicia alrededor del cuarto día y termina durante el sexto día, posterior a la eclosión para iniciar el crecimiento acelerado. En forma similar, en los casos en que no se observa evidencia de período crítico, es a partir del sexto día en que la larva está en condiciones de aprovechar el alimento disponible e iniciar el crecimiento vigoroso.

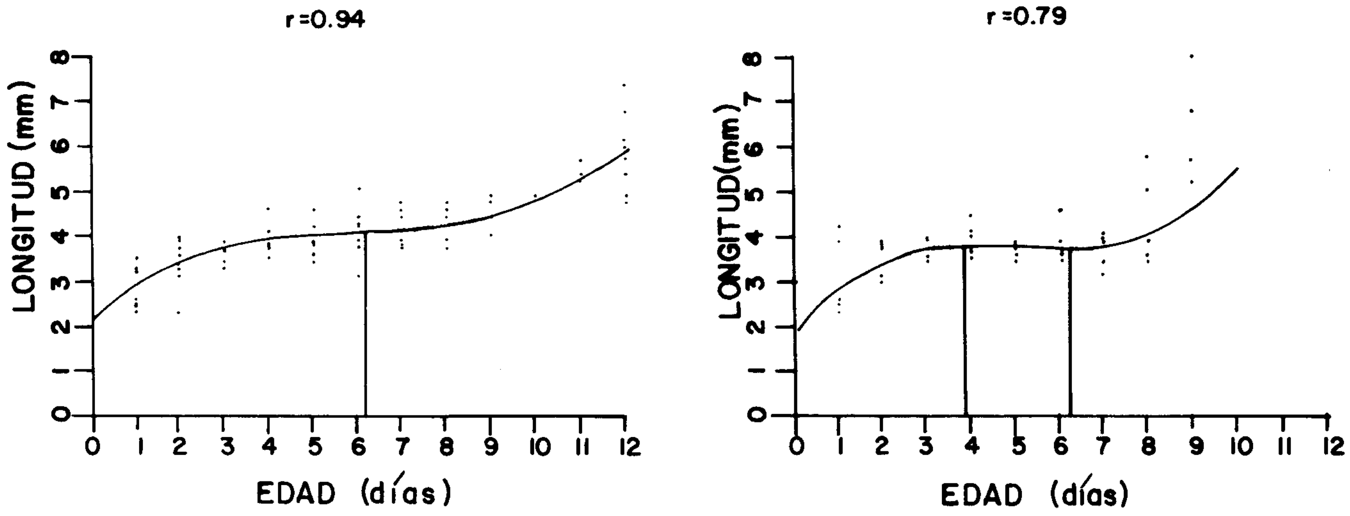
TABLA 1
Parámetros del Modelo Polinomial y Duración del Experimento

Condiciones de alimentación	Parámetros *a*	*b*	*c*	*d*	Duración (días)[a]
MOP-microzooplancton	2.12	0.86	−0.13	0.007	12
MOP-*Tetraselmis* sp	1.86	1.26	−0.26	0.017	10
Tetraselmis sp-microzooplancton	1.98	1.04	−0.16	0.009	12
Inanición	0.84	1.88	−0.39	0.025	8

[a] Días después de la eclosión

TABLA 2
Edades del Punto de Inflexión (PI), Máximo Local (E_1), y Mínimo Local (E_2) en el Crecimiento de Larvas de *Engraulis mordax*

Condiciones de alimentación	*PI*	E_1 (días)	E_2
MOP-microzooplancton	6.19		
MOP-*Tetraselmis* sp		3.96	6.23
Tetraselmis sp-microzooplancton	5.92		
Inanición		3.79	6.6


(a) FUENTE DE ALIMENTACION: Espuma Orgánica - Microzooplancton

(b) FUENTE DE ALIMENTACION: Espuma Orgánica-Tetraselmis sp.

(c) FUENTE DE ALIMENTACION: Tetraselmis - Microzooplancton

(d) FUENTE DE ALIMENTACION: Inanicion

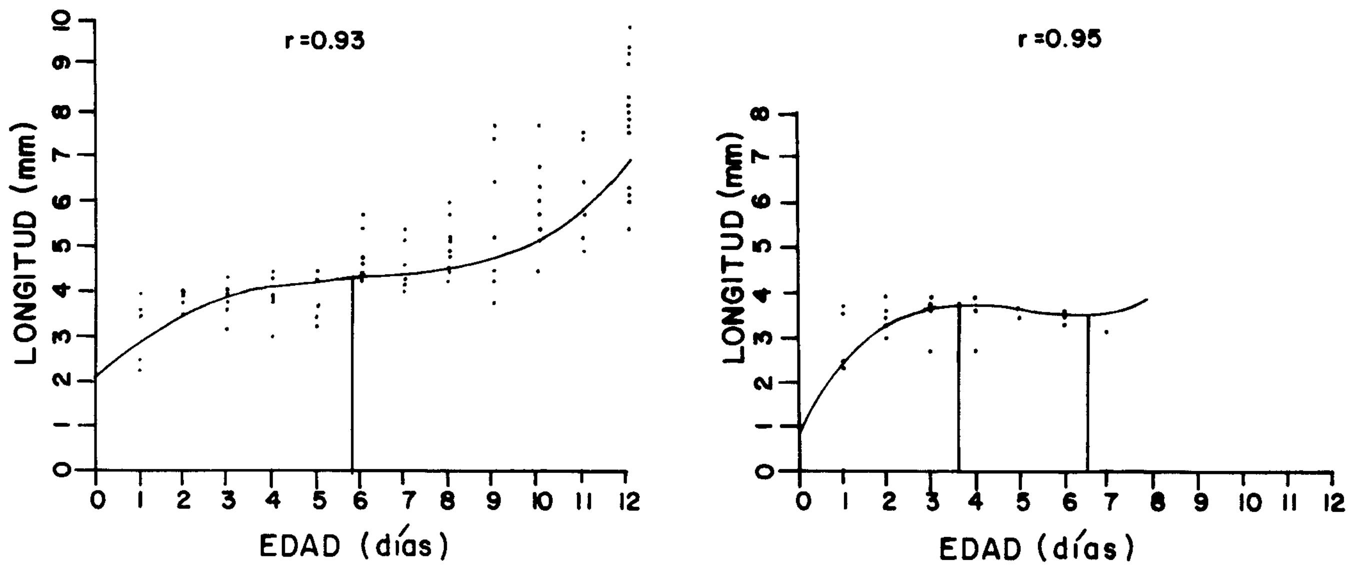


Figura 2. Gráfica del modelo y diagrama de dispersión del crecimiento individual de larvas de *Engraulis mordax*, bajo diferentes condiciones de alimentación.

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OFFSHORE ENTRAINMENT OF ANCHOVY SPAWNING HABITAT, EGGS, AND LARVAE BY A DISPLACED EDDY IN 1985

PAUL C. FIEDLER
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

In early 1985, a recurrent anticyclonic eddy, normally located about 400 km southwest of Point Conception, was displaced toward the offshore limit of the northern anchovy spawning range in the Southern California Bight. The anomalous location of the eddy, and surface flow patterns associated with it were determined from hydrographic data and satellite imagery. Productive surface waters of 14°-15°C, characteristic of the preferred spawning habitat of northern anchovy, were entrained from within the Southern California Bight by the eddy. Eggs were found 150 km farther offshore than in 1980-84, because of a combination of spawning habitat extension and advection. The eggs and subsequent larvae were removed from the usual larval feeding grounds within the bight. This extraordinary displacement apparently had little or no effect on recruitment in fall 1985.

RESUMEN

A principios de 1985, un vórtice anticiclónico de carácter periódico, normalmente ubicado alrededor de 400 km al Sureste de Point Conception, fue desplazado hacia el límite externo de la zona de desove de la anchoveta norteña en la Bahía del Sur de California. La ubicación anómala de este vórtice, y los patrones de circulación superficial asociados con el mismo fueron determinados por medio de información hidrográfica e imágenes de satélite. Aguas superficiales productivas con temperaturas de 14°-15°C, características del habitat de desove preferido de la anchoveta norteña, fueron atrapadas por el vórtice desde el interior de la Bahía del Sur de California. Se encontraron huevos a 150 km, mar adentro, en relación a aquellos colectados en 1980-84, debido a una extensión del habitat combinada con una advección de los productos de desove. Estos huevos y las posteriores larvas fueron sacados de las áreas de alimentación larval normales en la bahía. Este desplazamiento extraordinario de los productos de desove tuvo, aparentemente, muy poco o ningún efecto sobre el reclutamiento en el otoño de 1985.

INTRODUCTION

The Southern California Bight is the center of spawning activity for many pelagic fishes, including the large central stock of northern anchovy (*Engraulis mordax*). The bight is a particularly favorable spawning habitat, with a semienclosed gyral pattern of geostrophic flow (the Southern California Eddy) over a wide and topographically complex continental shelf; a relatively stable density structure of near-surface waters; and weak offshore Ekman transport and turbulent mixing (Husby and Nelson 1982; Parrish et al. 1983). The main axis of the California Current and the persistent eddy field seaward of that axis are normally farther from the coast along southern California than they are to the north of Point Conception (Figure 1). Peak anchovy spawning in February-April coincides with the seasonal minimum of offshore velocity in the surface mixed layer (Bakun 1985). Thus, minimizing the offshore dispersion of eggs and larvae from the coastal spawning habitat appears to be an important component of the spawning strategy of northern anchovy and other fishes in the Southern California Bight (Parrish et al. 1981).

This generalization is based on mean patterns of spawning activity and environmental variables. The Southern California Bight, however, is part of the highly variable California Current system, which is dominated by low-frequency, interannual changes in physical and biological factors (Chelton et al. 1982). Much of this variability is caused by tropical El Niño and mid-latitude warm events (Norton et al. 1985), which have had demonstrated effects on northern anchovy spawning activity (Fiedler et al. 1986).

The anchovy is a multiple spawner, with each female producing several batches of eggs per year. Eggs remain near the surface and hatch two to four days after spawning. Some spawning activity is observed year-round, but three-quarters of the yearly spawnings occur in February-April (Parrish et al., in press). Abundance and spatial distribution of anchovy eggs have been measured on biomass surveys during peak spawning months since 1980 (Figure 2. Stauffer and Picquelle 1980, 1981[1]; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986).

Substantial variations in egg distribution were caused by the 1982-84 California El Niño. In 1983 the

[Manuscript received February 12, 1986.]

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[1] Stauffer, G.D., and S.J. Picquelle. 1981. The 1981 egg production estimates of anchovy spawning biomass. Southwest Fisheries Center, unpublished report.

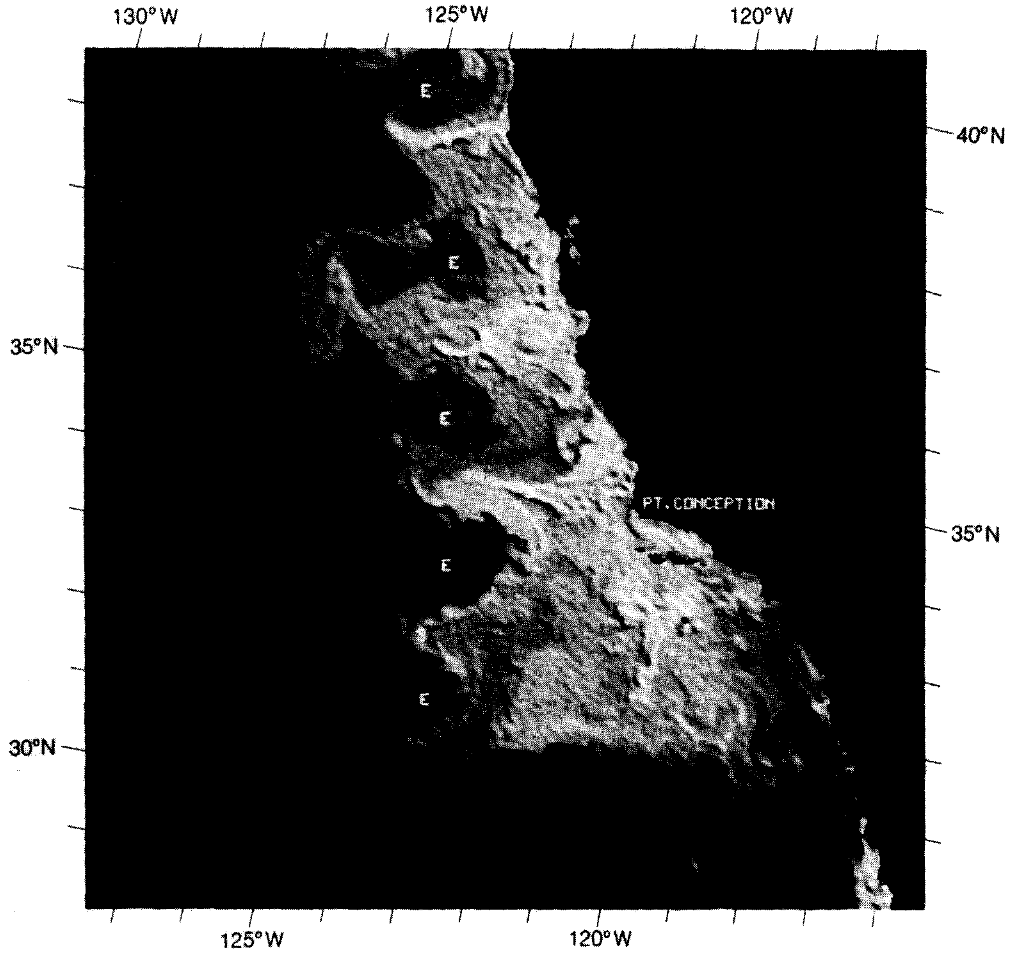

Figure 1. CZCS phytoplankton pigment image, June 15, 1981, showing a series of offshore eddies (E) in the California Current region off California. The recurrent eddy is the second from the bottom, to the left of Point Conception. Distance of eddies from coast increases north to south, from 100 to 400 km. Lighter shades indicate higher pigment concentrations on a logarithmic scale, with an additional enhancement to emphasize gradients.

boundary normally formed by the ~14°C surface isotherm had shifted far to the north of Point Conception; spawning range extended unusually far to the north, as well as offshore in the region of the Channel Islands. In 1984 the cold-water boundary was present, but spawning range again extended somewhat farther offshore than in 1980-82. On the 1980-84 surveys, eggs were sampled as far as 250 to 280 km from shore in the central region of the Southern California Bight (i.e., between CalCOFI lines 86.7 and 92).

The 1985 egg distribution was very unusual. First, small but significant numbers of eggs were found in cold (< 13°C) water to the north of Point Conception. Then, large numbers of eggs began to be taken along line 90. Sampling was extended offshore to station 80 on lines 91.7 to 95. Eggs were found up to 400 km offshore on these lines, 120-150 km beyond the farthest offshore eggs in 1980-84.

The anomalous offshore extension of the 1985 egg distribution would have important consequences for the stock if these eggs, and the larvae hatched from them, were irretrievably lost from inshore larval feeding grounds. What could have caused the peculiar egg distribution pattern? Offshore Ekman transport (coastal upwelling) is a primary mechanism of offshore transport in eastern boundary current systems. However, coastal upwelling off California is near its seasonal minimum in February and does not produce extensive coastal jets or plumes within the Southern California Bight. Another mechanism is needed to explain the observations.

An anticyclonic eddy located about 400 km SW of Point Conception is a recurrent component of the offshore eddy field of the California Current system; January-April 1949-65 CalCOFI data indicate that its mean postion is 32.1°N, 123.4°W, ± 1.2° (Simpson et al. in press). A sporadic, but not unusual, phenomenon associated with this eddy has been noted: onshore displacement may cause enhanced entrainment of cool coastal water and its associated biological community (Haury et al. in press). In this paper, I will exploit the extensive, detailed, and repetitive coverage of the sea surface by satellite-borne sensors to locate the eddy and estimate surface flow associated with it. I wish to

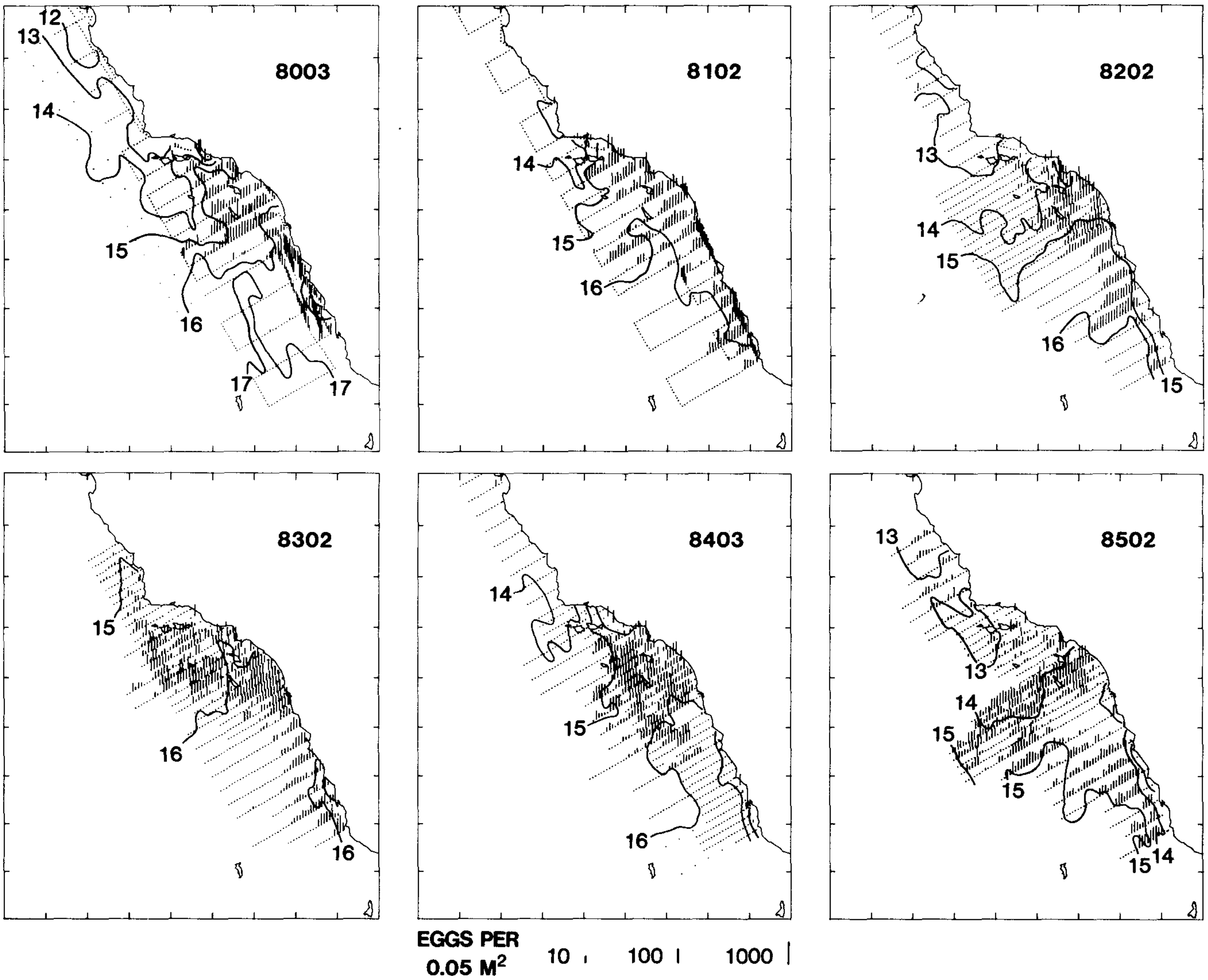

Figure 2. Surface isotherms (°C) and anchovy egg distributions on anchovy biomass cruises (CalCOFI 8003-4, 8102, 8202, 8302, 8403, and 8502). From Fiedler et al. (1986).

thank Jim Simpson for pointing out the possible manifestation of the displaced eddy in the data from CalCOFI cruise 8502.

METHODS

Satellite data were received, archived, and processed at the Scripps Satellite Oceanography Facility. Thermal infrared data from channel 4 (11 μm) of the Advanced Very High Resolution Radiometer (AHVRR) on the NOAA-7 and NOAA-9 satellites were corrected for the effect of thin low clouds, when necessary, using channel 2 (0.7-1.1 μm) near-infrared data (Gower 1985). No further correction was implemented for absorption of sea-surface radiance by atmospheric water vapor. Although multichannel correction algorithms produce more accurate temperature estimates, they do so at the cost of amplifying the noise in the sensor signal. Preserving small-scale patterns of sea-surface temperature variability was considered a higher priority for this study.

Visible radiance data from the Coastal Zone Color Scanner (CZCS, Nimbus-7 satellite) were processed using an algorithm based on Gordon et al. (1983) to remove effects of Rayleigh and aerosol scattering and to derive phytoplankton pigment concentrations from corrected blue/green radiance ratios. Surface flow patterns were derived by tracking movement of submesoscale features in sequential AVHRR images (Vastano and Borders 1984).

RESULTS

In Figure 3, two AVHRR sea-surface temperature images show mesoscale variability off southern California in January 1984 and 1985. In both images, the

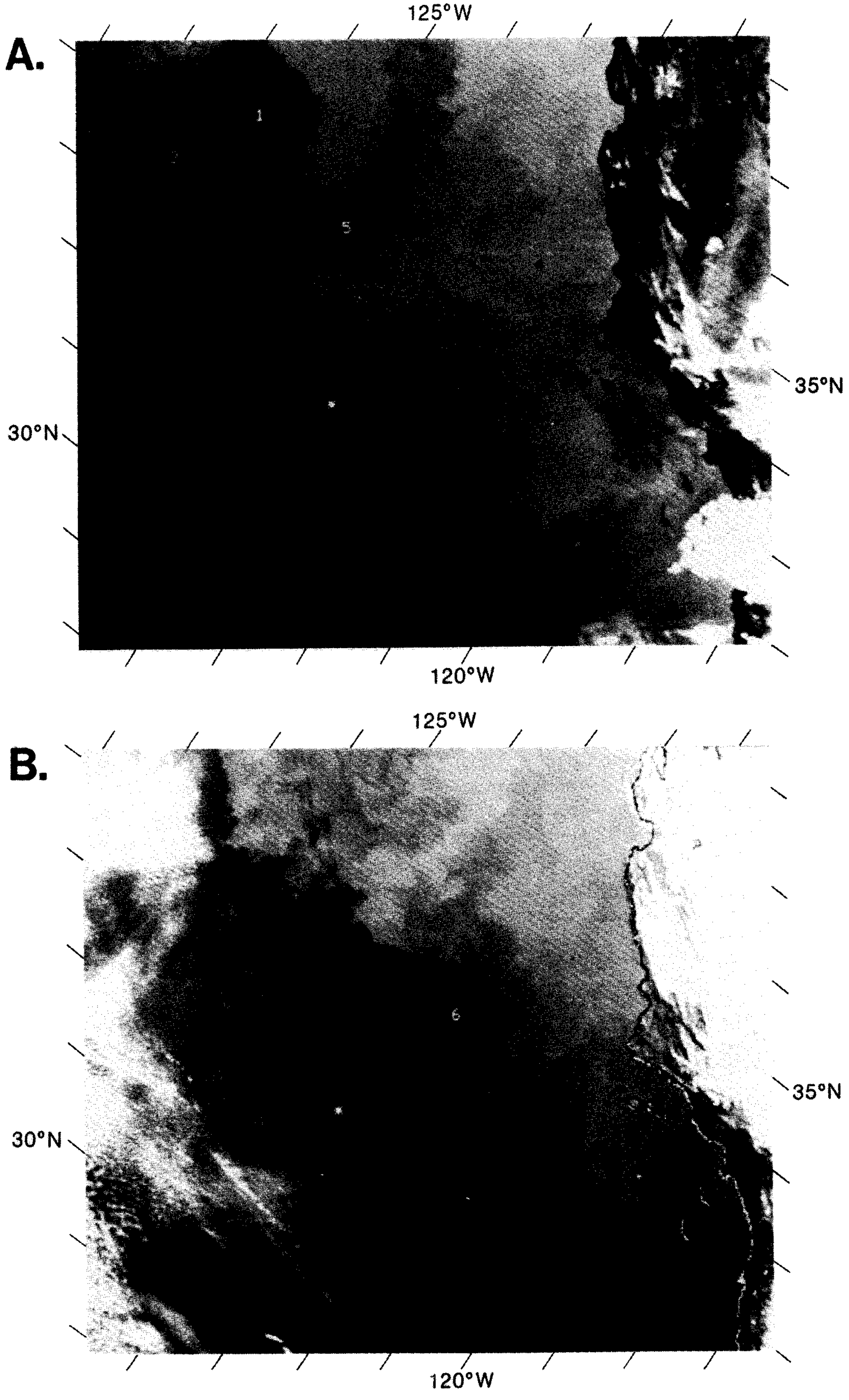

Figure 3. AVHRR sea-surface temperature images from *(A)* January 26, 1984 (1 = anticyclonic eddy, 2 = cold streamer, 3 = warm streamer, 4 = cold streamer from coast, 5 = secondary warm streamer) and *(B)* January 1, 1985 (6 = anticyclonic eddy, 7 = cold streamer from coast, 8 = cold-water plume from Point Conception). The asterisk (*) marks the mean January-April location of the recurrent eddy (Simpson et al., in press). Water temperatures range from 10.5°C (light grey) to 17°C (dark grey).

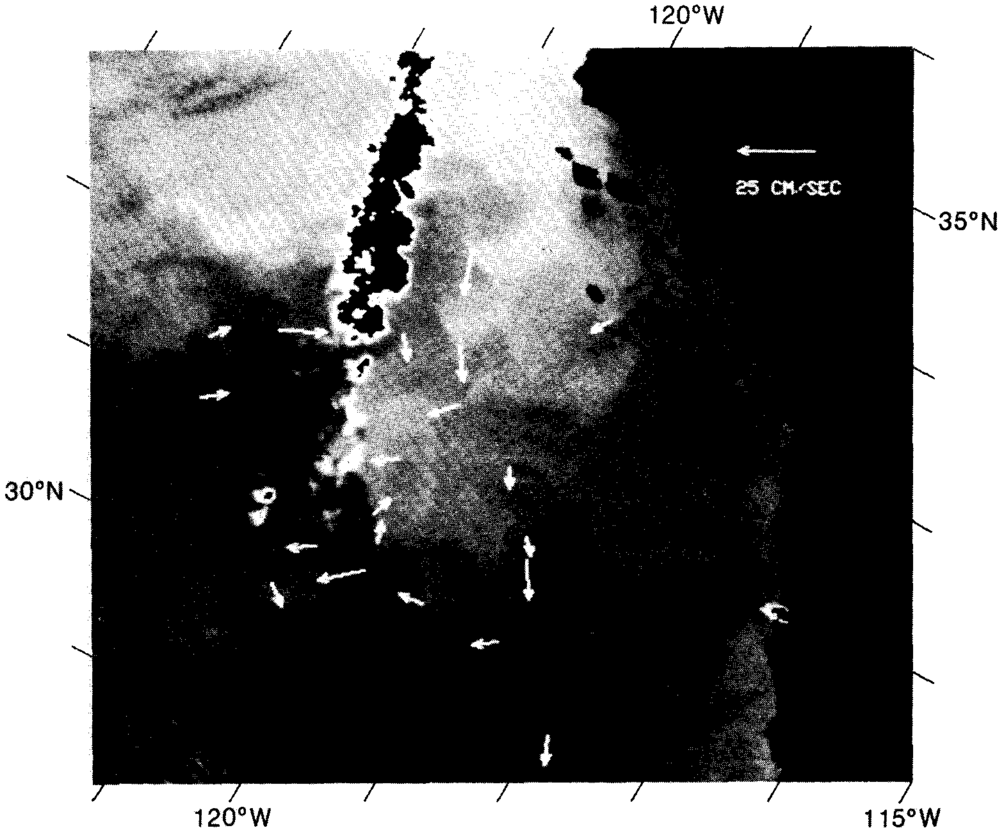

Figure 4. AVHRR sea-surface temperature image from February 21, 1985, with surface current vectors (arrows) derived from movements of submesoscale features visible on February 21 and 24, 1985. Temperatures range between 10° and 13.6°C. Clouds and land are masked with black.

coldest water (lighter grey shades) is along the coast to the north of Point Conception. This is California Current water augmented by seasonally weak coastal upwelling. The cold surface water extends south of Point Conception as a streamer or plume that separates from the coast. This pattern is obscured by clouds in Figure 3a, but is clearly visible in Figure 3b, where warmer nearshore water in the Southern California Bight can also be seen. The warmest water in both images is found to the south and offshore.

On January 26, 1984, a warm-water anticyclonic eddy is clearly visible at 34.2°N, 126.4°W (Figure 3a). This is 360 km northwest of the mean historical position, at the extreme of the range observed by Simpson et al. (in press). A well-defined cold streamer, with a source outside the image to the north, is wrapped around the inshore side of the eddy. A warm streamer from an offshore, oceanic source is wrapped around the offshore side of the eddy. The temperature of surface water within the eddy is intermediate between the temperatures of the surrounding warm and cold streamers. A large cold streamer (~400 km long) extends from the coast north of Point Conception out toward the eddy. Instead of becoming entrained by the eddy, this streamer is deflected to the south around a secondary warm streamer surrounding the inshore edge of the eddy.

On January 1, 1985, a warm-water anticyclonic eddy is at 33.8°N, 122.5°W—370 km east of the January 1984 eddy and 210 km northeast of the mean position (Figure 3b). A cold streamer flowing along the southern edge of the eddy is anchored on the coast in the vicinity of Point Conception and can be traced almost 500 km offshore. Some water from within the Southern California Bight appears to be entrained in this streamer.

On February 21, 1985, the eddy was located at 32.6°N, 122.5°W (Figure 4). It was then 130 km south of its position on January 1 and 100 km east-northeast of the mean postion. A surface velocity field derived from the February 21 and 24 images is included in Figure 4. Current vectors were more easily measured at the edges of the eddy than in the cool coastal water mass inshore of the eddy, because the submesoscale features serving as tracers are most visible at strong temperature gradients. Although cloud cover prevented complete coverage of the eddy, and the discernable flow pattern is complex, anticyclonic rotation is apparent on the northern and inshore edges, where velocities are 7-15 cm/sec, dominated by an offshore component of 7-10 cm/sec.

Figure 5 is a Coastal Zone Color Scanner image showing that the cool coastal water being entrained offshore by the eddy was relatively rich in phytoplank-

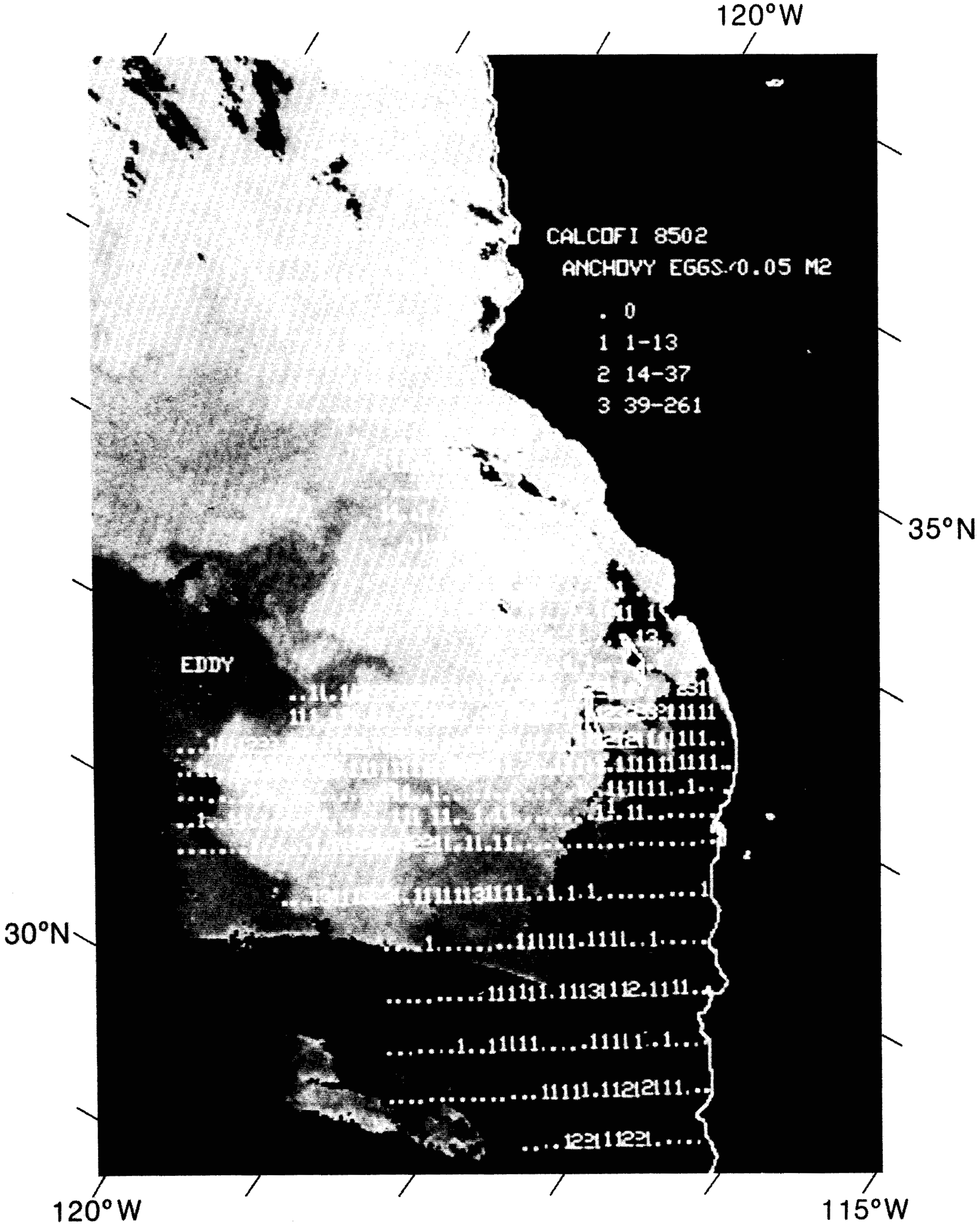

Figure 5. CZCS phytoplankton pigment image from February 28, 1985. Pigment concentrations range between 0.12 and 4.7 mg/m^3 (dark to light). Clouds and land are masked with black. Relative abundance of anchovy eggs in vertical egg tows (CALVET) on CalCOFI cruise 8502, R/V *David Starr Jordan*, January 28-March 8, 1985.

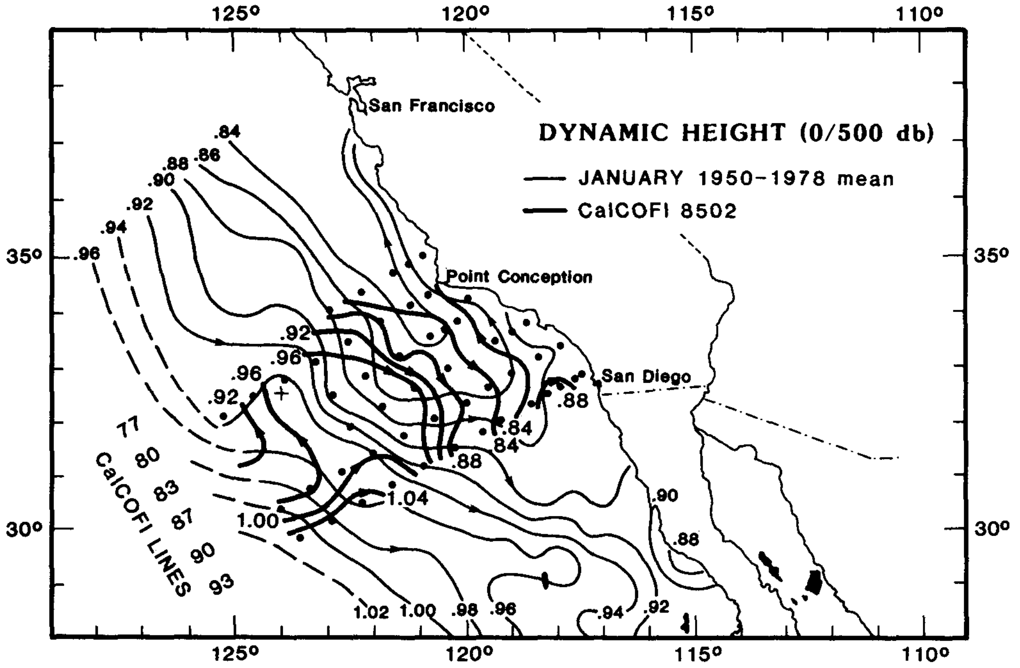

Figure 6. Dynamic height and geostrophic flow at the surface: January 1950-78 mean (Lynn et al. 1982) and CalCOFI cruise 8502, February 19-March 5, 1985 (Scripps Institution of Oceanography 1985). + = mean postion of recurrent anticyclonic eddy (Simpson et al., in press).

ton pigment. The offshore extension of anchovy eggs is contained in this cool, rich surface water. Note, however, that there are few eggs in the even colder and richer water to the north toward Point Conception.

DISCUSSION

In the mean January hydrography, this recurrent anticyclonic eddy appears as a local elevation in dynamic height within a geostrophic current meander (Figure 6), and as local depressions of isopycnal surfaces (sigma-t = 25.0 in the top of the thermocline at ~80 m; sigma-t = 25.8 at ~140 m; and sigma-t = 26.6 at ~280 m; Lynn et al. 1982). Dynamic topography at the sea surface in February 1985 shows an unusual pattern of meanders centered at 32°N, 122°W (Figure 6). The local high, and the direction of flow on three sides of it suggest that the eddy was embedded within this pattern. The revised CalCOFI grid, with no offshore sampling between lines 80 and 90, unfortunately missed the center of this eddy. However, the data show the enhanced entrainment of coastal water expected from such a displacement: the direction of surface flow at coastal stations along CalCOFI lines 90 and 93, inshore of the eddy, was more offshore than the long-term mean. The observed egg distribution is consistent with entrainment in anomalously strong offshore flow associated with the displaced eddy: the offshore extension of anchovy eggs is within the region of anomalous offshore flow.

Power (in press) analyzed larval anchovy drift from the spawning center in the Southern California Bight. His 30-day simulation model of advection-diffusion incorporated mean seasonal geostrophic currents and Ekman transport and a constant eddy diffusivity. In March, most larvae move inshore from the points where they were spawned. Monthly mean offshore Ekman velocities in the bight range between .05 and 2.0 cm/sec, assuming negligible Ekman transport below 50 m (Husby and Nelson 1982). Power found that significant seaward transport of larvae occurred only if Ekman velocities were increased to three times the long-term mean, or up to 6 cm/sec.

During an intensive study in January 1981, the anticyclonic eddy was located at 32.4°N, 124°W and was found to be entraining both cold coastal waters and warm oceanic waters into its surface and near-surface layers. In this "normal" case, the source of the coastal waters was north of Point Conception (Simpson et al. 1984). Satellite imagery shows that this eddy was displaced 100-200 km inshore of the normal position in January and February 1985. Surface waters from within the Southern California Bight were entrained toward the eddy. Apparent offshore velocities were up to 10 cm/sec, or five times greater than normal mean offshore Ekman velocities.

Eggs that hatch in three days could move only 30 km at this speed. Therefore, anomalous advection of eggs cannot entirely explain the 150 km offshore extension. Spawning must have been taking place offshore of the normal range. Ken Mais provides maps of major concentrations of adult anchovies in the central stock from February acoustic and midwater trawl surveys of the central stock (California Department of Fish and Game Cruise Reports 80-A-1, 81-X-1, 82-X-1, 83-X-1, 84-

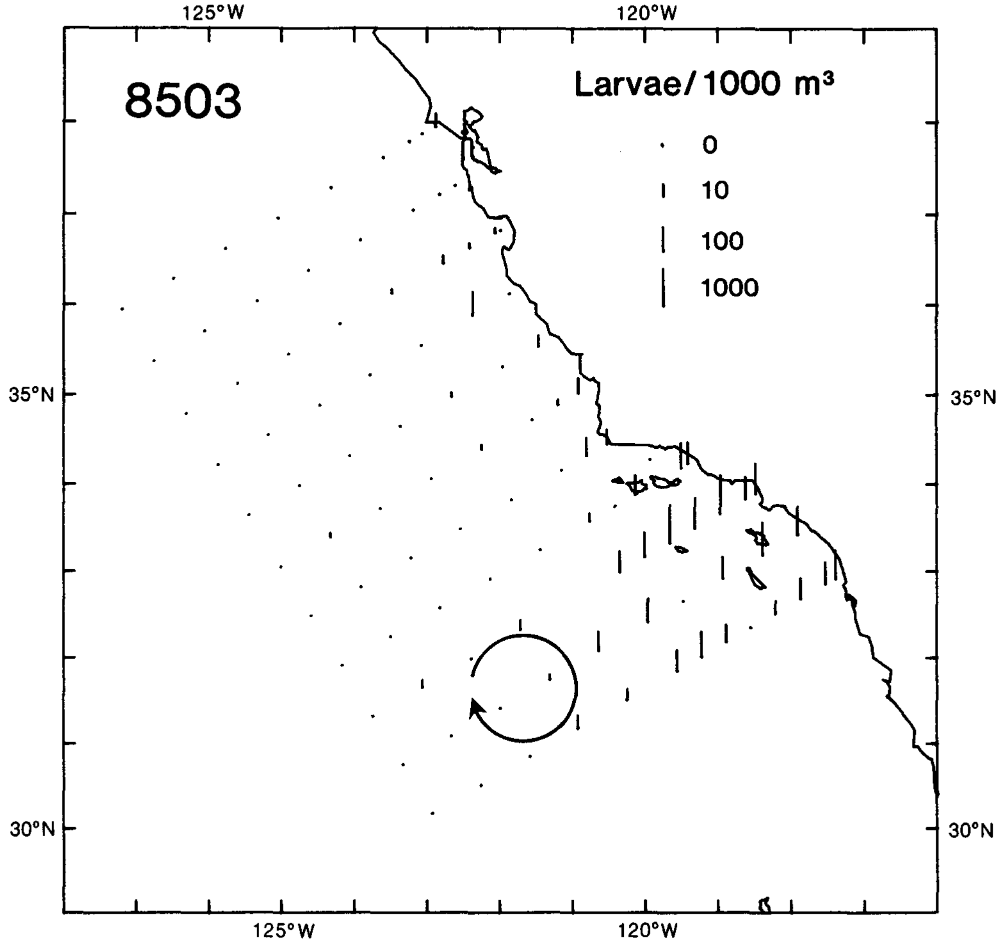

Figure 7. Anchovy larvae abundance from bongo net tows, 333-μm mesh, on CalCOFI cruise 8503, R/V *McArthur*, March 15–April 5, 1985. The location of the eddy on February 21, 1985, is indicated schematically.

X-1, and 85-X-1). These maps show a maximum offshore extent of anchovies of 230 km in 1985, compared with 80-190 km (mean = 142 km) in 1980-84. Mais reported that the 1985 distribution was more offshore and southward than in any previous survey, and that "the bulk of the population was located in an arc of 80 miles west to south, and 30 miles east to south of San Clemente Island." This distribution encompasses the region of anomalous offshore flow illustrated in Figure 6.

Adult spawners in winter 1985 moved offshore within the cool coastal water mass being entrained by the displaced eddy. The eggs spawned by these fish were advected for a short distance by this offshore flow. We can assume that offshore advection continued as the eggs hatched and larvae developed. Ultimately, the larvae may have been trapped in the surface convergence within the eddy or spun off to the south and offshore. A few larvae were found offshore in the vicinity of the eddy in March 1985 (out to station 100 on line 87; Figure 7). Unfortunately, no sampling was done south of the U.S.-Mexico border.

Available evidence indicates that the displacement of spawning habitat and products had little, if any, effect on recruitment of the 1985 anchovy year class. Central stock spawning biomass in February 1985 was about average for the post-1979 period (Bindman 1986). A September California Department of Fish and Game anchovy recruitment survey north of the U.S.-Mexico border found evidence of a relatively weak 1985 year class: mean catch rate of juveniles ranked seventh among nine surveys conducted since 1976 (K. F. Mais, California Department of Fish and Game Cruise Report 85-X-14). A limited trawl survey in February-March 1986 again found a relatively small proportion of 1985 year-class fish (K. F. Mais, California Department of Fish and Game Cruise Report 86-X-4). However, the year class appeared relatively strong in the Ensenada fishery south of the border in fall 1985 (R. Methot, Southwest Fisheries Center, pers. comm.).

The best estimate as of April 1986 is that the 1985 year class is neither stronger nor weaker than expected from the 1985 spawning stock. Two major environmental perturbations in recent years—the 1982-84 California El Niño and the displaced offshore eddy in 1985—have caused observable changes in central stock spawning activity without a resultant effect on stock size. The northern anchovy seems to be resistant to such perturbations, perhaps because of compensatory responses in the juvenile stage that we are only beginning to sample adequately.

ACKNOWLEDGMENTS

I thank the many NMFS scientists, technicians, and ship personnel who contributed to the sampling and analysis involved in the anchovy egg production surveys, as well as the staff of the Scripps Satellite Oceanography Facility (SSOF) for receiving and archiving satellite data. SSOF activities are partially funded by a NSF/NASA/ONR block grant to the Scripps Institution of Oceanography.

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PREY SIZE SELECTIVITY AND FEEDING RATE OF LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX* GIRARD

PATRICIA D. SCHMITT
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

A series of laboratory feeding experiments was conducted with larvae of the northern anchovy, *Engraulis mordax*, at 10, 20, 30, and 40 mm SL. The larvae were fed wild zooplankton in high (100 prey/liter) and low (10 prey/liter) concentrations. The 10-mm larvae consumed primarily rotifers, probably because of their past feeding history. The 20-40-mm larvae tended to select large copepods at high concentrations, and medium and large copepods at low concentrations. The ability of late larvae to select the largest prey available is similar to the foraging behavior of adult anchovies reported by previous workers. The foraging of 40-mm larvae was probably restricted by the size of the experimental tanks.

Feeding rates as a function of larval size and prey concentration were estimated and compared to a conservative estimate of basal metabolic costs. Only 20- and 30-mm larvae feeding at 100 prey/liter consumed enough food to grow at rates similar to those observed in the sea, which indicates that even late larvae require somewhat concentrated patches of food.

RESUMEN

Una serie de experimentos de alimentación en laboratorio se llevó a cabo con larvas de anchoveta del norte, *Engraulis mordax*, de 10, 20, 30, y 40 mm (largo estándar). Las larvas fueron alimentadas con concentraciones altas (100 presas/litro) y bajas (10 presas/litro) de zooplancton silvestre. Las larvas de 10 mm consumieron principalmente rotíferos, probablemente debido a su historial de alimentación previo. Las larvas de 20 a 40 mm LS seleccionaron principalmente copépodos grandes a altas concentraciones, y copépodos medianos y grandes a concentraciones bajas. La habilidad de las larvas maduras para escoger las presas disponibles más grandes es similar al comportamiento depredador de las anchovetas adultas de acuerdo a lo informado por otros investigadores. La predación de las larvas de 40 mm probablemente fue restringida por el tamaño del tanque experimental.

Las tasas de alimentación fueron calculadas como función del tamaño larvario y de la concentración de presas y fueron comparadas con una estimación de los costos en metabolismo basal. Sólo las larvas de 20 a 30 mm, quienes consumieron 100 presas por litro, se alimentaron lo suficiente como para crecer a tasas similares a las observadas en el mar. Esto indica que incluso las larvas maduras requieren la presencia de sus presas concentradas en "manchas."

INTRODUCTION

In order to understand the factors affecting recruitment and year-class strength, scientists have done much research on the early life history of the northern anchovy, *Engraulis mordax* Girard. The rationale behind this work has been that year-class strength may be determined by the growth and mortality rates of larvae in the first month of life (5-15 mm SL), especially during the transition from the yolk-sac stage to planktivorous feeding (Lasker 1975). However, correlation of the densities of early larvae (less than 15 mm SL) with the strength of the subsequent year class has shown that only exceptionally small recruitment can be predicted, not medium or large recruitment (Smith 1981). Smith and Lasker (1978) note that an increase of an order of magnitude occurred in the anchovy population between 1951 and 1969, while the annual average daily production of 20-day-old larvae remained relatively constant. From this observation it is apparent that variations in survival during the late larval phase (20-35 mm SL, ca. 1-3 months old) are also important in determining recruitment (Smith 1985). The late larval and juvenile stages are presently the least understood phases of *E. mordax*.

Feeding and growth characteristics of northern anchovy show gradual changes from early to late larval stages. Northern anchovy larvae of all sizes feed by visually mediated biting (Blaxter and Hunter 1982). Filter feeding begins only after metamorphosis (35-40 mm SL). As a larva grows, it requires more food of a larger size to maintain a given rate of growth. However, there seems to be no further increase in food size after larvae reach about 12 mm SL, even though the mouth width, and therefore the size of particles ingestible, continues to increase (Hunter 1981). In the field, there are far more food particles of the size taken by first-feeding larvae (50-100 μm) than there are of larger particles needed by older larvae (ca. 200 μm and larger) (Arthur 1977; Hunter 1981). The maximum

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naupliar biomass in waters of the California Current occurs at a naupliar width of about 70 μm (Arthur 1977). Measurements of the standing stocks of pelagic organisms indicate that there is approximately equal biomass over logarithmically equal size ranges (Sheldon et al. 1977); in other words, the number of organisms decreases exponentially as size of organisms increases linearly (Vlymen 1977).

Jack mackerel larvae inhabiting the same general environment as the anchovy are able to secure increasingly larger food particles as they grow (Arthur 1976). This suggests that factors other than mouth size, such as the relatively slow swimming speed of engrauliid larvae, may limit the size of food captured by *E. mordax* (Hunter 1981). Late larvae are thought to continue to feed on smaller prey and to take larger copepods when available, although this apparently has not been examined in either field-caught or laboratory-reared larvae larger than 20 mm SL (Arthur 1976; Hunter 1981).

Methot (1981) reports that late larvae grow at a slower rate (0.30-0.35 mm/day) than early larvae (0.47-0.70 mm/day) or early juveniles (0.40-0.60 mm/day). The ratio between weight and length seems similar during all stages (Methot 1981); therefore, the reason for slower length-specific growth during the late larval stage may lie in feeding ecology, energetic requirements, and assimilation efficiency. Methot (1981) suggests that the decline in growth through the late larval period may be due to the inability of larvae to find and capture large particles.

Here I present the results of laboratory experiments conducted with *E. mordax* larvae fed wild zooplankton to determine how prey-size selectivity and feeding rates differ between larvae of various sizes that are feeding on different densities of prey. The results are used to infer whether larvae can obtain enough food at the experimental prey concentrations to meet metabolic and growth requirements.

METHODS

Larvae of *Engraulis mordax* were reared from eggs at 18°C in the laboratory at the Southwest Fisheries Center, La Jolla, California, using the methods presented by Hunter (1976). Larvae were fed the dinoflagellate *Gymnodinium splendens*, the rotifer *Brachionus plicatilis*, and the harpacticoid copepod *Tigriopus californicus*, all reared in the laboratory.

Wild zooplankton for the feeding experiments was collected in Mission Bay from October 25, 1984, to February 21, 1985. Collections were made from a skiff, with 0.5-m ring nets of 64-μm and 333-μm nylon mesh. The nets were fitted with solid cod ends. The two nets were towed sequentially for 5 minutes each at approximately 1 m/sec, and the catches from six sets of tows were combined. The most abundant organisms collected were calanoid copepods of the genus *Acartia*. Also common were the cyclopoid copepods *Corycaeus* spp. and *Oithona* spp., and the harpacticoid copepod *Euterpina acutifrons*. Gastropod veligers and rotifers were occasionally abundant.

Experimental Design

The experimental design was orthogonal, with two main factors—larval length (10, 20, 30, and 40 mm SL) and prey concentration (10/liter and 100/liter). The larval lengths were chosen to cover the entire larval life in this species. The prey concentrations were chosen to approximate high and low average densities of microzooplankton prey sampled in areas inhabited by anchovy larvae in the California Current (Arthur 1977). Each combination of factors and levels was replicated twice. Only two tanks were available for experiments; therefore, experiments with the two prey concentrations were done simultaneously for a particular size of fish. The size-composition of wild plankton varied between experiments because of natural variations in the plankton collections. The order of experiments was randomized so that any seasonal change in plankton composition was interspersed among sizes of larvae.

Experimental Procedure

One to three days before an experiment, I transferred 20-30 reared larvae to each experimental tank. The experimental tanks were as similar as possible to the rearing tanks in construction (400-liter, 1.2-m-diameter, black fiberglass), aeration, lighting, and temperature. Larvae were starved and acclimated for 1-3 days, depending on size, until guts were empty and behavior seemed normal.

Fresh plankton was collected each morning (0800-1200 hrs), and experiments were conducted in the afternoon (1400-1800 hrs). Immediately before the experiment, I stopped the aeration. I then added the appropriate amount of plankton to create the target concentration. To determine the actual concentration and distribution of prey in each tank, I took samples with plexiglas tubes (7-cm diameter) lowered onto rubber stoppers that had been placed on the bottom before I added plankton. Sample volume ranged from 500-750 ml, depending on the volume of water in the tank. I preserved five replicate samples in 5% buffered Formalin for later enumeration. I used size-frequency data from samples in the high-density tank (100/liter) to determine size-frequency in the low-density tank (10/liter). Pilot studies indicated a coefficient of variation between replicate samples of 8%-74%.

I measured swimming speed for two 10-minute periods before and after plankton was added. To measure the speed, I randomly selected an individual fish, and then, with the aid of 1-cm and 3-cm grid patterns on the bottom of the tank, estimated the distance the fish traveled in 2 seconds. The number of fish observed in 10 minutes ranged from 35 to 142. I converted speeds into body lengths/sec, using the mean standard length of the fish in each tank.

I terminated the experiments after 30-60 minutes by anesthetizing all fish with MS_{222}, at a concentration of 0.1 g/l. This was done to prevent the larvae from defecating or regurgitating their gut contents during handling (June and Carlson 1971). After 10 minutes, I collected fish with a dip net as quickly as possible, and preserved them in 10% buffered Formalin for later measurement and enumeration of gut contents. Duration of the experiments was assumed to be less than the time required for larvae to fill their guts at the experimental prey concentrations or to defecate prey ingested during the experiment (G. Theilacker, pers. comm.).

Laboratory Analyses

All prey items were identified in three categories: nauplii, copepods (including copepodites and adult copepods), and others. I measured items across the maximum width, excluding appendages. Initially I grouped the measurements into 50-μm size categories, and later regrouped them into five categories for data analysis: nauplii ($<$ 150 μm wide), small copepods ($<$ 100 μm wide), medium copepods (100-300 μm wide), large copepods ($>$ 300 μm wide), and others (predominantly rotifers $<$ 200 μm; also gastropod and bivalve veligers).

Plankton samples were stained with Biebrich scarlet, and counted in either a settling chamber with an inverted microscope at 50-100×, or a Plexiglas counting dish under a dissecting microscope at 25-50×. In the settling chamber, some plankters were found in the supernatant after the settling period of 12-15 hr. I estimated the percentage of error (i.e., the proportion of plankters not settling completely) from 20 samples; it averaged 15.1% for nauplii and copepods. There was no significant size-bias in the error factor. All counts made with settling columns were subsequently corrected.

I examined the guts of ten larvae from each experiment (except for one experiment with 10-mm larvae, when only eight larvae were available). I measured the fish (SL), and dissected the guts in glycerin. I teased out the gut contents with fine needles, and stained them with Chlorazol Black E in lactic acid and ethyl alcohol (Judkins and Fleminger 1972). All prey items were counted and measured under a compound microscope.

I determined the live length of each fish by using the shrinkage correction factors of Theilacker (1980) for 10 min of net treatment followed by preservation in 10% Formalin. Shrinkage rates due to MS_{222} and net treatment were similar. For 10-mm larvae, the shrinkage from 10 min in 0.1 g/l MS_{222} followed by Formalin preservation was 13.1% ($n = 20$), compared to 15% from 10 min of net treatment followed by Formalin preservation (Theilacker 1980).

Gut contents and plankton data were converted from numbers of prey to dry weight, taking into account the size-frequency of prey by 50-μm width classes before the data were combined into the five larger prey classes for analysis. The width-specific volumes of copepods and nauplii were calculated from ocular micrometer measurements of the length, width, and depth, assuming nauplii to be ellipsoids, and copepods to be ellipsoids (cephalothorax) plus cylinders (abdomen). I determined volume-to-width relationships for nauplii [ln volume $= -14.20 + 3.08$ (ln width), $r^2 = 0.902$, $n = 42$] and copepods [ln volume $= -13.56 + 3.02$ (ln width, $r^2 = 0.993$, $n = 75$]. The width-specific dry weight of fresh, mixed-species copepod samples was determined following the methods of Theilacker and Kimball (1984). I rinsed samples with isotonic ammonium formate solution (3.4%), sorted them into 50-μm size classes, and dried them overnight on glass slides at 60°C. I prepared 14 slides, each containing from 3 to 95 individuals, depending on the size of copepods. Following drying, samples were removed from the slides and weighed on a Cahn electrobalance. I determined the dry-weight-to-volume relationship by linear regression with intercept set equal to 0 [dry weight $= 0.19$ (volume), $p < .001$, $n = 14$], and used the relationship to calculate dry weights of nauplii and copepods from their volume. The dry weight used for the prey category "others" was the average for rotifers $<$ 200 μm wide (0.30 μg) given by Theilacker and Kimball (1984).

Data Analyses

Prey-size selectivity was determined using the alpha index (α) (Chesson 1978). I chose this index because it allows comparisons of selectivity between experiments with different prey compositions (Chesson 1983), and also because it is possible to test the apparent selectivity against a random model (Manly 1974). The index is calculated as:

$$\alpha_i = \frac{r_i/p_i}{\sum_{i=1}^{m} r_i/p_i}$$

where m = number of prey types = 5
r_i = proportion of prey type i consumed
p_i = proportion of prey type i available.

p_i was assumed to be constant for the duration of each experiment; i.e., the initial prey concentration was assumed to be not significantly depleted by larvae feeding during the experiment. r_i was determined from gut content analyses.

I calculated the alpha index for each of the five prey categories, for each larva that fed during experiments. The values so obtained were not suitable for parametric statistical analyses, because the variances remained heterogeneous after arc sine transformation. Therefore, I examined the median values and the quartiles above and below the median. The observed values are compared with the value expected if feeding was random on all categories of prey ($\alpha = 1/m = 0.20$).

In order to compare feeding rates between sizes of larvae at the target concentrations, I fitted feeding-rate data for each 10-mm size class of larvae to a log-linear multiple regression model:

$$\ln(\text{rate} + 1) = \ln(a) + b_1(\text{SL}) + b_2(\text{concentration})$$

I backtransformed the resulting estimates, taking into account the variance of the regression, and calculated 95% confidence limits (Beauchamp and Olson 1973).

I calculated the metabolic and growth requirements using the following values and assumptions:

1. Larvae fed at the estimated mean feeding rates throughout a 12-hr feeding day.

2. Daily minimum metabolic requirement (24 hr) was calculated from the following model presented by Theilacker[1] for anchovy larvae at 15.5°-16°C:

$$Q = 4.269\, W^{0.697}$$

where Q = metabolic rate in μl O_2/day
W = fresh dry weight in mg

and converted to μg prey material using the following factors: 0.00463 cal/μl O_2 and 4.9×10^{-3} cal/μg, for copepod prey (Theilacker and Kimball 1984).

3. Assimilation efficiency was 70% for larvae of all sizes, a rough extrapolation from Theilacker's results.[2]

4. Weight-specific growth rates of larvae in the sea were taken from Methot (1981). The surface temperatures reported in that study (generally representative of anchovy spawning areas) ranged from 13° to 19°C, with the mode at approximately 15°-16°C.

5. Fresh dry weights were calculated from the formula in Hunter (1976) for 10-30-mm larvae, and from unpublished data of Hunter for 40-mm larvae.

RESULTS AND DISCUSSION

The target and actual larval lengths and prey concentrations are given in Table 1, along with the feeding incidence (% of larvae with one or more prey in gut). Because 10-mm larvae did not feed at 10 prey/liter, I tested them at 100 and 1000 prey/liter. Feeding incidence tended to increase with both larval length and prey concentration; similar results have been reported for other species of fish larvae (Houde and Schekter 1980).

Swimming Activity

The mean swimming speed, measured as body lengths/sec (bl/s), in each experiment is shown in Table 2, along with t-tests of the equality of means before feeding (after 1-3 days of food deprivation) and during feeding. For 10-mm larvae, mean speed was always less than 1 bl/s, and showed no changes with the addition of food. My results contrast with those of a previous study in which anchovy larvae from 4-8 days old (< 6 mm SL) swam slower when inside a dense patch of food cells (up to 260 cells/ml) than when outside such a patch (Hunter and Thomas 1974). The difference in these results could be because the "patches" created by adding food in my experiments were 3 to 4 orders of magnitude less dense than those used by Hunter and Thomas.

For 20-40-mm larvae, mean swimming speed ranged from 0.6 to 3.3 bl/s and tended to increase during feeding (9 of 11 t-tests with $p < .10$). However, there was no difference in the relative increase in speed during feeding between high and low prey concentrations; i.e., larvae did not swim faster while feeding on high prey concentrations (Table 2).

Prey Selectivity

The mean proportion of various prey types consumed by various sizes of larvae at high and low concentrations is compared to the mean available size composition in Figure 1. The 10-mm larvae consumed primarily rotifers (the "others" category), although they consumed some nauplii and copepods at 1000 prey/liter. The 20-40-mm larvae tended to consume a higher proportion of nauplii at low concentrations than at high concentrations, and higher proportions of medium and large copepods at high concentrations than at low concentrations. Medium copepods (100-300 μm wide) formed the largest proportion (50%-80%) of prey consumed, both by numbers and by weight for 20-40-mm larvae at both concentrations.

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[1] Theilacker, G.H. MS. Feeding ecology and growth energetics of larval northern anchovy, *Engraulis mordax*.

[2] Ibid.

TABLE 1
Comparison of Target Values for Standard Length of Northern Anchovy Larvae and Prey Concentrations with the Mean Values for Two Experiments

Target		Actual			
SL (mm)	Conc. (no./liter)	SL (mm)	Conc. (no./liter)	Conc. (μg./liter)	Feeding incidence (%)
10	100	10.2 (1.8)	278.1 (61.0)	148.1 (25.5)	77.8
	1,000		1,173.0 (148.8)	969.2 (53.6)	72.2
20	10	22.2 (2.2)	36.9 (16.4)	23.6 (13.2)	50.0
	100		92.2 (19.8)	64.6 (10.5)	95.0
30	10	28.4 (3.0)	19.5 (9.5)	9.0 (3.7)	85.0
	100		127.3 (18.7)	92.9 (42.7)	100.0
40	10	43.0 (5.0)	10.2 (0.4)	7.9 (4.3)	100.0
	100		166.0 (58.5)	264.9 (165.9)	100.0

Standard deviation is shown in parentheses below mean values.

TABLE 2
Mean Swimming Speed (Body Lengths/Sec) of Northern Anchovy Larvae Before and During Feeding Experiments, and Results of t-Tests of the Equality of Means

		Swimming speed (body lengths/sec)			
SL (mm)	Prey conc.	Before	During	t	*p*
10	Low	0.8 (0.3)	0.8 (0.3)	0	ns
	High	0.8 (0.3)	0.7 (0.3)	1.5	>.10
	High	0.5 (0.4)	0.5 (0.4)	0	ns
	Low	0.7 (0.4)	0.7 (0.4)	0	ns
20	Low	0.6 (0.4)	1.8 (1.2)	−10.2	<.001
	High	1.3 (1.2)	2.0 (0.9)	−5.2	<.001
	Low	1.2 (0.6)	2.3 (1.1)	−6.9	<.001
	High	1.5 (1.2)	1.9 (1.1)	−1.9	<.10
30	Low	2.6 (1.2)	3.0 (1.4)	−1.8	<.10
	High	3.3 (0.9)	2.2 (0.7)	8.7	<.001
	Low	2.3 (1.1)	2.1 (0.8)	−1.2	>.20
	High	1.3 (0.6)	1.6 (0.6)	−2.9	<.001
40	Low	1.4 (0.8)	1.6 (0.6)	−1.8	<.10
	High	1.2 (0.5)	1.9 (0.5)	−9.1	<.001
	High	1.0 (0.4)	2.7 (0.6)	−18.2	<.001

Standard deviation is shown in parentheses after each mean. The number of observations for each mean ranged from 35 to 142.

The alpha indexes of selectivity are presented in Figure 2, and compared to the random feeding value of 0.20. The 10-mm larvae were highly selective for rotifers. This could have been influenced by two factors. First, there was a large proportion of rotifers in the tank during the experiment. The rotifers came both from the plankton used for the experiment (collected by chance during a rotifer bloom) and from the rearing tanks when the fish were transferred. Before the experiments began, I attempted to remove the transferred rotifers using an air-lift pump, but was not entirely successful. The second factor was the larvae's lack of experience with wild zooplankton as food. The 10-mm larvae were accustomed to eating cultured rotifers, and may have been unable to adjust to wild plankton in the time allowed by the experiment. However, in the field, anchovy larvae select prey smaller than the largest they are capable of ingesting (Arthur 1976). In the laboratory, herring larvae (12-19 mm SL) selected wild zooplankton narrower than the widest available and ingestible during feeding experiments, even though they were accustomed to wild zooplankton as food during rearing (Checkley 1982). The fact that 10-mm anchovies ate more medium copepods at 1000/liter than at 100/liter suggests that they were better able to capture

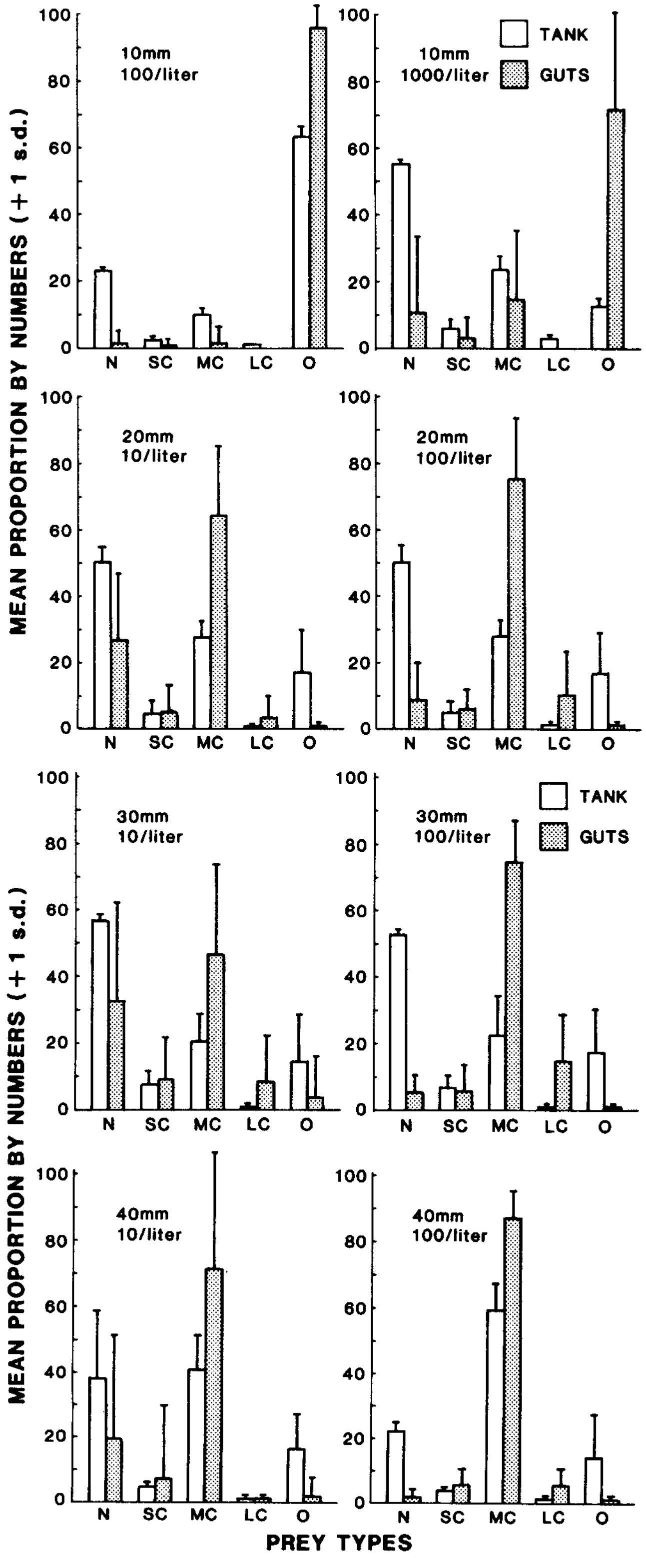

Figure 1. Comparisons of the proportions of various prey types consumed versus the proportions available to northern anchovy larvae of 10, 20, 30, and 40 mm SL, feeding at high and low prey concentrations. Mean values for two experiments are indicated by bars, with 1 standard deviation shown by a line above each bar. Prey types are abbreviated as follows: N, nauplii < 150 μm wide; SC, small copepods < 100 μm wide; MC, medium copepods 100-300 μm wide; LC, large copepods > 300 μm wide; and O, others (mainly rotifers < 200 μm wide, and gastropod and bivalve veligers).

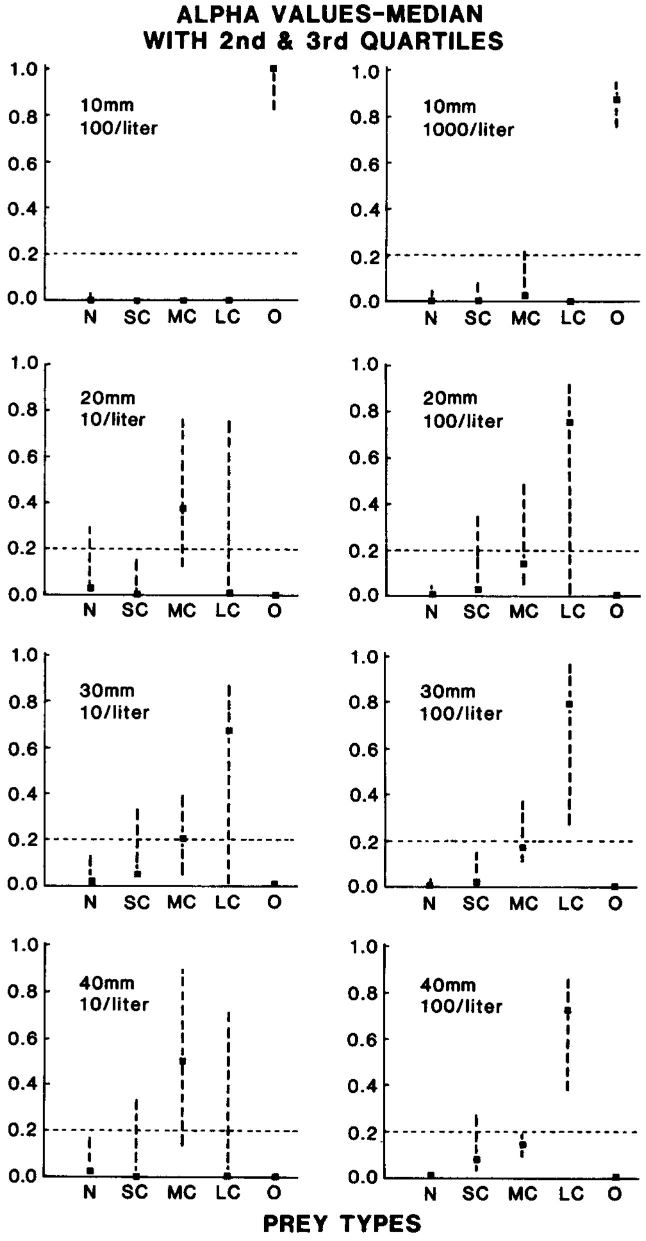

Figure 2. Values of the alpha index of selectivity for each prey type, size of northern anchovy larvae, and prey concentration. The median value from two experiments (number of fish = 20) is shown by the square symbol, with the quartiles above and below the median indicated by the vertical dashed lines. The random feeding value (α = 0.20) is shown by the horizontal dashed line on each graph. The prey types are abbreviated as in Figure 1.

larger prey at high density, regardless of previous experience. The larger larvae (20-40 mm) had all been previously exposed to wild plankton as an occasional food source in the rearing tanks.

The 20-40-mm larvae tended to select large copepods at high concentrations, and to select medium and large copepods at low concentrations. There is obviously much individual variation in selectivity. No clear pattern of difference in selectivity or size composition of prey consumed appears to exist between 20-, 30-, and 40-mm larvae; all tended to select the largest prey available. Adult northern anchovy in the Southern California Bight showed similar selectivity for the largest prey available while feeding in schools on a variety of plankton assemblages of prey genera and sizes overlapping those used here (Koslow 1981).

There was some indication that the 20-40-mm larvae may have significantly reduced the concentration of larger prey during some experiments, but this depletion was not quantified. Such a violation of the assumption of constant p_i would tend to make the alpha values presented here an underestimation of the actual degree of selectivity (Chesson 1978, 1983; Manly 1974).

Feeding Rates

Estimated feeding rates (Figure 3), given both as numbers per minute and as dry weight per minute, were calculated from multiple regression equations describing feeding rate as a function of larval size and prey concentration for each 10-mm size class (Table 3). Feeding rate was higher at 100/liter than at 10/liter for all sizes of larvae. At 100 prey/liter, 40-mm larvae consumed 1.5-2 times more items than did 20- and 30-mm larvae. However, in terms of dry weight of prey consumed/min, 40-mm larvae consumed less than did 30-mm larvae, indicating that 40-mm larvae ate more small prey than did 30-mm larvae. This may be because the experimental tank was small relative to the searching abilities of 40-mm larvae, and because 40-mm larvae apparently depleted the tank of large copepods during the experiment.

Metabolic and Growth Requirements

The results of the calculations of food consumed and metabolic costs are presented in Table 4. For all sizes of larvae at all concentrations (except 20-mm larvae at 10/liter), larvae ingested enough food to meet their basal metabolic needs. However, the consumption rates used here are probably somewhat high for two reasons: (1) feeding rates were measured during the first 30-60 minutes of feeding after a period of starvation, and were thus higher than an average 12-hour rate (Hunter 1972); and (2) feeding rates were measured at 18°C, whereas minimum metabolic requirements and field growth rates are more representative of larvae at 15°-16°C.

Nevertheless, estimated growth rates as a percentage of body weight are compared with the weight-specific growth rates of field-caught larvae (Methot 1981) to determine if larvae could grow at observed rates at the prey concentrations tested (Table 4). Neither 10-mm nor 40-mm larvae could grow at field growth rates at any of the food concentrations tested, but I do not believe the results for these two size classes are reliable.

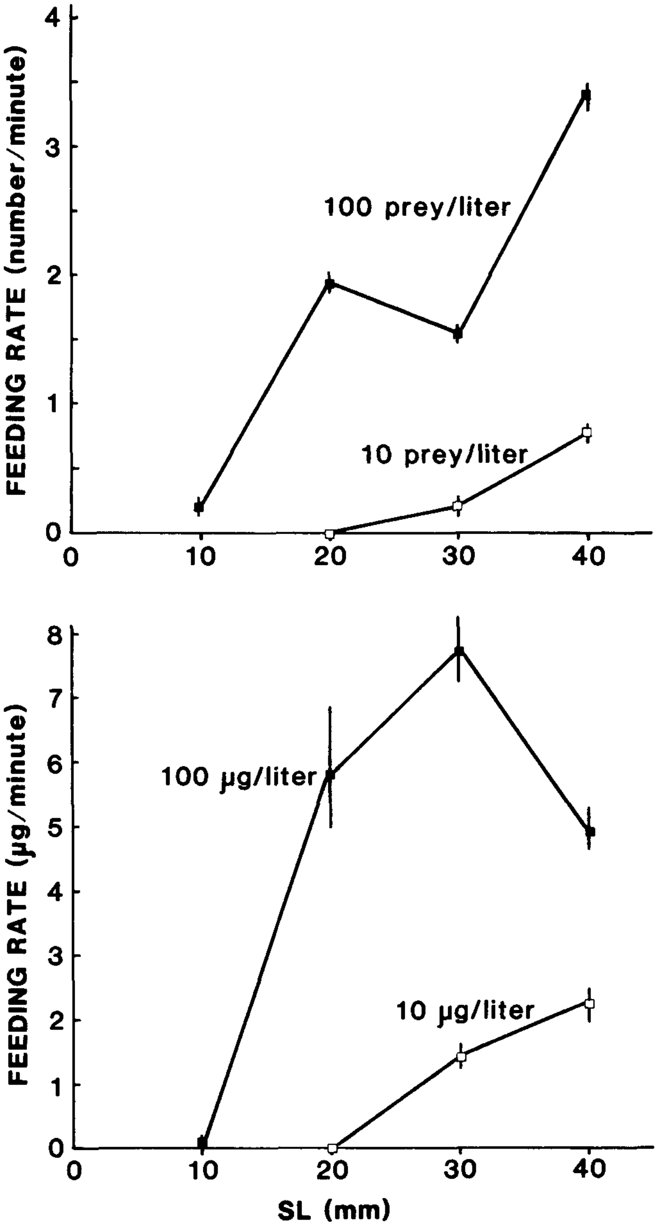

Figure 3. Estimated feeding rates of northern anchovy larvae of various sizes at two standardized prey concentrations. Rates are expressed as numbers of prey per minute and as weight of prey consumed per minute. The 95% confidence limits are indicated by vertical lines through each estimate.

The feeding of 10-mm larvae was probably not typical, because prior feeding was only on rotifers. Foraging of 40-mm larvae was probably affected by tank size.

According to the estimates, the 20- and 30-mm larvae would consume enough food to grow at observed rates at prey concentrations of 100/liter, but not at 10/liter. Thus, even late larvae (20-30 mm), which are able to select large prey, may require somewhat concentrated patches of food. On the other hand, 100 prey/liter is substantially lower than estimated food densities required for survival and growth in past studies (Hunter 1981), and is in keeping with the more recent

TABLE 3
Parameters for Multiple Linear Regression Equations* Describing Feeding Rate (ln rate + 1) in Relation to Larval Length (x_1) and Prey Concentration (x_2) for Northern Anchovy Larvae

SL (mm)	b_1	(Standard error)	b_2	(Standard error)	ln a	mult. r^2	F	p
Numbers of prey per minute								
10	−0.006	(0.012)	−0.7E-4	(0.5E-4)	0.243	0.107	1.97	0.16
20	0.025	(0.032)	0.013	(0.002)	−0.815	0.472	16.53	0.00
30	−0.015	(0.022)	0.008	(0.001)	0.491	0.556	23.18	0.00
40	−0.014	(0.017)	0.010	(0.001)	0.900	0.749	55.30	0.00
20-40	0.016	(0.005)	0.010	(0.001)	−0.463	0.666	116.64	0.00
Weight of prey per minute								
10	−0.002	(0.004)	−0.2E-4	(0.2E-4)	0.076	0.067	1.18	0.32
20	0.130	(0.041)	0.022	(0.004)	−3.032	0.557	23.25	0.00
30	0.052	(0.035)	0.014	(0.002)	−1.040	0.546	22.28	0.00
40	−0.037	(0.026)	0.007	(0.001)	2.282	0.664	36.62	0.00
20-40	0.002	(0.008)	0.008	(0.001)	0.556	0.528	65.31	0.00

*Model: ln (rate + 1) = ln a + b_1x_1 + b_2x_2

literature for larvae in general (Houde and Schekter 1980; Munk and Kiorboe 1985).

The prey concentrations used here were chosen to approximate high and low densities of prey suitable for *E. mordax* larvae in the field. Arthur (1977) states that the usual densities in areas where most anchovy larvae are found are about 1.5-4 copepodids/liter and about 13-30 nauplii/liter. The highest concentrations he reported from several studies in California Current waters were 36 copepodids/liter and 195 nauplii/liter. There are many difficulties in estimating field concentrations of appropriate-size prey on spatial scales relevant to larvae, especially because both prey sizes and foraging ranges change as larvae grow. Such estimates involve significant problems in sampling and data interpretation, since no single type of zooplankton gear adequately samples the entire size range of prey at one time and place, and different types of gear integrate densities over different scales—e.g., water bottles on a scale of decimeters (Owen 1981), pumps and nets over meters to kilometers (Beers and Stewart 1967; Arthur 1977). The prey distribution used in my experiments was skewed toward larger prey, with most experiments offering about 40% copepodids and adult copepods (range 30%-60%). This is about four times as many copepodids as larvae would normally encounter in the wild (Arthur 1977; Sheldon et al. 1977).

TABLE 4
Bioenergetic Estimates for *Engraulis mordax* Larvae Feeding at Two Prey Concentrations, Calculated for a 24-hr Period, with a 12-hr Feeding Period

SL (mm)	Dry weight (mg)	Metabolic requir. (μg)	Prey conc. (μg/l)	Consump. (μg)	Growth potential* (μg)	Growth body wt. (%)	Field growth (%)
10	0.316	1.808	100	43.2	28.4	9.0	15-20
			1,000	28.8	18.4	5.8	
20	4.185	10.941	10	0		—	—
			100	4,183.2	2,917.3	69.7	8-9
30	31.930	45.102	10	1,015.2	665.5	2.1	5-6
			100	5,400.0	3,734.9	11.7	
40	105.82	103.95	10	1,641.6	1,045.2	1.0	3-4
			100	3,715.2	2,496.7	2.4	

*calculated as consumption × assimilation efficiency − metabolic requirement.

In conclusion, these experiments indicate that feeding ability of northern anchovy larvae changes most dramatically between 10 and 20 mm SL. By 20 mm, the larvae's size selectivity is functionally similar to that of adults, in that larvae are capable of selecting the largest prey available over the range of sizes normally encountered. Koslow (1981) calculates that a spawning stock of 1.32-2.35 × 10^6 anchovies in the Southern California Bight would consume 10% to more than 100% of the secondary production available in the area. This implies that growth rates of late larvae may be limited by (1) intraspecific competition for large prey items with adults, (2) low prey concentrations, and (3) the stochastic interaction of these two factors.

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DEVELOPMENT AND DISTRIBUTION OF LARVAE AND PELAGIC JUVENILES OF OCEAN WHITEFISH, *CAULOLATILUS PRINCEPS*, IN THE CALCOFI SURVEY REGION

H. GEOFFREY MOSER, BARBARA Y. SUMIDA, DAVID A. AMBROSE, ELAINE M. SANDKNOP, AND ELIZABETH G. STEVENS
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Ocean whitefish larvae occurred in 88 tows taken on CalCOFI plankton surveys from 1954 to 1981. The robust larvae develop a distinctive array of spines and spiny ridges in the head region. The body becomes covered with minute spines, which develop on each scale. Larvae also have a characteristic pattern of melanistic pigmentation, which makes it possible to identify early stages that have not yet developed head spines.

Larvae occurred from Ensenada (CalCOFI line 100) to Magdalena Bay (line 140) and seaward to Guadalupe Island. Occurrences were concentrated off central Baja California; only 20% of the positive tows were north of Sebastian Viscaino Bay. It is apparent from the distribution of larvae that ocean whitefish populations off southern California are recruited from Baja California.

RESUMEN

Larvas oceánicas de *Caulolatilus princeps* estuvieron presentes en 88 arrastres de plancton realizados durante el programa CalCOFI entre 1954 y 1981. Estas robustas larvas desarrollan un claro conjunto de espinas y zonas espinosas en la región de la cabeza. El cuerpo se cubre con espinas diminutas, las cuales crecen sobre cada escama. Las larvas tienen, además, un patrón de pigmentación melánico característico que permite identificar estadíos tempranos que aún no han desarrollado espinas en la cabeza

Se encontraron larvas desde Ensenada (CalCOFI línea 100) hasta Bahía Magdalena (línea 140) y mar afuera de la Isla Guadalupe. Las larvas se concentraron frente a la zona central de Baja California; sólo un 20% de los arrastres con larvas ocurrió al Norte de la Bahía Sebastián Vizcaíno. La distribución de las larvas indica que las poblaciones oceánicas de *Caulolatilus princeps* en el Sur de California son formadas por reclutas provenientes de Baja California.

INTRODUCTION

The ocean whitefish, *Caulolatilus princeps*, ranges from Vancouver Island, British Columbia, to Peru and is a prominent coastal bottomfish off southern California and Baja California (Miller and Lea 1972; Dooley 1978). Southern California commercial passenger fishing boat catch from 1972 to 1983 ranged from 11,000 to 61,000 fish per year, with an average catch of 32,000 fish for the 12-year period[1]. Ocean whitefish ranked tenth in a survey of landings of the southern California private sport fishery (Wine 1978). Commercial landings declined steadily from a catch of 100,000 pounds in 1946 to less than 2,000 pounds in 1956 and have not increased appreciably since (Fitch and Lavenberg 1971). The species is an excellent food fish, and related species in the family Malacanthidae command a high market price, especially in Japan, where they are used for sashimi (S. Kato, National Marine Fisheries Service, Tiburon, California, pers. comm.).

What little is known about the biology of *C. princeps* is summarized in Fitch and Lavenberg (1971). Fourmanoir (1970) briefly described some juveniles taken from tuna and lancetfish stomachs. Kramer and Smith (1973) briefly summarized the distribution of ocean whitefish larvae from CalCOFI surveys of 1955-60. Johnson (1984) summarized rostral spination in *Caulolatilus* larvae in comparison with other malacanthid genera. Detailed descriptions of larvae and juveniles of other malacanthid species (Okiyama 1964; Fahay and Berrien 1981; Fahay 1983) show that in its early life history stages this family is among the most highly developed of all teleosts.

Larvae of *C. princeps* are relatively rare in California Cooperative Oceanic Fisheries Investigations (CalCOFI) plankton collections; however, this may result partly from their distribution off coastal Baja California, where sampling has been relatively low. The purpose of this paper is to describe the larvae and pelagic juveniles of *C. princeps* and summarize their distribution in CalCOFI samples taken during 1954-81.

MATERIALS AND METHODS

A total of 163 *C. princeps* larvae and 8 pelagic juveniles was available for study. Larval specimens ranged from 1.7 mm NL to 7.9 mm SL, and pelagic juveniles ranged from 15.5 to 44.5 mm SL. A developmental series was established to study general morphology,

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[1] Reports of fish caught by the California commercial passenger fishing boat fleet. California Department of Fish and Game, Marine Resources Division, Long Beach.

TABLE 1
Measurements (mm) of Larvae and Pelagic Juveniles of *Caulolatilus princeps*

Station	Body length	Snout-anus length	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length
6107 123.45	2.6	1.0	0.59	0.42	0.13	0.27	0.68	0.19	0.19	—
6608 120.45	2.8	1.2	0.65	0.57	0.18	0.33	0.83	0.22	0.31	—
6608 120.45	3.0	1.6	0.80	0.56	0.24	0.33	0.86	0.21	0.37	—
5410 130.55	3.3	1.5	1.0	0.73	0.32	0.38	1.0	0.28	0.35	—
5707 120.35	3.7	1.8	1.1	0.80	0.32	0.40	1.2	0.27	0.48	—
5707 120.35	4.0	1.9	1.2	0.83	0.35	0.47	1.2	0.32	0.57	—
5907 133.45	4.2	2.0	1.2	0.95	0.30	0.48	1.3	0.33	0.62	—
6007 130.35	4.5	2.1	1.3	1.0	0.35	0.58	1.4	0.40	0.65	—
5908 123.55	4.7	2.3	1.5	1.2	0.36	0.60	1.5	0.37	0.64	0.02
5904 137.35	5.0	2.4	1.6	1.2	0.34	0.60	1.6	0.40	0.68	0.03
6107 133.35	5.3	2.7	1.7	1.2	0.30	0.65	1.8	0.50	0.69	0.05
H-5706 120.35	5.7	2.9	1.9	1.2	0.53	0.80	2.1	0.67	0.76	0.06
H-5706 120.35	6.1	3.4	2.2	1.3	0.55	0.87	2.3	0.70	0.82	0.04
5102 140.30	7.1	4.2	2.8	1.7	0.70	1.0	2.9	1.0	1.0	0.43
5302 100.30	7.9	4.7	3.1	1.8	0.93	1.2	3.2	1.3	1.0	0.71
6509 107.40	15.5	9.5	5.6	2.8	1.5	2.1	6.0	—	1.4	—
5706 130.60	16.9	10.0	5.9	3.1	1.6	2.1	6.3	3.0	1.5	2.2
5510 123.50	27.8	17.2	9.2	4.6	1.8	3.2	9.2	4.4	1.9	3.7
7510AX 130.30	33.9	18.8	10.3	5.4	2.2	3.9	10.1	5.8	2.3	4.3
6010B 117.30	44.5	25.8	12.7	6.1	3.2	4.0	12.8	7.5	2.8	6.2

Specimens between dashed lines are in the notochord flexion stage; those below the solid line are pelagic juveniles.

morphometry, and pigmentation. Additional specimens from the collection were used to define variability of these features. Subsequently, the series was stained with Alizarin Red-S and cleared in a graded series of KOH and glycerin to determine the sequence of formation of ossified fin rays, head spines, and scale patches. Most of the small specimens were poorly ossified because of calcium leaching in preservation and, for these specimens, only the appearance of unossified fin rays could be noted. The descriptive methods and terminology follow Ahlstrom et al. (1976) and Moser et al. (1977). Head spines are named for the bones from which they originate. Prior to the completion of notochord flexion, body length is measured from the tip of the snout to the tip of the notochord and is designated "NL." In postflexion specimens body length is measured to the posterior edge of the hypural plate and is termed "SL."

DESCRIPTION

General Morphology

Larvae of *C. princeps* are characterized by a robust body form and the development of larval features at a comparatively small size (Tables 1-3; Figures 1 and 2). Our smallest intact specimen (2.6 mm) has a relatively large head and a compact coiled gut with no evidence of yolk. At the beginning of notochord flexion (about 5.7 mm NL) the larva is highly robust and deep-bodied, with a massive head, triangular-shaped gut mass, and large eye. Notochord flexion is completed at about 7.0 mm SL, and this body form is maintained throughout the postflexion stage. Development of the larval morph is shown by changes in body proportions (Table 2). Relative snout-anus length, head length, head width, snout length, and body depth increase throughout the larval period. Each of these propor-

TABLE 2
Average Body Proportions (% ± Standard Deviation) for Larvae and Pelagic Juveniles of *Caulolatilus princeps*

	Snout-anus length	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin length	Pelvic fin base depth	Pelvic fin length
Stage	Body length	Body length	Head length	Head length	Head length	Body length	Body length	Body length	Body length
Preflexion	47.2±4.05	28.8±3.25	21.6±2.66	25.9±4.30	41.1±4.46	30.6±2.06	7.9±0.70	12.6±2.25	~1.0±0.00
Flexion	53.5±3.54	34.5±2.12	21.0±0.00	26.5±2.12	41.0±1.41	37.5±0.71	11.5±0.71	13.0±0.00	1.0±0.00
Postflexion	59.0±0.00	39.0±0.00	23.5±0.71	27.5±3.54	37.5±2.12	41.0±0.00	15.0±1.41	13.5±0.71	7.5±2.12
Juvenile	59.0±2.74	32.6±3.05	16.6±1.67	24.0±3.32	36.6±3.78	33.6±3.34	17.0±0.82	7.6±1.34	13.2±0.50

TABLE 3
Sequence of Development of Head Spines in Larvae of *Caulolatilus princeps*

	Body length (mm)													
Spine	.2.6	2.8	3.1	3.3	3.7	4.0	4.4	4.7	5.0	5.3	5.7	6.1	7.1	7.9
Preopercle margin—angle	—	+	+	+	+	+	(2)	(2)	(2)	(3)	(6)	B	(6)	(11)
Preopercle margin—upper series	—	1	1	2	2	3	3	3	4	4	4	5	5	6
Preopercle margin—lower series	—	—	1	2	3	3	4	3	4	4	5	5	5	5
Preopercle ridge—upper series	—	—	—	—	—	—	—	—	—	—	1	3	2	4
Preopercle ridge—lower series	—	—	1	1	2	2	4	3	4	4	5	6	6	6
Frontal—1st transverse ridge series	—	—	1	2	3	3	5	5	4	5	6	9	9	9
Frontal—2nd transverse ridge series	—	—	—	—	1	2	3	4	4	5	5	5	8	9
Frontal—3rd transverse ridge series	—	—	—	—	—	2	3	3	3	4	5	B	9	9
Frontal—secondary transverse ridges*	—	—	—	—	—	—	—	—	1	1	2	2	5	5
Frontal—longitudinal ridge series	—	—	—	—	—	1	3	3	3	3	4	B	7	8
Frontal—anterior longitudinal ridge series	—	—	—	—	—	1	2	3	3	4	4	5	5	7
Frontal—supraocular shelf series	—	—	—	—	1	3	4	4	4	6	7	10	10	13
Posttemporal—upper series	—	—	1	3	3	3	4	4	6	7	7	9	10	12
Posttemporal—lower series	—	—	—	—	1	2	2	2	2	4	3	3	5	5
Supracleithrum series	—	—	—	—	—	1	1	1	2	2	3	3	4	5
Dentary series	—	—	—	4	3	6	6	7	6	8	9	12	11	12
Pterotic series	—	—	—	—	—	—	1	1	1	1	2	4	4	5
Interopercle series	—	—	—	—	—	—	1	2	2	2	2	2	2	3
Subopercle series	—	—	—	—	—	—	—	—	—	—	1	1	1	2
Opercle	—	—	—	—	—	—	—	—	—	—	1	1	1	1
Nasal—lateral series	—	—	—	—	—	—	—	—	1	2	3	4	6	7
Nasal—median series	—	—	—	—	—	—	—	—	—	2	3	4	4	4
Nasal—ventral series	—	—	—	—	—	—	—	—	—	—	1	1	3	3
Lacrimal—upper series	—	—	—	—	—	—	—	—	—	—	4	4	6	8
Lacrimal—lower series	—	—	—	—	—	—	—	—	—	—	3	6	6	9
Extrascapular—upper series	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Extrascapular—lower series	—	—	—	—	—	—	—	—	—	—	—	—	1	2

*Number of ridges indicated, not the number of spines.

Numbers of spines in each series are listed. Spinules on preopercular angle spine are enclosed in parentheses. Symbols: + = present; B = broken.

tions, except relative snout-anus length, decreases in pelagic juveniles as the body becomes more streamlined.

Larvae of *C. princeps* develop a remarkable array of head spines. Preopercular spines develop in larvae less than 3.0 mm NL. The spine at the angle of the preopercle develops first, then spines are added above and below it throughout the larval period (Table 3; Figures 1 and 2). The angle spine develops prominent spinules late in the larval period. A second preopercular series forms on a ridge anterior to the preopercular margin.

Numerous spinous ridges develop on the frontal bone. Each begins with one or two broad-based spines and gradually adds spines to form a serrate ridge. Initially a transverse ridge forms above the eye; two additional transverse ridges form posterior to it, and two longitudinal ridges form anterior to it. Later in the larval period several secondary transverse ridges develop anterior to the original three; these curve forward to form a pattern that appears heart-shaped from dorsal view. The longitudinal ridges become aligned with the lateral ridges of the nasal bone. These series of ridges are joined anteriorly by a transverse ridge at the point of fusion of the nasal bones to form a long troughlike structure that projects beyond the upper jaw. In addition to these ridges, a spinous supraocular shelf forms at the margin of the frontal bone and projects laterally over the eye. A spinous ridge develops on the pterotic bone posterior to the supraocular shelf, and, late in the larval period, ridges develop on the extrascapular bone in the epiotic region (Table 3; Figures 1 and 2).

Ornate spinous ridges develop on the posttemporal and supracleithral bones early in the larval period. The upper series on the posttemporal forms first and becomes antlerlike at full development (Table 3; Figures 1 and 2). The lower posttemporal and supracleithral ridges are less ornate, and fuse to form a continuous structure.

Ventrally on the head, spinous ridges develop on the upper and lower margins of the lacrimal bone and along the ventral margin of the dentary bone. Two spines form on the subopercle, three form on the inter-

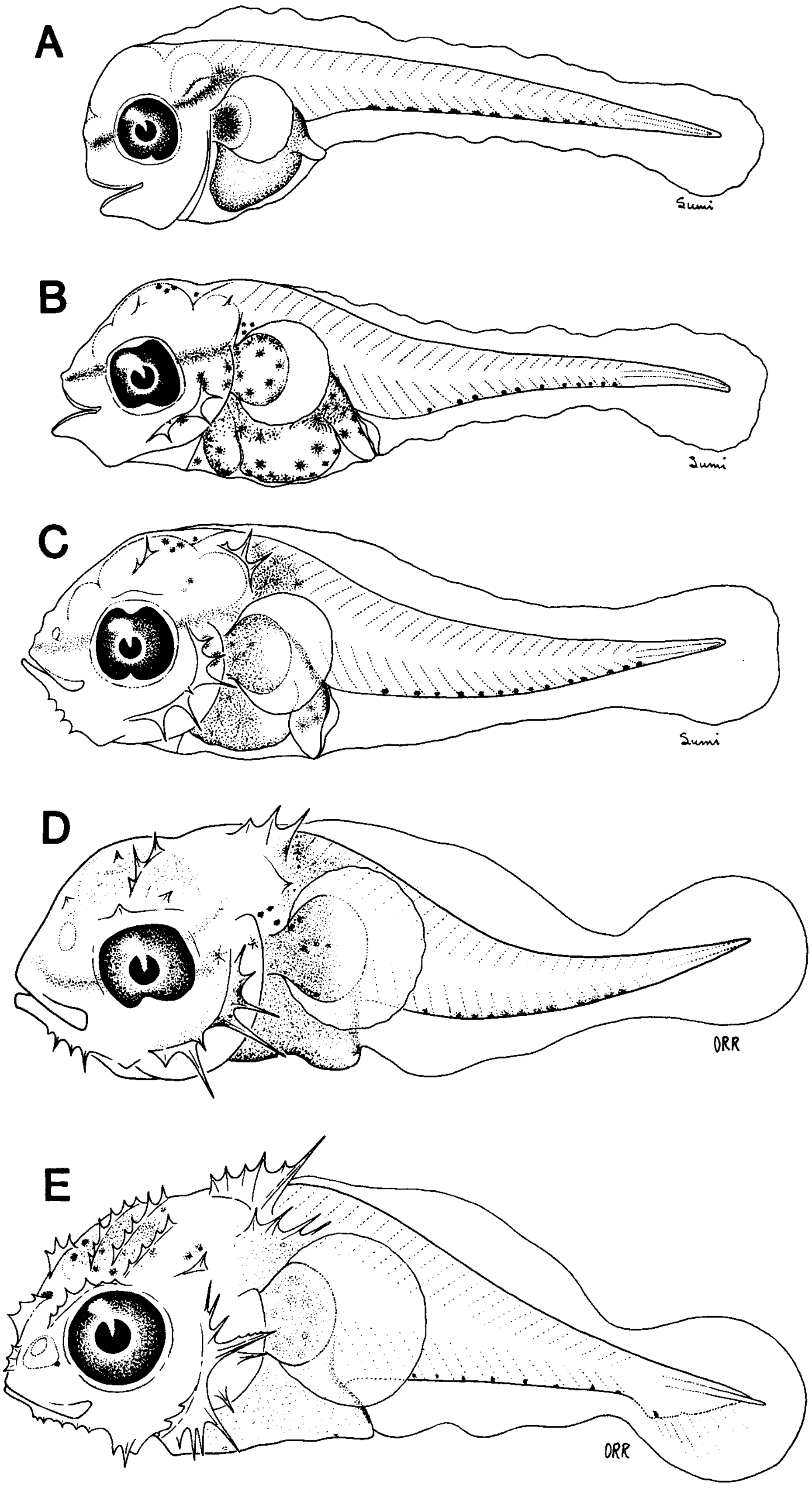

Figure 1. Preflexion larvae of *Caulolatilus princeps:* (*A*) 2.6 mm; (*B*) 3.0 mm; (*C*) 3.3 mm; (*D*) 3.8 mm; (*E*) 5.3 mm.

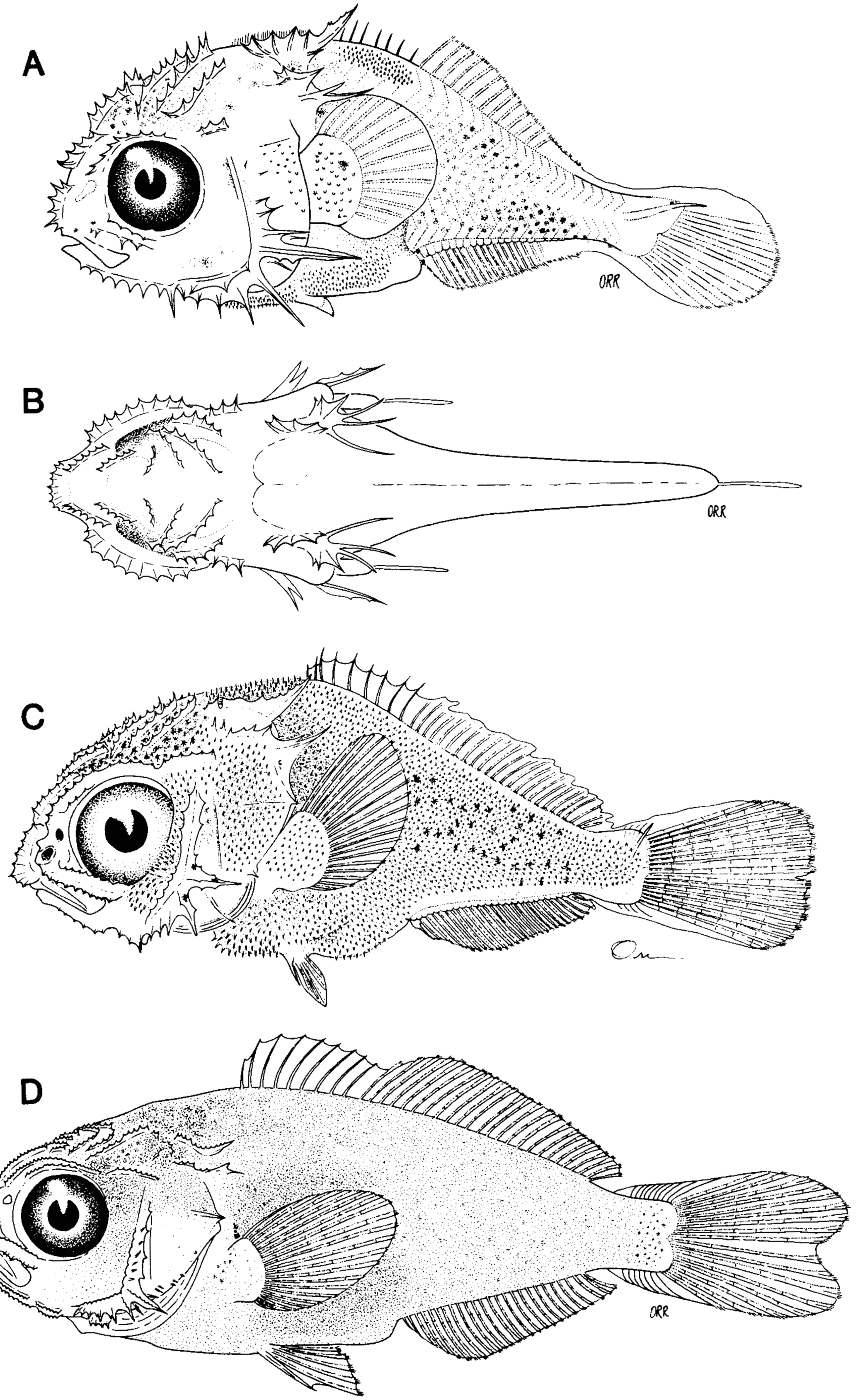

Figure 2. Developmental stages of *Caulolatilus princeps:* (*A*) 6.2-mm larva, flexion stage; (*B*) 6.2-mm larva, dorsal view; (*C*) 7.9-mm larva; (*D*) 16.8-mm pelagic juvenile.

TABLE 4
Meristics of Stained Specimens of *Caulolatilus princeps*

Length	Principal caudal fin rays		Procurrent caudal fin rays		Branchio-stegal rays		Pectoral fin rays		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
(mm)	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
3.7	—	—	—	—	1	1	—	—	—	—	—	—	—
4.0	—	—	—	—	4	4	—	—	—	—	—	—	—
4.1	—	—	—	—	3	3	—	—	—	—	—	—	—
4.2	—	—	—	—	4	4	—	—	—	—	—	—	3
4.4	—	—	—	—	5	5	—	—	—	—	—	—	6
4.5	(1)	(1)	—	—	5	5	—	—	—	—	—	—	7
4.7	(1)	(1)	—	—	5	5	—	—	—	—	—	—	7
5.0	(1)	(1)	—	—	5	5	—	—	—	—	—	—	9
5.1	(4)	(4)	—	—	6	6	(6)	(5)	(7)	(VIII,4)	—	—	13
5.3	4	4	—	—	6	6	(5)	(5)	(7)	(VIII,5)	—	—	14
5.7	(6)	(6)	—	—	6	6	(7)	(7)	(I,12)	(VIII,10)	—	—	15
6.1	(8)	(7)	—	—	6	6	—	(12)	(I,17)	(IX,17)	—	—	17
7.1	9	8	—	—	6	6	12	12	II,22	IX,20	I,3	I,3	27
7.9	9	8	4	4	6	6	19	19	II,25	IX,24	I,5	I,5	—
15.5	9	8	13	11	6	6	19	19	II,25	IX,24	I,5	I,5	—
16.8	9	8	11	11	6	6	18	18	II,24	IX,25	I,5	I,5	—
17.1	9	8	12	12	6	6	19	19	II,25	IX,26	I,5	I,5	—
38.6	9	8	13	12	6	6	19	19	II,25	IX,26	I,5	I,5	—

Specimens between dashed lines are undergoing notochord flexion. Numbers in parentheses indicate unstained fin elements.

opercle, and the opercle has one. In pelagic juveniles the spines on the ridges become less prominent, but the ridges increase in number as multiple ridges develop at the supracleithral shelf, lacrimal, dentary, and preopercular bones.

In addition to head spines, larvae of *C. princeps* develop spinous scales on the head and body. These appear initially in flexion-stage larvae as patches of small conical spines lacking the ossified scale. Flexion-stage larvae develop the following patches: (1) a linear patch on each side of the nape, (2) a linear patch on each side of the spinous dorsal fin, (3) a patch on the opercle, (4) one on the outer surface of the pectoral fin base, (5) one on the ventral midline posterior to the isthmus, (6) a rounded patch on the posteroventral surface of the gut, (7) an elongate patch on the trunk extending posteriad along the midlateral region of the tail. All of these patches enlarge in postflexion larvae, and the supporting scales become ossified. The patches at the nape and fin base enlarge to fill in the body region above the lateral line; the trunk patch enlarges to fill in the area below the lateral line. The gut patch extends anteriad and dorsad to cover the gut area, and the ventral midline patch expands in a broad triangular shape to cover that region. A patch also forms on the cheek posterior to the eye.

In early pelagic juveniles the entire body is covered with scales that have one to several spines located on their posterior regions. The head is also covered, except for the frontal ridge region and the ventral region. In late-stage pelagic juveniles each scale has typically 4-6 spines in a cluster at the posterior central region of the scale.

Fin Formation/Meristics

The first elements to ossify are the branchiostegal rays at about 3.7 mm NL (Table 4). Specimens larger than 5.0 mm NL have the full complement of 6 branchiostegal rays. The sequence of initial ossification of fin rays could not be determined because of calcium leaching during preservation; however, the appearance of unstained rays could be noted, and these are indicated in Table 4. Principal caudal rays appear at about 4.5 mm NL, and the full complement of 9 + 8 rays is present in early preflexion larvae. Procurrent caudal rays begin forming late in the postflexion stage; the full complement is formed in pelagic juveniles (Table 4). Dorsal and anal fin rays appear in 5-mm larvae, and the full complements (D. VIII-IX, 23-26; A. I-II, 23-25) are present in our largest larva (7.9 mm SL).

The pectoral fins have a large rounded base and blade in preflexion larvae. Rays begin to form in 5-mm larvae and are fully formed by the end of the larval period. The pelvic fins are the last to develop and are fully formed in postflexion larvae (Table 4). Vertebrae begin to ossify in 4-mm larvae; all centra (27) are ossifying by the end of the notochord flexion.

Pigmentation

The melanistic pigment pattern present on the smallest larvae of *C. princeps* persists throughout most of the larval period. Melanophores cover all surfaces of the gut and continue dorsally and internally to the anterior region of the trunk (Figure 1). The trunk pigment continues internally through the otic region to the base of the neurocranium and extends forward to the snout. Before the larvae reach 3.0 mm NL, melanophores appear on the nape region, the lateral and medial surfaces of the pectoral fin base, the preopercular-opercular region, the cardiac region, and on the optic and cerebellar lobes of the brain. Pigment on all of these regions intensifies during the remainder of the larval period.

A postanal series of melanophores along the ventral midline is present in the smallest larvae available (Figure 1). The series begins on the third to fifth postanal myomere and extends posteriad to the caudal fin anlage. There are typically 11-14 melanophores in the series; occasional specimens have as few as 9. At the end of the preflexion stage, the hypaxial musculature begins to mask the anterior melanophores in the series; coalescence further reduces the number so that they are not visible in specimens larger than 7.0 mm SL.

The principal change in pigmentation during later larval stages is the gradual posteriad extension of the trunk pigment to cover the entire body. This begins at about 5.0 mm NL, when the region dorsal to the gut becomes covered with large melanophores. This melanistic sheath extends posteriad to about half the distance to the caudal fin in flexion-stage larvae. The pigment sheath covers the entire body posteriad to the hypural region in the largest larva (7.9 mm SL). At this stage only the ventral region of the head and the jaws are unpigmented. The hypural region is fully pigmented in 40-mm juveniles.

DISTRIBUTION

A total of 88 occurrences of *C. princeps* larvae can be documented for CalCOFI plankton surveys during 1954-81. All but 10 of these are from the 1954-69 period, when coverage of the stations off central and southern Baja California was most complete. Ocean whitefish larvae were not identified in survey collections from 1951 through 1953; however, 7 large larvae were found in these collections during the present study. The paucity of occurrences in the surveys of 1972, 1975, and 1978 reflects the limited station coverage in central and southern Baja California during the summer months.

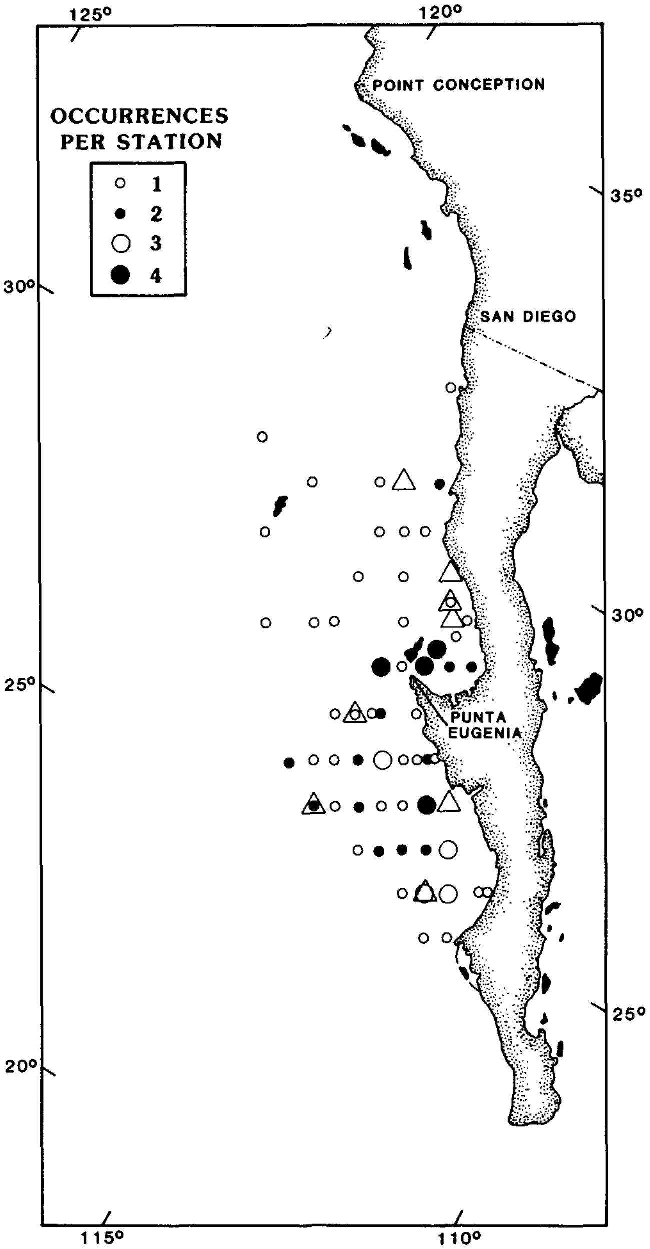

Figure 3. Pooled numbers of occurrences of *Caulolatilus princeps* larvae (circles) and pelagic juveniles taken in standard CalCOFI tows from 1954 to 1981. Triangles indicate single occurrences of pelagic juveniles.

Larvae of *C. princeps* were taken as far north as Ensenada, Baja California, (CalCOFI line 100) and south to Magdalena Bay, Baja California, (CalCOFI line 140). Lack of larvae from stations south of line 140 reflects the infrequent occupancy of stations on CalCOFI lines 143-157. The fact that only 20% of the occurrences were north of Sebastian Viscaino Bay emphasizes the warm-water affinity of ocean whitefish. Larvae were concentrated in a band within about 100 miles of the coast, although some were found at nearly twice that distance—as far seaward as station 70 on some lines (Figure 3). Pelagic juveniles were even more closely associated with the coast.

Larvae occurred principally in summer: 33% of the occurrences were in July, 25% in August. Larvae were taken in all other months except December, with the number of occurrences ranging from two to eight. Juvenile occurrences were highly clustered seasonally, with 6 of the 8 specimens coming from October cruises.

The number of specimens per tow was small ($\bar{x}$ = 1.85 ± 2.69SD), with 72% of the positive tows represented by a single larva. Larval size ranged from 1.7 mm NL to 7.9 mm SL ($\bar{x}$ = 4.3 mm NL ± 1.093SD), with a paucity of postflexion specimens: only 9 of the 126 measured specimens were larger than 6.0 mm SL. The 8 pelagic juveniles were taken on separate tows; their length measurements were 15.5, 16.8, 17.1, 27.8, 33.9, 38.6, 43.2, and 44.5 mm SL.

It is apparent from the distribution of ocean whitefish larvae that populations in southern California, and perhaps northern Baja California, are recruited from central and southern Baja California. This pattern is seen in other transboundary species like white seabass, yellowtail, and bonito. Although ocean whitefish larvae do not occur off southern California, adults of this population may contribute to production of larvae off central and southern Baja California by periodic migration. Alternatively, they may spawn unsuccessfully in southern California or may be reproductively inactive. A study of the seasonal changes in the gonads of southern California ocean whitefish could solve a part of this puzzle.

ACKNOWLEDGMENTS

The initial identification of ocean whitefish larvae was made by Elbert H. Ahlstrom. H. Orr provided illustrations for Figures 1D and E and 2A-D. Richard Charter helped with the CalCOFI data base.

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DISTRIBUTION OF FILTER-FEEDING CALANOID COPEPODS IN THE EASTERN EQUATORIAL PACIFIC

FERNANDO ARCOS
Instituto Oceanográfico de la Armada
P.O. Box 5940
Guayaquil
Ecuador

ABRAHAM FLEMINGER
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093

ABSTRACT

Zooplankton samples taken in the Eastern Equatorial Pacific between 5°N and 5°S by two Eastropac cruises (August-September 1967 and February-April 1968) were examined to determine the distribution of 21 species of epiplanktonic calanoid copepods. The distributions were considered relative to oceanographic conditions and circulations in the Eastern Equatorial Pacific Ocean. Distributional groups of species were defined by cluster analysis and correlation coefficients. The distributional groups were associated with waters influenced by the Peru Current, the warm equatorial and central waters, and the transition waters between them. The distribution patterns of the species varied in response to seasonal changes in the circulation of surface waters.

RESUMEN

Muestras de zooplancton tomadas en el Pacífico Ecuatorial Oriental entre 5°N y 5°S en dos cruceros Eastropac (agosto-septiembre 1967 y febrero-abril 1968) fueron examinadas para determinar la distribución de 21 especies de copépodos calanoídeos epipelágicos. Las distribuciones fueron consideradas en relación a las condiciones oceanográficas y a la circulación en el Océano Pacífico Ecuatorial Oriental. Los grupos de distribución estaban relacionados con masas de agua influenciadas por la corriente del Perú, aguas cálidas ecuatoriales y centrales, y masas de agua de trancisión entre ellas. Los patrones de distribución de las especies varían de acuerdo a cambios estacionales en la circulación de las aguas superficiales.

INTRODUCTION

This work focuses on the qualitative and quantitative distribution of herbivorous planktonic copepods of the mixed layer within the Eastern Equatorial Pacific (EEP), a complex region marked by surface currents, countercurrents, and undercurrents. The area studied lies off the coasts of Colombia, Ecuador, and northern Peru, and is part of the Panamic Province (Figure 1). It is overlain by tropical surface water and equatorial surface water of the Eastern Tropical Pacific (Wyrtki 1966).

Knowledge of the distribution of copepods in the EEP is relatively sparse. Works dealing with the taxonomy and geographical occurrence of calanoid copepods in this area have been published by Giesbrecht (1895) and Wilson (1950), from collections by the U.S. Fisheries steamer *Albatross*. Wilson (1942) lists species from the Carnegie expedition; later contributions to specific taxa include Bowman (1955) on *Mesocalanus*, Grice (1964) on five species from the Galápagos Islands, Fleminger (1967, 1975) on coastal-water *Labidocera*, Frost and Fleminger (1968) on *Clausocalanus*, Fleminger (1973) on *Eucalanus*, Bradford (1974) on *Euchaeta*, Fleminger and Hulsemann (1973) on *Pontellina*, and Mullin and Evans (1976) on *Neocalanus*. Of the very few descriptions and reports made for the coast of Ecuador, most are from the Gulf of Guayaquil (Johnson 1964; Fleminger 1975; Arcos 1978). Studies performed in waters

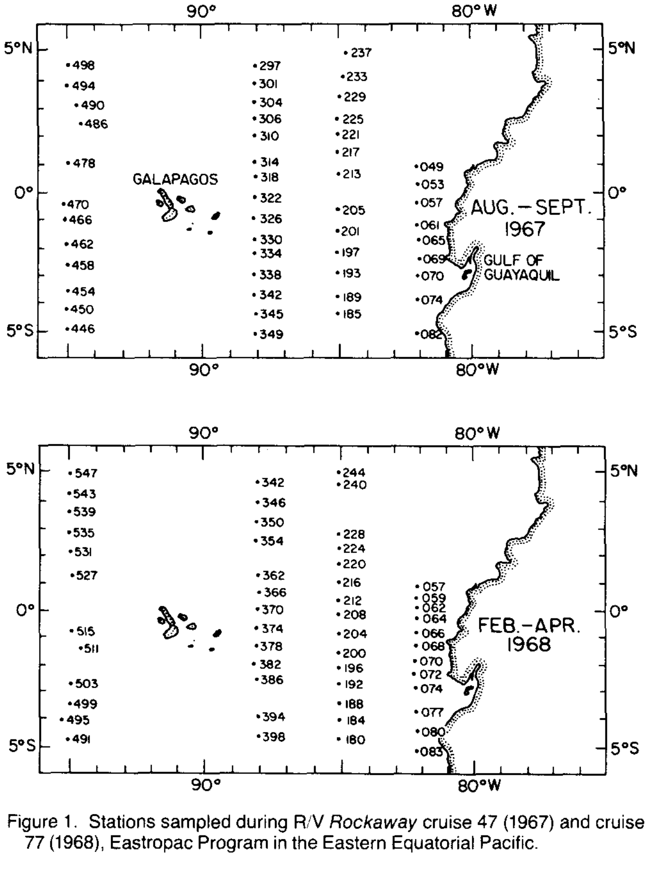

Figure 1. Stations sampled during R/V *Rockaway* cruise 47 (1967) and cruise 77 (1968), Eastropac Program in the Eastern Equatorial Pacific.

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adjacent to the area of our concern are by Heinrich (1960, 1973), who discusses horizontal distributions in the Equatorial Pacific (EP) and the Peru Current regions; by Timonin and Voronina (1977), who discuss vertical distribution related to the stratification of water masses on the equator between 100°W and 160°W; by Grice (1961), who reports on the systematics of copepods in the EP west of 120°W; by Gómez (1982), who refers to some calanoids at 9°S in the Peru Current; by Gueredrat (1971), who reports on the transpacific distribution of copepods in the upper 200 meters at the equator; by Lang (1964), who discusses systematics and distribution of the Eucalanidae in the Western and Central Pacific; by Manrique (1977), who discusses seasonal variation in the Gulf of California; and by Brinton et al. (1986), who review the plankton biota in the Gulf of California.

Of the more than 200 species of calanoids described in the literature cited above for the mixed layer in the EEP, 140 species have been reported from the area of this study (5°N-5°S and 82°W-95°W).

Here we establish the quantitative distribution of the individual species sampled by the Eastropac Program during R/V *Rockaway* cruises 47 (August-September 1967) and 77 (February-April 1968). A second objective is to determine whether the distributions display discernible patterns that are coherent with the major circulation systems of the study area.

MATERIALS AND METHODS

The zooplankton samples examined here were obtained from the region limited by 5°N and 5°S, and between 82° and 95°W, within the Eastern Equatorial Pacific. The samples were collected on two cruises of the Eastropac Program: 49 stations from R/V *Rockaway* cruise 47 in August-September 1967 and 52 stations from R/V *Rockaway* cruise 77 in February-April 1968 were examined (Figure 1). The distance between stations within the meridional lines was 70 km, and the distances between lines were 300 km east of the Galápagos, and 700 km west of the Galápagos.

The samples were taken by oblique hauls made with a 1-m zooplankton net constructed of nylon cloth (mesh aperture 0.505 mm), with approximately a 5:1 ratio (pore area to mouth area) of effective straining surface. Detailed description of the towing procedure is given by Love (1972a). The positions of the stations, as well as the numbers of organisms per 100 m^3 are given in an appendix that can be obtained by mail from either author. The estimated maximum depths of the 101 samples ranged from 100 to 266 m, with a mean of 200 m and a standard deviation of 24 m. The samples were taken at the time of arrival at the station, without regard for day or night.

The zooplankton samples were originally divided with the aid of a Folsom plankton sample splitter (McEwen et al. 1954), half of each sample being sent to the Smithsonian Institution in Washington and half deposited in the zooplankton collection of Scripps Institution of Oceanography (SIO). From the 50% fractions held by SIO, aliquots were taken using a Folsom splitter. Aliquots ranging in volume from $1/32$ to $1/2$ were taken in order to count at least 100 individuals of the most abundant species. In 80% of the cases, the two portions given by the splitter were counted independently. An overall difference of less than 10% was observed between the two portions.

The copepods analyzed and listed below were adult females of the 21 most abundant species. Two species were lumped under *Cosmocalanus* spp., and the copepodite stage V of *Calanus chilensis* was also counted because of its high abundance in some samples.

Calanus chilensis Brodsky
Calanus chilensis copepodites stage V
Centropages calaninus (Dana)
Centropages furcatus (Dana)
Centropages gracilis (Dana)
Cosmocalanus spp.
Eucalanus hyalinus (Claus)
Eucalanus inermis Giesbrecht
Mesocalanus tenuicornis (Dana)
Nannocalanus minor (Claus)
Neocalanus gracilis (Dana)
Neocalanus robustior (Giesbrecht)
Pareucalanus attenuatus (Dana)
Pareucalanus sewelli (Fleminger)
Rhincalanus nasutus Giesbrecht
Rhincalanus rostrifrons (Dana)
Subeucalanus pileatus (Giesbrecht)
Subeucalanus subcrassus (Giesbrecht)
Subeucalanus subtenuis (Giesbrecht)
Temora discaudata Giesbrecht
Undinula vulgaris (Dana)

Over 64,000 organisms were identified and counted under a dissecting microscope, the mean per sample being 634 individuals (range, 132 to 3879). Most of the species studied are easy to identify. In the case of eucalanids, when the identification was uncertain, the specimens were sorted for examination of the pore signature. This procedure, described by Fleminger (1973), readily permits one to distinguish species of Eucalanidae.

The number of organisms calculated for each sample was standardized to the volume of 100 m^3. The mean volume of water filtered during the field sampling was 620 m^3.

The samples were arranged into assemblages using the Ward method (Anderberg 1973) for cluster analysis from a pool of 2,020 values. The program forms successively fewer, larger, groups until the total number of samples has been reduced to a small number of assemblages (in the extreme, one assemblage consists of all samples). As the number of assemblages is allowed to decrease in this process by agglomeration of samples, the faunal variability included within each assemblage increases, but the spatial pattern of assemblages becomes easier to visualize and interpret. The method deals with the sum of Euclidean distances (SED) between stations; the same level of SED was used for the two cruises. Pearson's correlation coefficient (Sokal and Rohlf 1981) was used for evaluating the correlations between species.

Water temperatures were available at 1-m intervals from the surface to about 750-m depth for each station at which an STD determination of salinity and temperature was made. Since most of the copepods studied are distributed in the upper 50 m, the values of temperature and salinity were integrated for the 0-50-m water column. For the integration we used six values at 10-m intervals.

The Eastropac atlases (Love 1972a, b and 1975; Love and Allen 1975) presented the physical, chemical, and biological information of the region. M. Tsuchiya provided unpublished tabulated data of temperature and salinity.

SYSTEMATIC NOTE

There is general acceptance of the systematic status of most of the species observed, but we want to comment on the use of the genera *Subeucalanus* and *Pareucalanus*.

Fleminger (1973) divided the species of the genus *Eucalanus* s.l. Dana into four groups based on the pattern of integumental pore distributions. These are (1) the subtenuis group (*E. subtenuis, E. mucronatus, E. crassus, E. longiceps*, and *E. monachus*); (2) the pileatus group (*E. pileatus, E. subcrassus*, and *E. dentatus*); (3) the elongatus group (*E. elongatus, E. hyalinus, E. inermis, E. bungii*, and *E. californicus*); and (4) the attenuatus group (*E. attenuatus, E. sewelli, E. parki*, and *E. langae*). Geletin (1976) subsequently defined three genera based on the fifth legs of males, and abdomen morphology of females: *Eucalanus* s.s. represents the elongatus group, *Subeucalanus* the subtenuis and pileatus groups, and *Pareucalanus* the attenuatus group. This revision was further supported by Bjornberg's (1986) study of the morphological characteristics of the nauplii. Since these independent characters suggest the same taxonomical groupings, we accept Geletin's genera.

In the area of study there are two species of *Cosmocalanus*—*C. darwini* (Lubbock) and *C. caroli* (Giesbrecht)—that overlap in their distribution. There are morphological characteristics to separate the adult males, but not the females, so the two species were united together as *Cosmocalanus* spp.

Hydrography of Studied Area, 1967 and 1968

A number of oceanographic expeditions have studied the Eastern Equatorial Pacific and delineated its principal oceanographic features (e.g., Wooster and Cromwell 1958; Austin 1960; Knauss 1960, 1966; Bennett 1963; Wyrtki 1966, 1967, 1977; Tsuchiya 1968, 1970, 1972, 1974, 1985; Stroup 1969; Donguy and Rotschi 1970; Leetmaa 1982; Leetmaa et al. 1981; Lukas 1981; Moreano 1983).

The main surface current in our area of study is the South Equatorial Current (SEC) moving to the west, with the northern limit at 4°N and the southern at 10°S (Wyrtki 1977). This current is fed from the northeast by a branch of the North Equatorial Countercurrent (NECC) that flows to the east, strikes the coast of Central America, and advects water northward to Costa Rica, and southward from the Panama Bight to the south and west. From the southeast the SEC meets the Peru Current, which flows to the north along the coast of Peru and then turns west toward the Galápagos, forming the limit of the Equatorial Front as it encounters the warm surface tropical waters from the north (Wooster 1969).

The SEC carries a tremendous volume of water that is supplemented by water coming from the Equatorial Undercurrent (EU) in addition to that supplied by the NECC and the Peru Current (Wyrtki 1977). Tsuchiya (1972, 1975) describes the circulation of the subsurface currents, pointing out the presence of the EU, originally described by Cromwell et al. (1954), flowing eastward along the equator, and the presence of the north and south Equatorial Subsurface countercurrents having the same direction and lying at 3°-6°N and 4°-8°S, respectively.

Figures 2 and 3 show the surface temperature and salinity for August-September 1967 and February-April 1968. From these charts one can visualize the Equatorial Front (EF) defined by the 20° and 25°C isotherms. The EF is normally weak or absent in February-March, as can be seen in monthly average sea-surface temperature maps (e.g., Wyrtki 1964; Robinson 1976). In February-March 1968, the front was present east of the Galápagos Islands. The upper layer temperature off South America was lower than normal in this period, and the development of the cold water mass east of the Galápagos (Figure 2) was unusually strong, resulting in a fairly intense front.

In 1967 warmer and less saline water remained north of the EF, and cooler and more saline waters were to

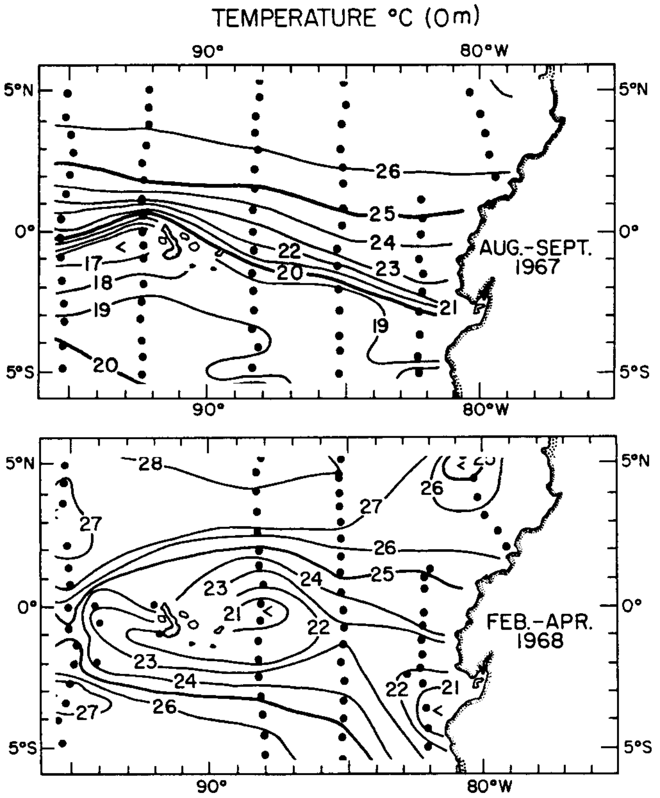

Figure 2. Distribution of surface temperature in the Eastern Equatorial Pacific in 1967 and 1968, reproduced from Love (1972a,b, 1975).

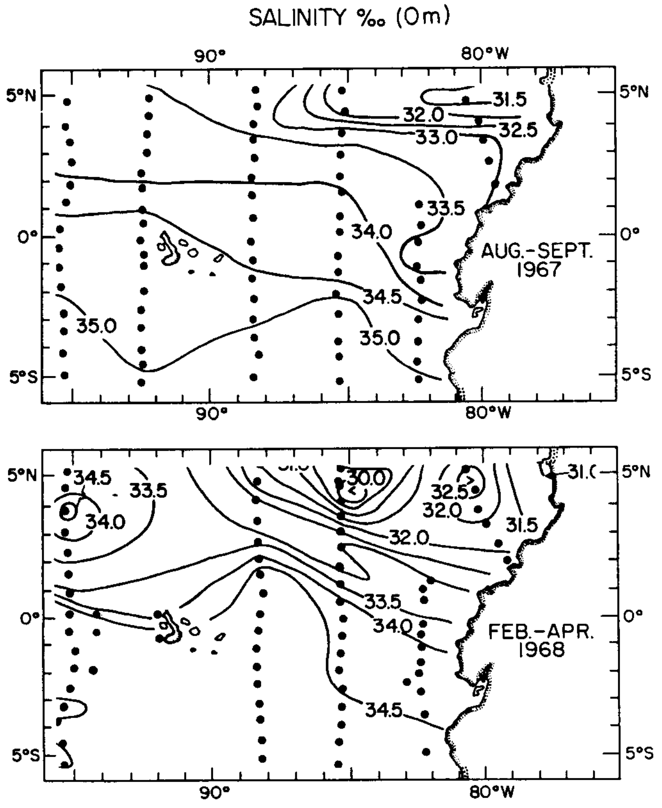

Figure 3. Distribution of surface salinity in the Eastern Equatorial Pacific in 1967 and 1968, reproduced from Love (1972a,b, and 1975).

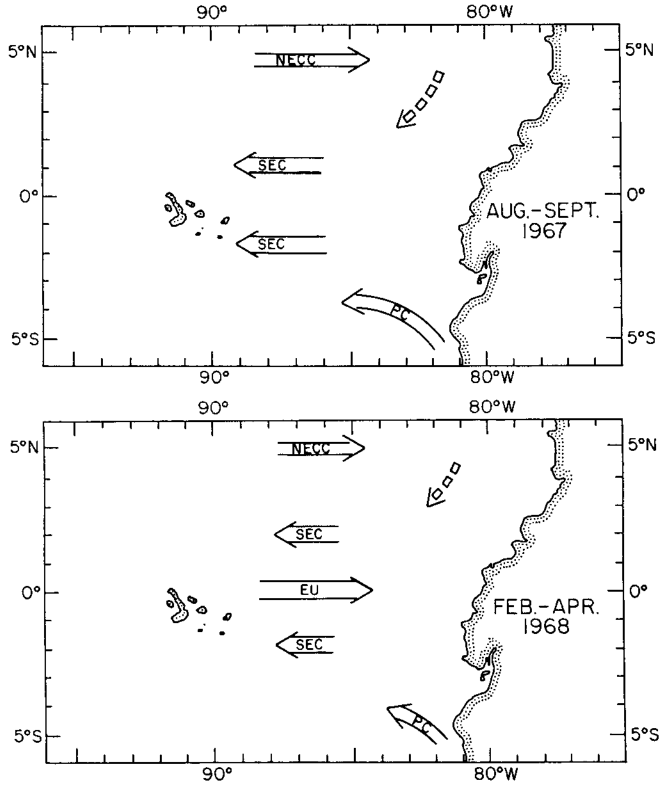

Figure 4. Trends of circulation of surface waters in the Eastern Equatorial Pacific in 1967 and 1968. See text for references.

the south. In 1968 temperatures lower than 21°C were not found; the 25°C isotherm was located at 1°N and 5°S in the east, and at 1°N and 2°S in the west. Waters warmer than 25°C were found north and south of the limits of that isotherm, with lower salinity to the north and higher salinity to the south.

In 1967 there was an indication of upwelling southwest of the Galápagos (Ahlstrom 1972), and in 1968 upwelling was evident east of the Galápagos and south of the Gulf of Guayaquil (Wyrtki et al. 1976; Moreano 1983).

The general trend of circulation (Figure 4) is based on data from Sverdrup et al. (1942), Wyrtki (1966, 1967), Tsuchiya (1972, 1975), Zambrano (1980), Sund et al. (1981), Moreano (1983), and Okuda et al. (1983). The North Equatorial Countercurrent, the South Equatorial Current and the Peru Current were stronger in 1967 than in 1968. Another primary difference between these two cruises is the surfacing in the latter of the Equatorial Undercurrent as it flows eastward along the equator (Jones 1969).

RESULTS

Abundance

Table 1 shows the mean abundance of species for all stations in each of the cruises. The most abundant species, exceeding 150 organisms (org.)/100m^3, for

TABLE 1
Mean Abundance of Individual Species (Org./100m^3) in August-September 1967 and February-April 1968

	1967	1968
Calanus chilensis	388	478
Calanus chilensis (stage V)	249	4,137
Centropages calaninus	1	0
Centropages furcatus	44	154
Centropages gracilis	—	2
Cosmocalanus spp.	188	150
Eucalanus hyalinus	—	1
Eucalanus inermis	11	74
Mesocalanus tenuicornis	34	29
Nannocalanus minor	249	495
Neocalanus gracilis	3	4
Neocalanus robustior	0	1
Pareucalanus attenuatus	9	4
Pareucalanus sewelli	66	50
Rhincalanus nasutus	260	116
Rhincalanus rostrifrons	12	8
Subeucalanus pileatus	39	20
Subeucalanus subcrassus	40	87
Subeucalanus subtenuis	374	202
Temora discaudata	71	144
Undinula vulgaris	14	12

TABLE 2
Occurrences of Individual Species for Each Cruise

	1967	**1968**	**Total**
Number of stations	49	52	101
Calanus chilensis	11	7	18
Calanus chilensis (stage V)	9	11	20
Centropages calaninus	8	2	10
Centropages furcatus	47	49	96
Centropages gracilis	16	14	30
Cosmocalanus spp.	47	45	92
Eucalanus hyalinus	9	12	21
Eucalanus inermis	18	27	45
Mesocalanus tenuicornis	45	47	92
Nannocalanus minor	49	52	101
Neocalanus gracilis	23	16	39
Neocalanus robustior	5	9	14
Pareucalanus attenuatus	18	17	35
Pareucalanus sewelli	48	48	96
Rhincalanus nasutus	34	41	75
Rhincalanus rostrifrons	33	31	64
Subeucalanus pileatus	34	30	64
Subeucalanus subcrassus	38	47	85
Subeucalanus subtenuis	49	51	100
Temora discaudata	46	45	91
Undinula vulgaris	27	24	51

the two cruises are *Calanus chilensis* (adults and stage V copepodites) (Figures 5 and 6), *Nannocalanus minor* (Figure 7), *Subeucalanus subtenuis* (Figure 8), *Rhincalanus nasutus* (Figure 9), and *Cosmocalanus* spp. (Figure 10). Intermediate abundance values, between 40 and 150 org./100m^3, are found for *Temora discaudata* (Figure 11), *Centropages furcatus* (Figure 12), *Pareucalanus sewelli* (Figure 13), *Eucalanus inermis* (Figure 14), and *Subeucalanus subcrassus* (Figure 15). Species showing the lowest abundance, below 40 org./100m^3, are *Mesocalanus tenuicornis* (Figure 16), *Subeucalanus pileatus* (Figure 17), *Undinula vulgaris* (Figure 18), *Rhincalanus rostrifrons* (Figure 19), *Pareucalanus attenuatus* (Figure 20), *Neocalanus gracilis* (Figure 21), *Centropages gracilis* (Figure 22), *Eucalanus hyalinus* (Figure 23), *Neocalanus robustior* (Figure 24), and *Centropages calaninus* (Figure 25).

Frequency

Table 2 shows the number of occurrences of each species from the total of samples studied and from each cruise. Species represented in more than 50% of the samples are *Nannocalanus minor, Subeucalanus subtenuis, Pareucalanus sewelli, Centropages furcatus, Cosmocalanus* spp., *Mesocalanus tenuicornis, Temora discuadata, Subeucalanus subcrassus, Rhincalanus nasutus, Subeucalanus pileatus, Rhincalanus rostifrons,* and *Undinula vulgaris*. Species represented in less than 20% of the samples are *Calanus chilensis* (adults and juveniles), *Neocalanus robustior,* and *Centropages calaninus*.

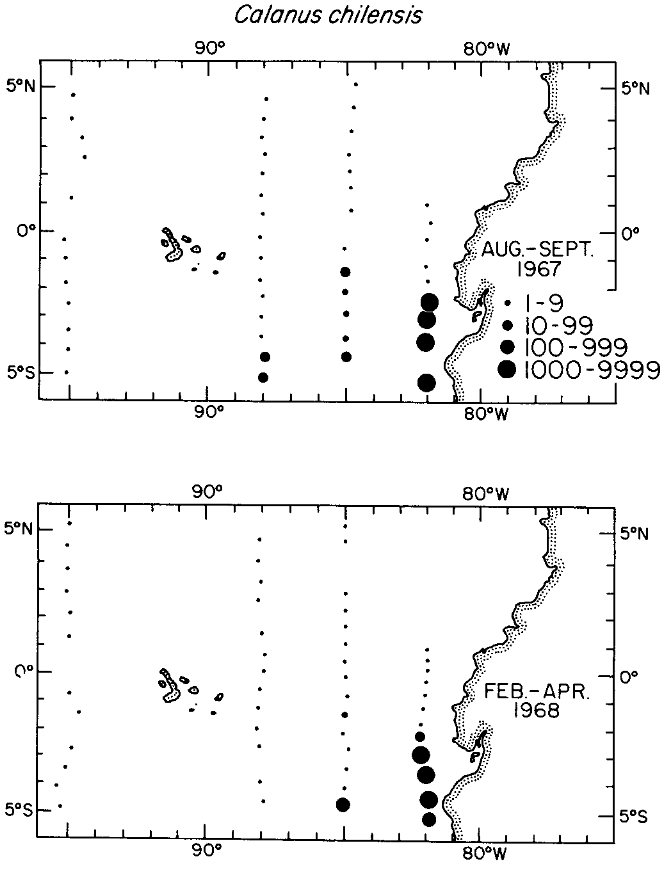

Figure 5. Distribution of abundance of adult females of *Calanus chilensis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

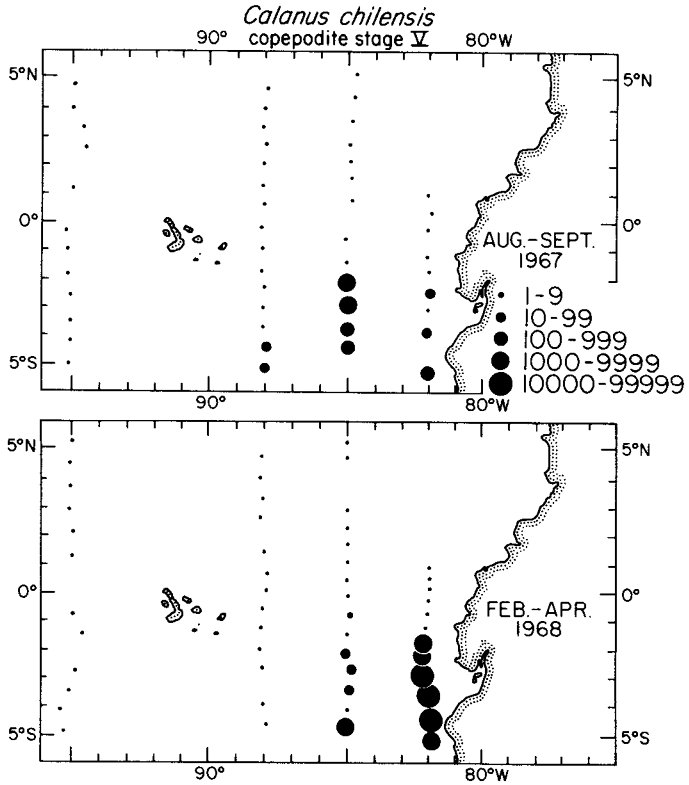

Figure 6. Distribution of abundance of *Calanus chilensis* stage V copepodites in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

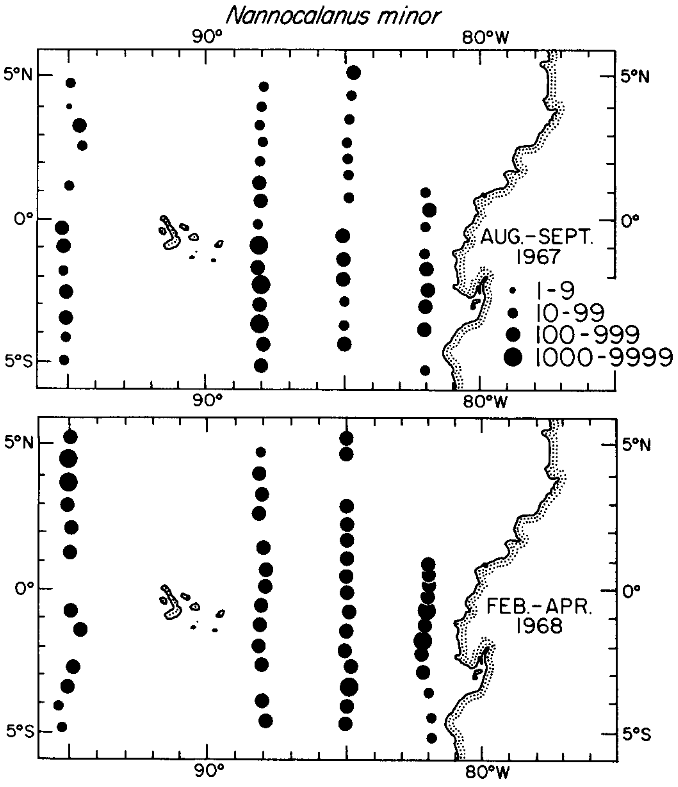

Figure 7. Distribution of abundance of adult females of *Nannocalanus minor* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

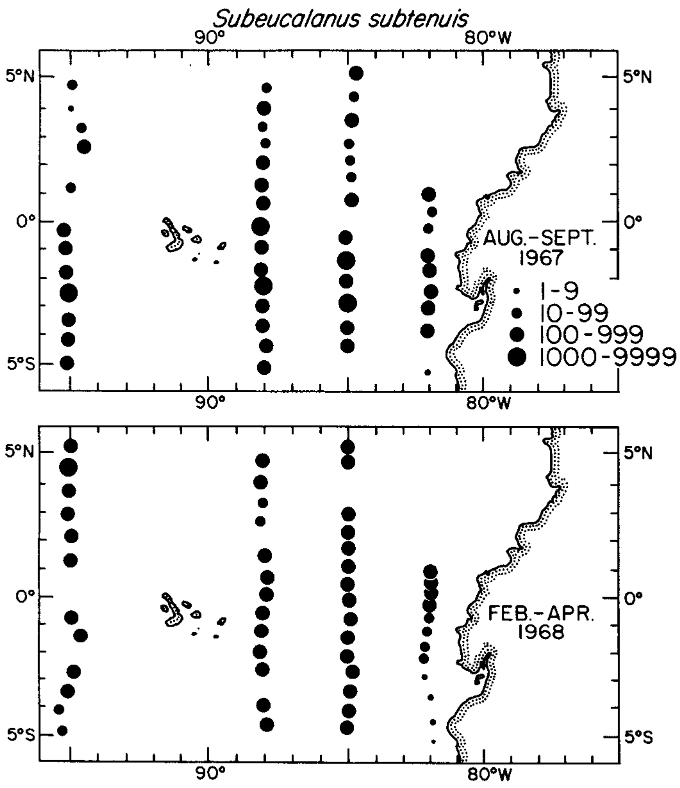

Figure 8. Distribution of abundance of adult females of *Subeucalanus subtenuis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

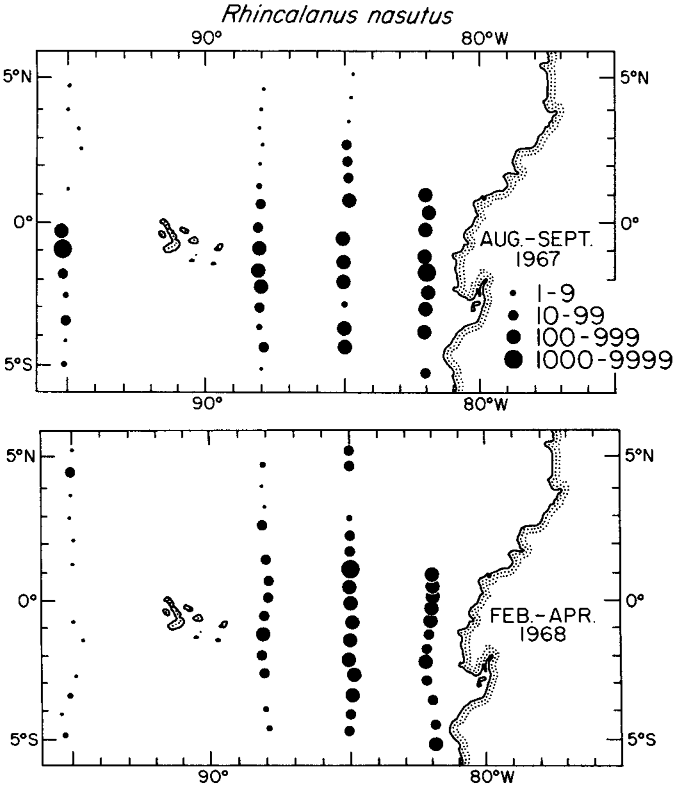

Figure 9. Distribution of abundance of adult females of *Rhincalanus nasutus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

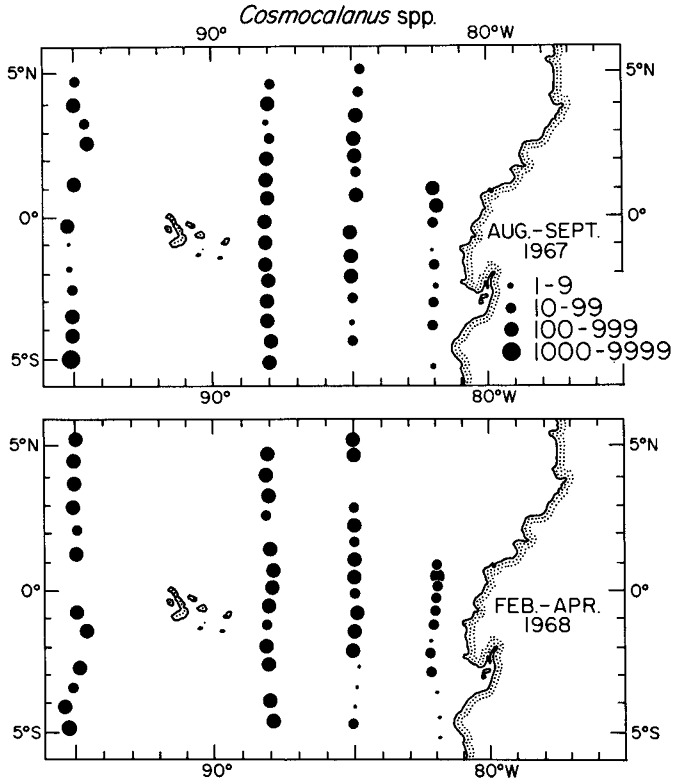

Figure 10. Distribution of abundance of adult females *Cosmocalanus* spp. in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

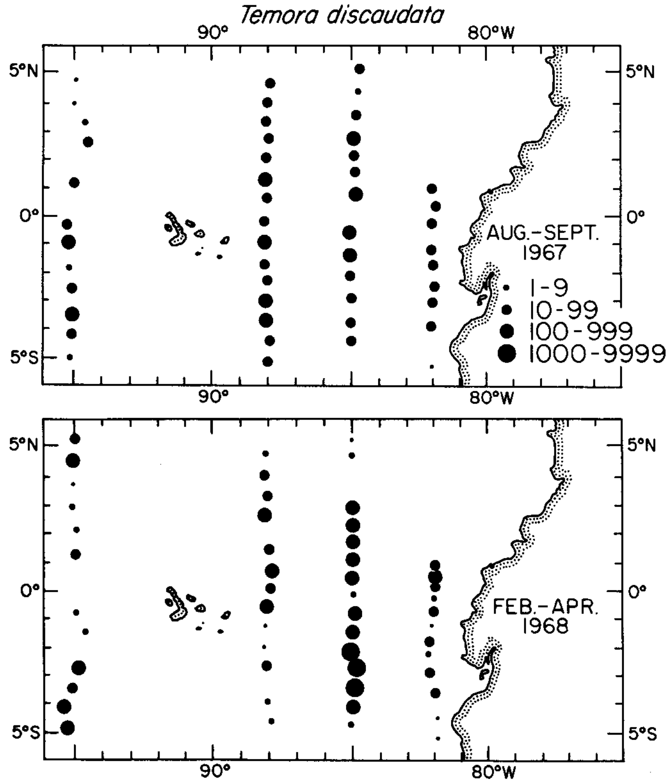

Figure 11. Distribution of abundance of adult females of *Temora discaudata* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

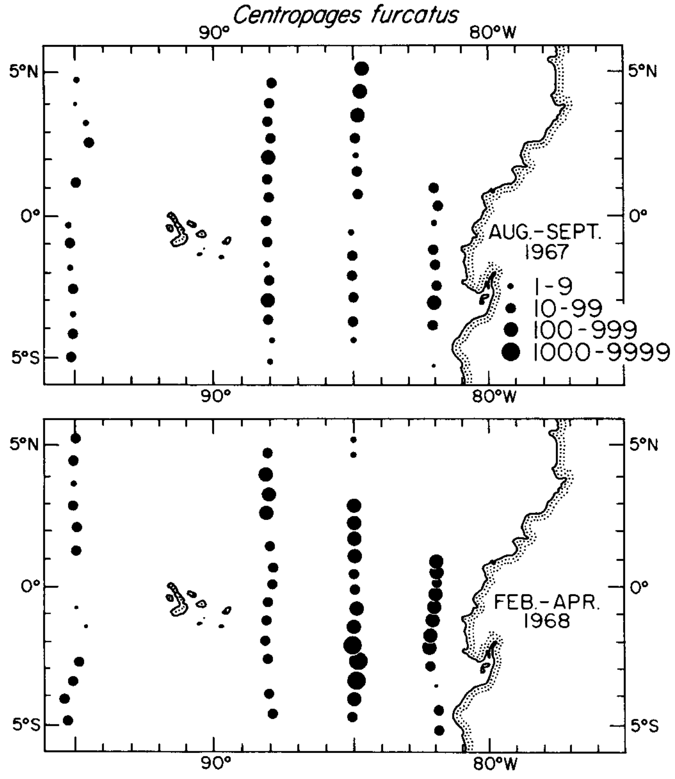

Figure 12. Distribution of abundance of adult females of *Centropages furcatus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

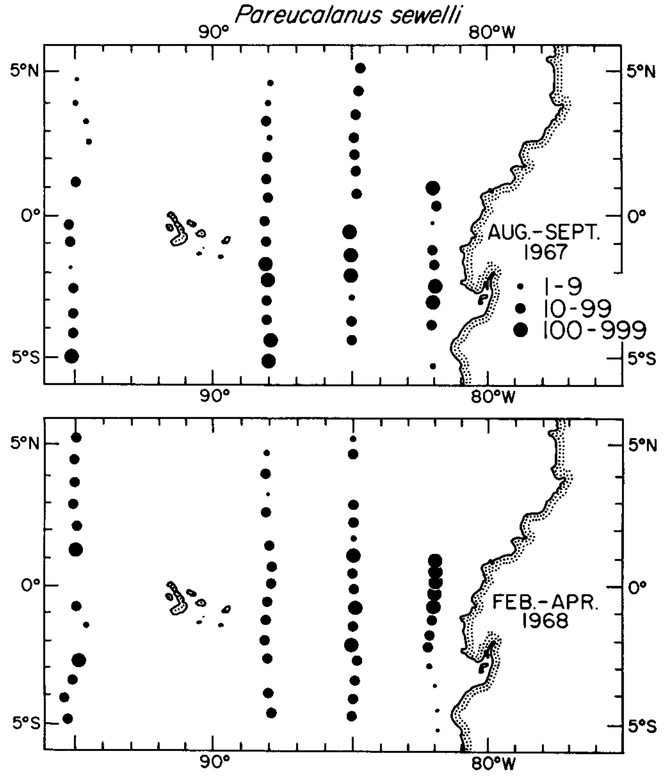

Figure 13. Distribution of abundance of adult females of *Pareucalanus sewelli* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

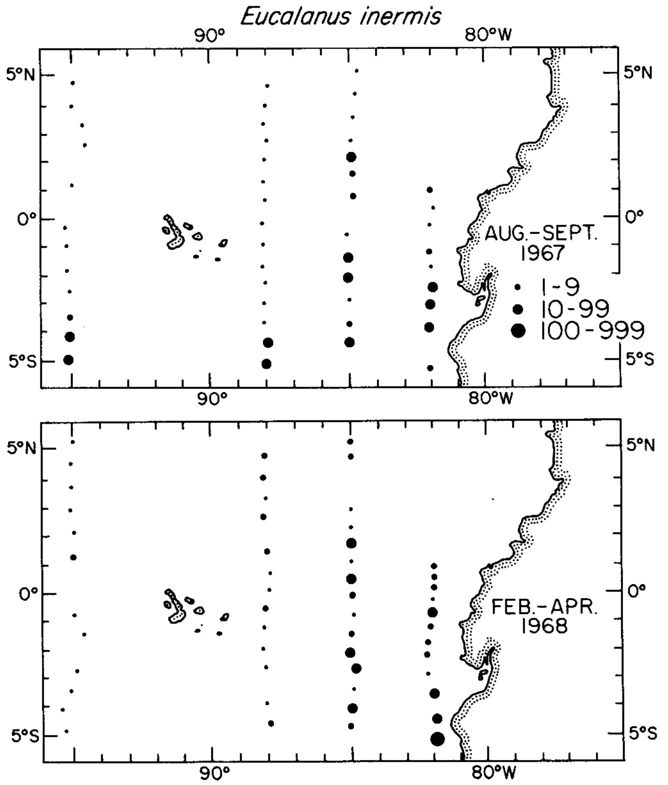

Figure 14. Distribution of abundance of adult females of *Eucalanus inermis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

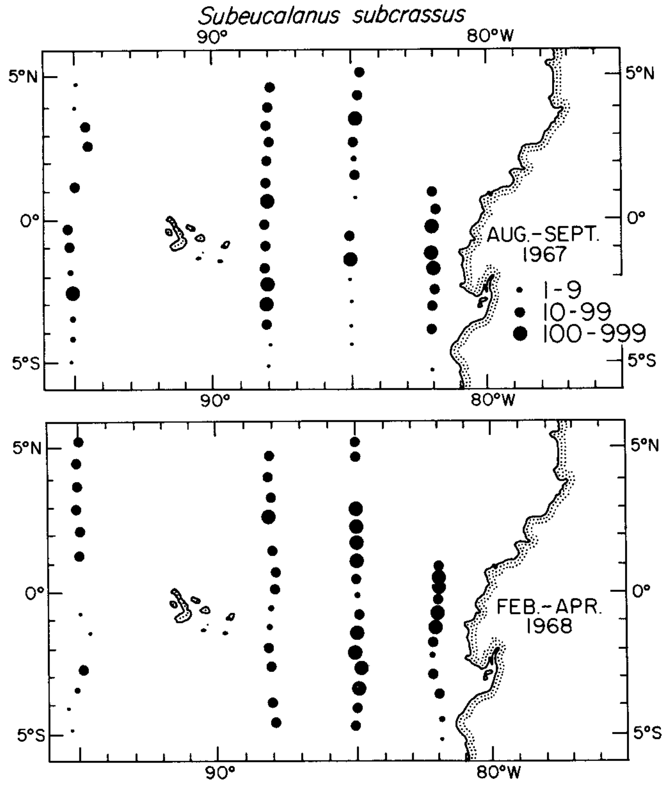

Figure 15. Distribution of abundance of adult females of *Subeucalanus subcrassus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

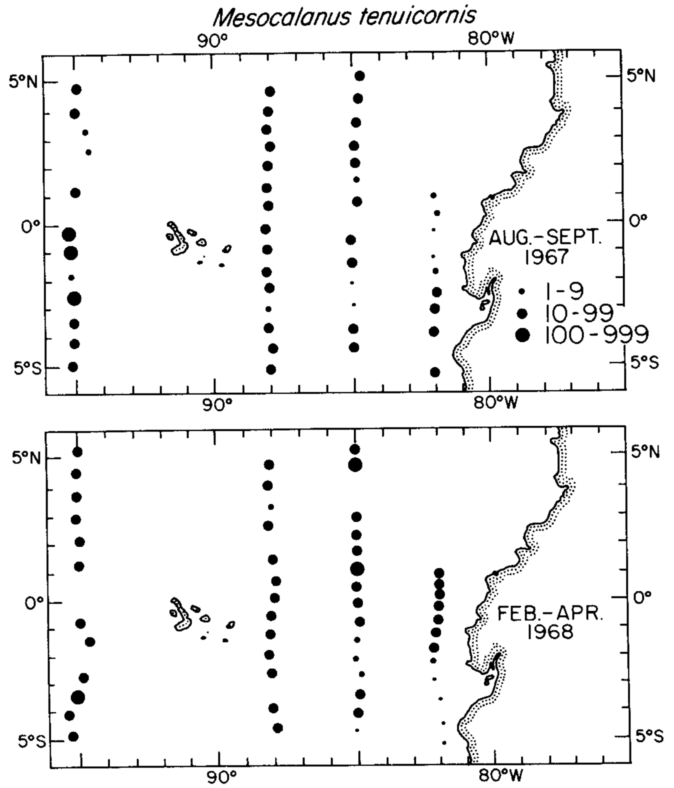

Figure 16. Distribution of abundance of adult females of *Mesocalanus tenuicornis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

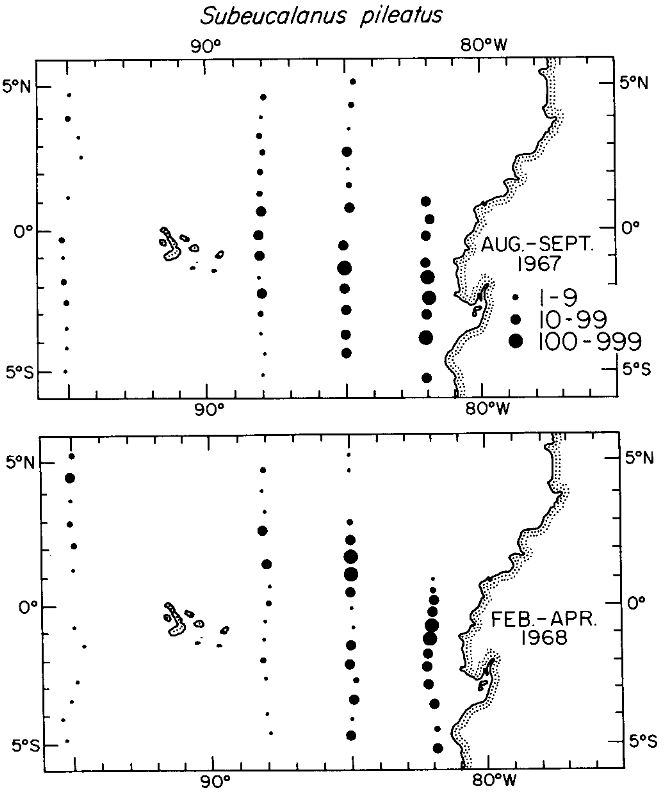

Figure 17. Distribution of abundance of adult females of *Subeucalanus pileatus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

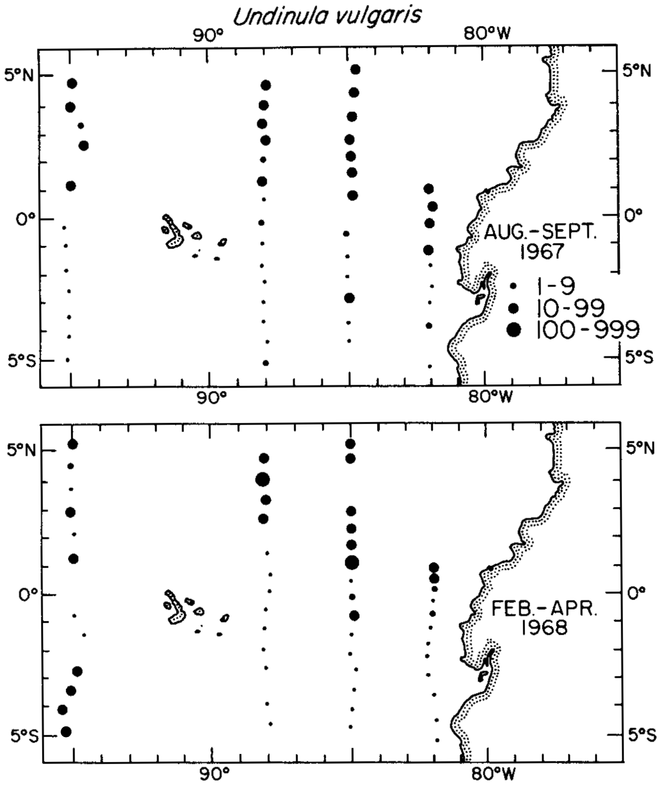

Figure 18. Distribution of abundance of adult females of *Undinula vulgaris* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

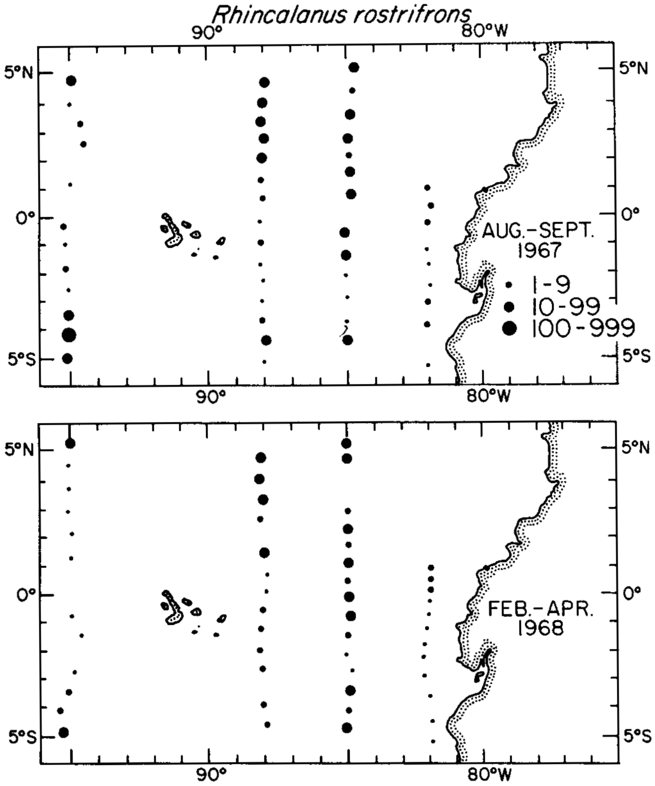

Figure 19. Distribution of abundance of adult females of *Rhincalanus rostrifrons* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

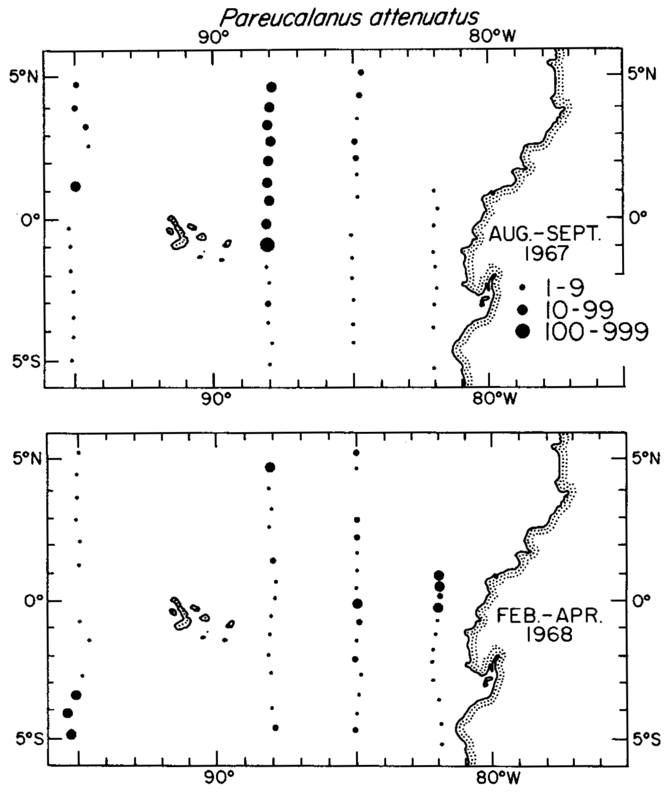

Figure 20. Distribution of abundance of adult females of *Pareucalanus attenuatus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

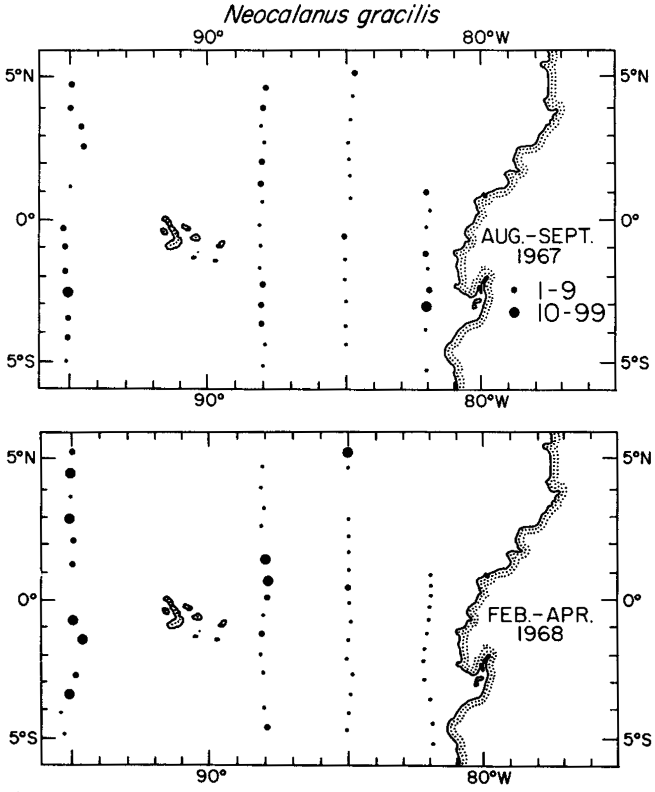

Figure 21. Distribution of abundance of adult females of *Neocalanus gracilis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

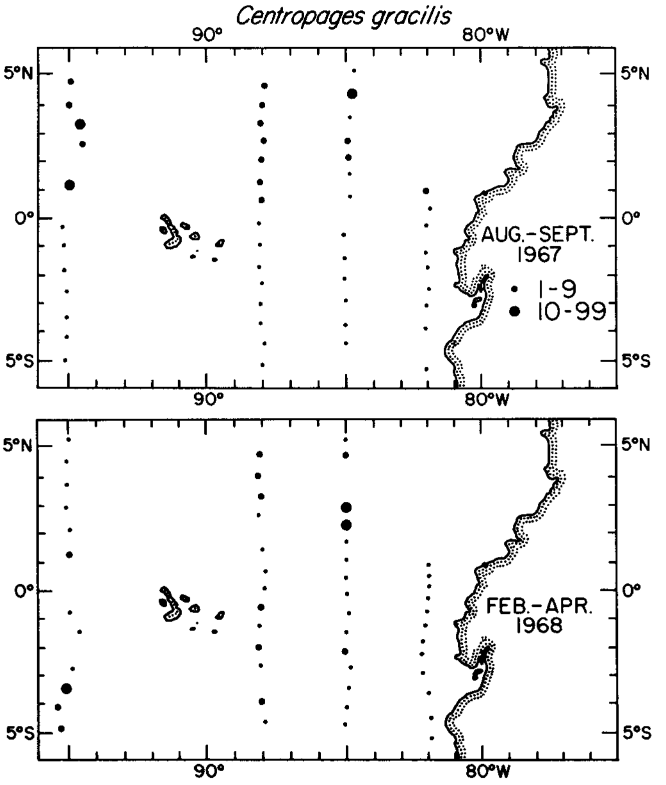

Figure 22. Distribution of abundance of adult females of *Centropages gracilis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

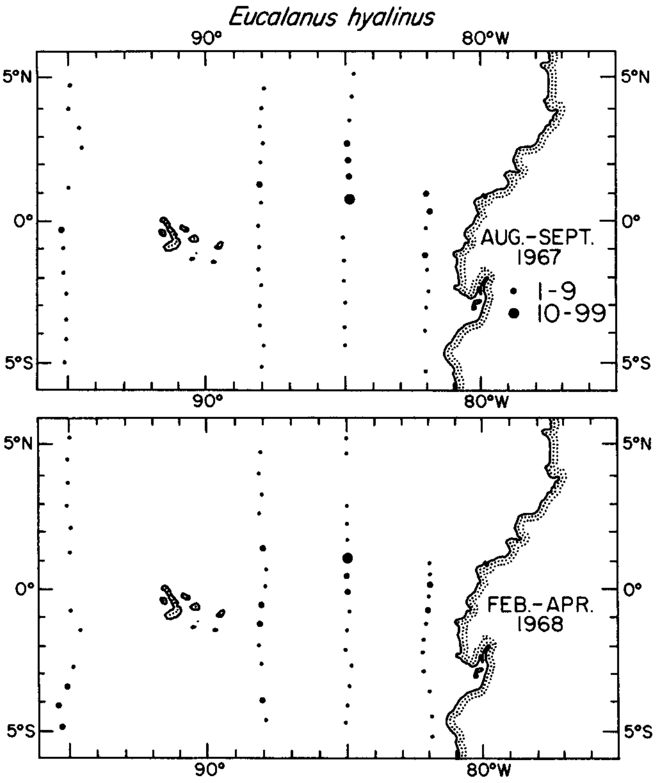

Figure 23. Distribution of abundance of adult females of *Eucalanus hyalinus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

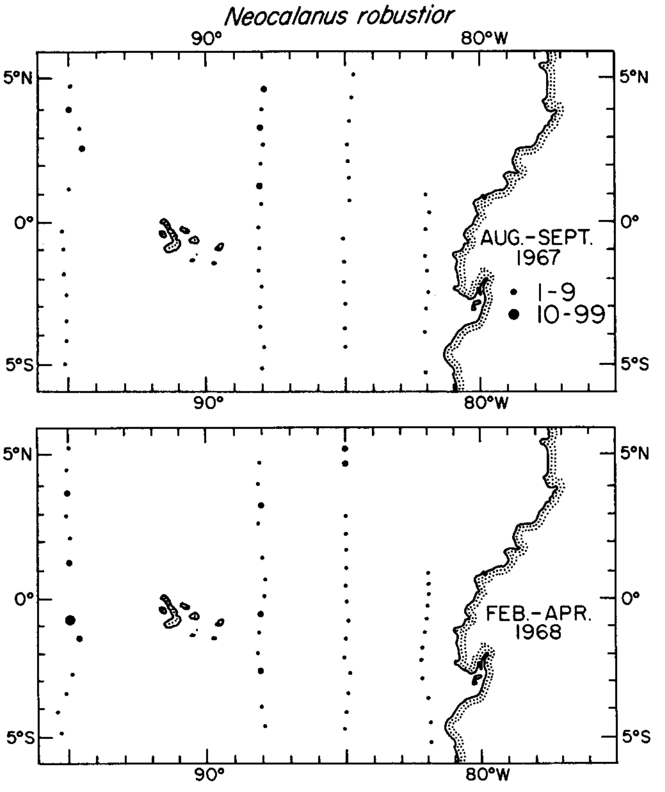

Figure 24. Distribution of abundance of adult females of *Neocalanus robustior* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

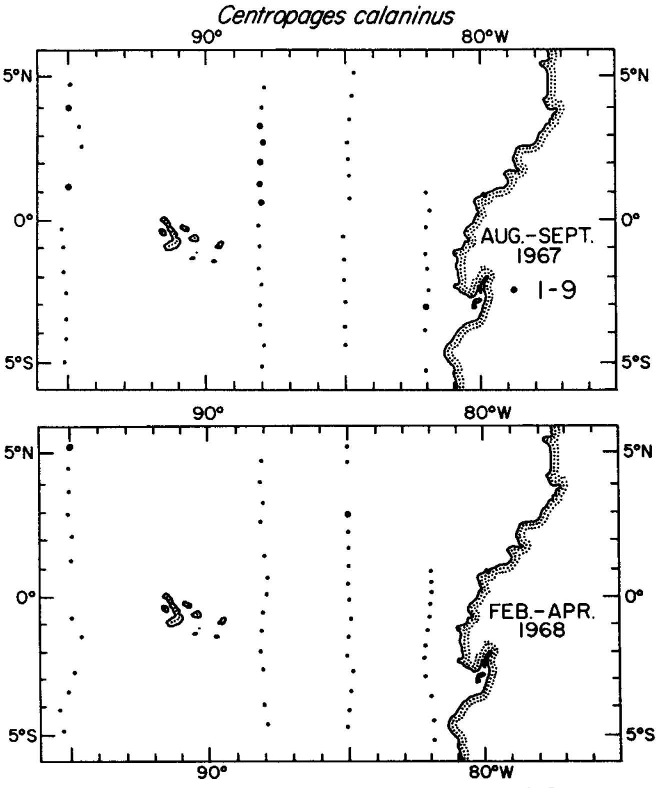

Figure 25. Distribution of abundance of adult females of *Centropages calaninus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

TABLE 3
Mean Abundance (Org./100m^3) in Night and Day Samples

	Night	Day
Calanus chilensis	270	111
Calanus chilensis (stage V)	639	853
Cosmocalanus spp.	248	176
Centropages calaninus	1	1
Centropages furcatus	120	104
Centropages gracilis	1	3
Eucalanus hyalinus	1	1
Eucalanus inermis	25	10
Mesocalanus tenuicornis	39	37
Nannocalanus minor	511	319
Neocalanus gracilis	4	4
Neocalanus robustior	1	1
Pareucalanus attenuatus	9	6
Pareucalanus sewelli	70	58
Rhincalanus nasutus	289	144
Rhincalanus rostrifrons	13	11
Subeucalanus pileatus	38	20
Subeucalanus subcrassus	80	49
Subeucalanus subtenuis	360	306
Temora discaudata	126	147
Undinula vulgaris	17	14

Day-Night Observations

Stations were divided according to day (0600-1759 h) and night (1800-0559 h) time of sampling, yielding 49 and 52 stations, respectively. Table 3 shows the mean abundance of each species in day and night samples. As expected, there were more organisms caught during the night. The overall difference of the total number of organisms between day and night was 19%. The day-night variability is less than station-to-station variability, and the diurnal variation of organisms shows no effect on the spatial coherence of the areas grouped in the analysis described below.

Differences between Cruises

Although some differences both in abundance and frequency are observable within the cruises, the numerical relationships among the species are very similar for both; that is, species correlated in 1967 were also correlated in 1968. Pearson's correlation coefficients were obtained, and the positive correlations between species with a significance of .01 or .001 are shown in Figure 26. There was almost total consistency of correlations within cruises. Of the 46 and 48 significant positive correlations in 1967 and 1968, all but 6 occurred during both years.

Dendrograms of Ward's Cluster Analysis

The sum of Euclidean distances (SED) provides information on differences between samples of relative rather than absolute abundance of species. The dendrograms of SED between stations grouped the stations in three major clusters (Figures 27 and 28). The stations grouped by the clusters have been plotted in the maps in order to determine the areas formed for each of the clusters. The three areas defined for each cruise are referred to as areas A, B, and C (Figure 29). The clusters were formed by the same species in both cruises, bearing out the correlations between species for the two cruises.

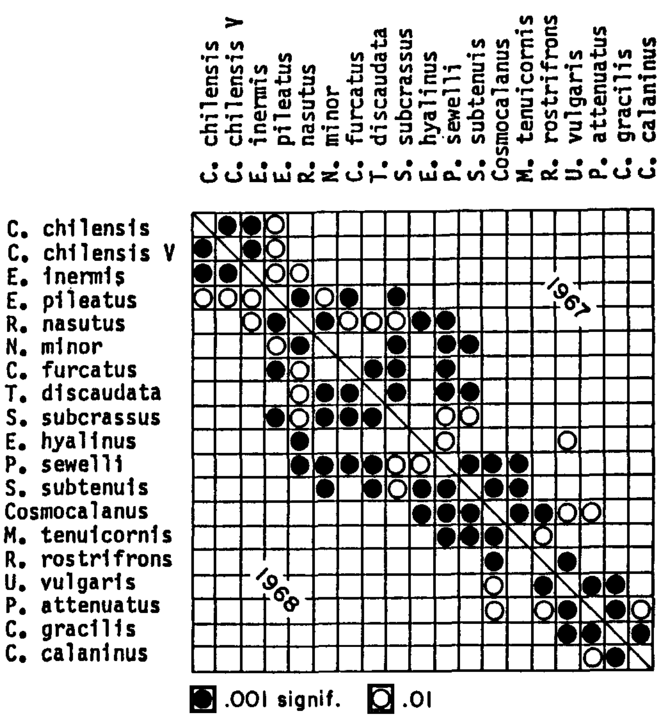

Figure 26. Significant positive Pearson's correlation coefficients between species in 1967 and 1968.

Area A is restricted to the southeast of the sampled area in both cruises; in 1967 this area extends farther westward than in 1968.

Area B in 1967 is almost parallel to area A, extending up to the equator. In 1968 area B is somewhat U-shaped, with the base facing the coast and the branches extending westward north and south of the equator; the northern branch extends farther westward. The northwest patch of area B is characterized by the species *Subeucalanus pileatus* and *Rhincalanus nasutus*, which share the highest abundance in both portions of area B.

Area C in 1967 occupies the northern region, limited zonally at the south by area B. In 1968, area C is found at the north, west, and southwest, surrounding most of area B, and meeting area A in the southeast.

Dendrograms of SED and Areas Formed by Deleting Neritic Species

To test the possibility that species of neritic origin may obscure the groups given by Ward's cluster

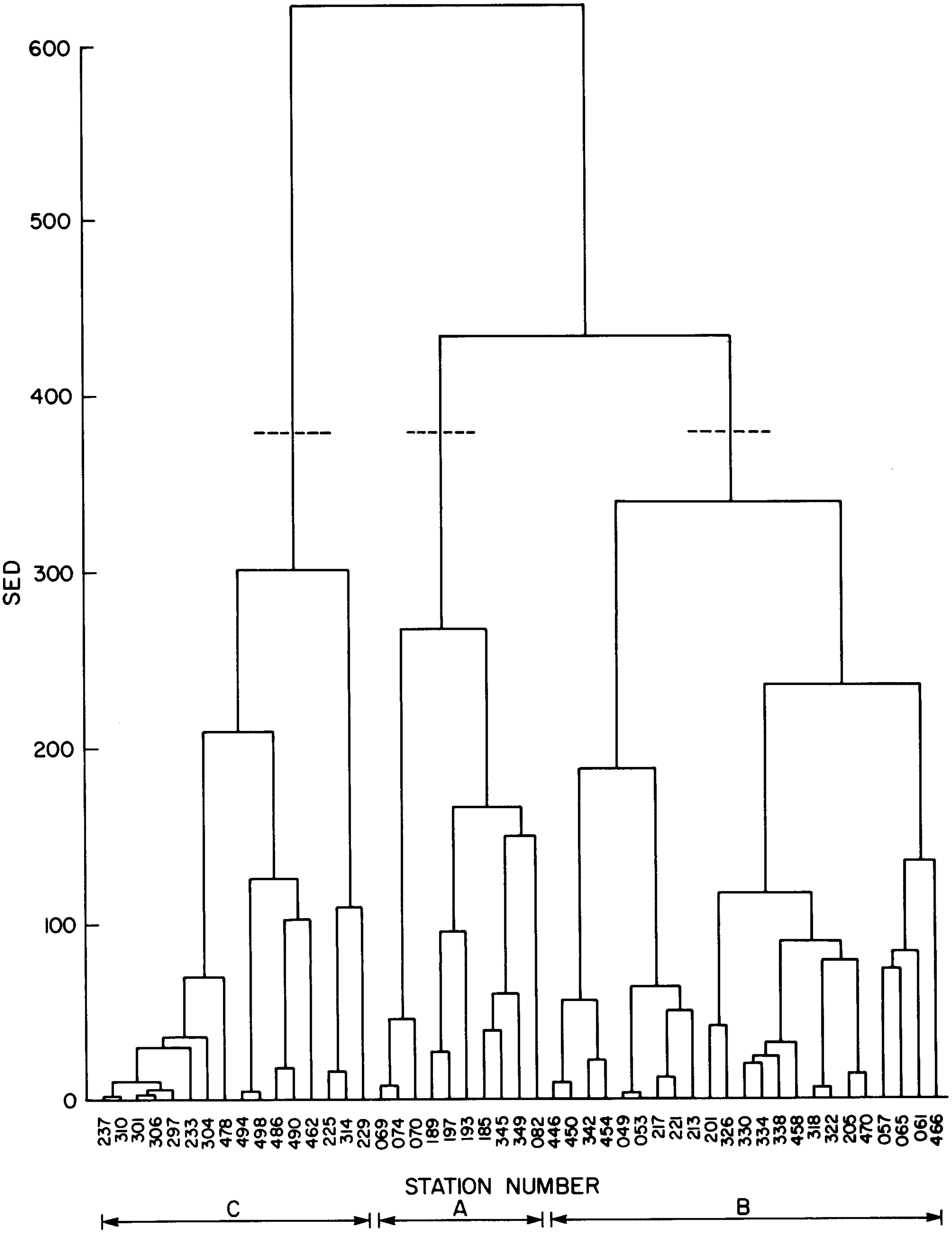

Figure 27. Dendrogram of the sum of Euclidean distances of 21 species for the stations in 1967.

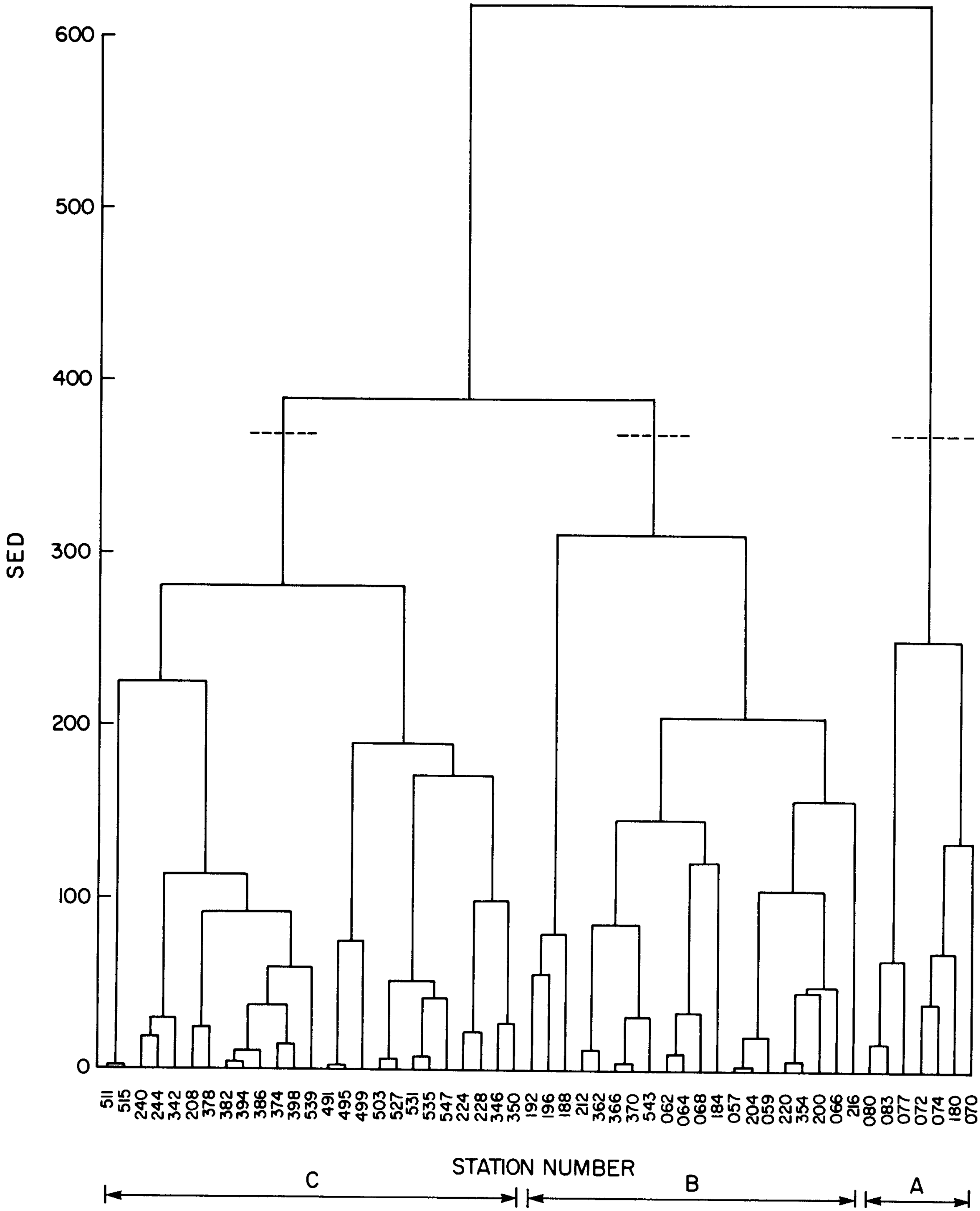

Figure 28. Dendrogram of the sum of Euclidean distances of 21 species for the stations in 1968.

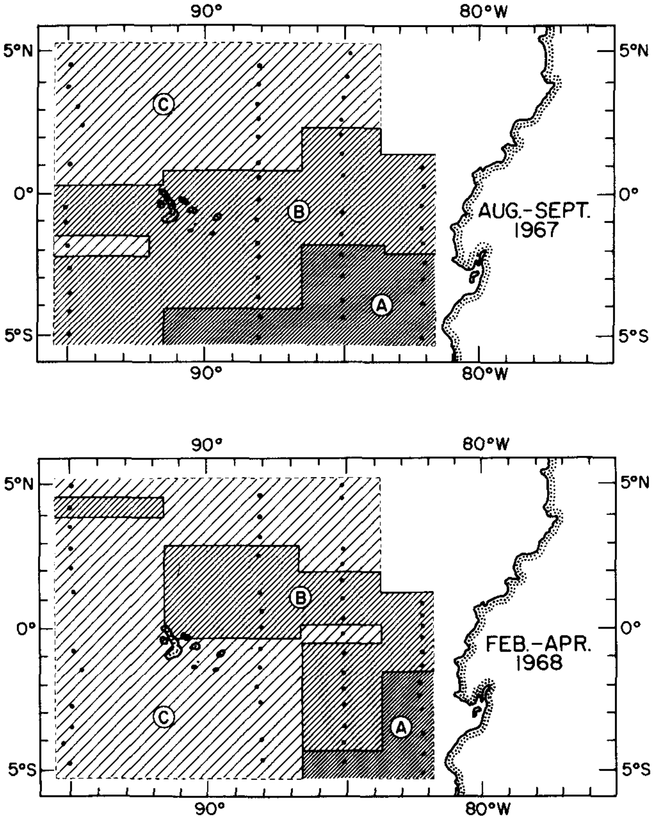

Figure 29. Areas of association defined by Ward's cluster analysis with 21 species in the Eastern Equatorial Pacific.

analysis, we reran the analysis excluding the neritic species, namely, *Undinula vulgaris, Subeucalanus pileatus, S. subcrassus, Temora discaudata,* and *Centropages furcatus* (Fleminger 1975, Fleminger and Hulsemann 1973). These neritic species succeed offshore, probably because of the large quantities of food in the upper mixed layer produced by the equatorial divergence system (see Discussion, below). The new areas formed by the clusters are substantively the same as those obtained with the full list of 21 species.

Abundance and Frequency by Cluster Area

This analysis includes all the species studied. Tables 4 and 5 show the mean abundance of each species and their occurrences in each of the areas (A, B, and C) for 1967 and 1968. Both abundance and frequency of some species characterize the areas, as discussed below.

Temperature and Salinity by Cluster Area

The mean values of temperature and salinity in the integrated 0-50-m water column for each of the areas is given in Table 6. This table shows the values to be consistently different for each area in both cruises. The lowest value of temperature and the highest of salinity are found in area A. The values are intermediate in area B. In area C, the temperature is the highest and the salinity is lowest.

TABLE 4
Distribution of the Mean Abundance (Org./100m^3) and Occurrence (in Parentheses) of Species in Groups Formed by the Ward Cluster Analysis, August-September 1967

	Area					
	A		B		C	
Number of stations per group		10		24		15
Calanus chilensis	1,164	(10)	1	(1)	0	(0)
Calanus chilensis (stage V)	747	(9)	0	(0)	0	(0)
Eucalanus inermis	27	(9)	6	(8)	0	(0)
Subeucalanus pileatus	74	(10)	44	(20)	2	(9)
Rhincalanus nasutus	246	(10)	514	(23)	1	(2)
Pareucalanus sewelli	108	(10)	73	(22)	18	(15)
Subeucalanus subtenuis	446	(10)	557	(24)	119	(15)
Cosmocalanus spp.	75	(10)	309	(20)	179	(15)
Temora discaudata	43	(9)	122	(24)	49	(13)
Nannocalanus minor	311	(10)	363	(24)	72	(15)
Subeucalanus subcrassus	17	(3)	64	(22)	38	(13)
Centropages furcatus	43	(9)	26	(24)	60	(14)
Mesocalanus tenuicornis	23	(8)	48	(22)	32	(15)
Rhincalanus rostrifrons	7	(4)	15	(14)	14	(13)
Undinula vulgaris	2	(3)	9	(9)	31	(15)
Neocalanus gracilis	3	(2)	3	(12)	2	(9)
Pareucalanus attenuatus	0	(0)	11	(5)	17	(13)
Eucalanus hyalinus	0	(0)	2	(6)	1	(2)
Centropages gracilis	0	(0)	1	(3)	2	(13)
Centropages calaninus	1	(1)	1	(1)	1	(6)
Neocalanus robustior	0	(0)	0	(0)	1	(5)

The species are ordered numerically by areas.

TABLE 5
Distribution of the Mean Abundance (Org./100m^3) and Occurrence (in Parentheses) of Species in Groups Formed by the Ward Cluster Analysis, February-April 1968

	Area					
	A		B		C	
Number of stations per group		7		20		25
Calanus chilensis	1,425	(6)	10	(1)	0	(0)
Calanus chilensis (stage V)	12,047	(7)	364	(4)	0	(0)
Eucalanus inermis	210	(6)	10	(13)	12	(5)
Subeucalanus pileatus	14	(7)	41	(17)	5	(13)
Rhincalanus nasutus	66	(7)	234	(20)	47	(14)
Pareucalanus sewelli	4	(4)	104	(20)	41	(25)
Subeucalanus subtenuis	8	(6)	363	(20)	236	(25)
Cosmocalanus spp.	9	(3)	187	(17)	253	(25)
Temora discaudata	12	(5)	343	(19)	76	(21)
Nannocalanus minor	301	(7)	780	(20)	403	(25)
Subeucalanus subcrassus	8	(6)	211	(20)	43	(21)
Centropages furcatus	58	(6)	353	(20)	52	(23)
Mesocalanus tenuicornis	2	(2)	43	(20)	41	(25)
Rhincalanus rostrifrons	1	(1)	10	(12)	15	(11)
Undinula vulgaris	0	(0)	15	(9)	20	(21)
Neocalanus gracilis	0	(0)	4	(4)	7	(9)
Pareucalanus attenuatus	1	(1)	4	(7)	7	(8)
Eucalanus hyalinus	0	(0)	2	(5)	2	(7)
Centropages gracilis	0	(0)	1	(1)	4	(13)
Centropages calaninus	0	(0)	0	(0)	1	(2)
Neocalanus robustior	0	(0)	0	(0)	2	(9)

The species are ordered numerically by areas.

Characteristics of the Cluster Areas

Area A is a region strongly influenced by waters from the Peru Current and is characterized by low mean temperature and high salinity. The species positively correlated in abundance (r = .001) are *Calanus chilensis* and *Eucalanus inermis*. *C. chilensis* (adults and stage V copepodites) is very important numerically, reaching up to 18,000 org./100m^3. The northern limit of distribution is south of the equator in both seasons (Figures 5 and 6). This species has been previously reported from the coast of Chile and Peru (Brodsky 1959; Herman and Mitchell 1981; Gómez 1982). Arcos (1978) reported the presence of *C. chilensis* (as *Calanus* sp.) in the Gulf of Guayaquil, associated with a tongue of cold and saline water from the Peru Current. This study confirms that the northern limit of the species is related to the northernmost influence of the Peru Current south of the equator. *E. inermis* (Figure 14) was more frequent and had more than 80% of its individuals in Area A in both cruises.

TABLE 6
Mean Temperature and Salinity of the Integrated 0-50 m in Groups Formed by the Ward Cluster Analysis, 1967 and 1968

	Area	Temperature	Salinity
1967	A	17.68	35.01
	B	19.33	34.64
	C	22.96	34.02
1968	A	17.43	34.80
	B	19.30	34.55
	C	22.17	34.25

Species significantly correlated in area B (r = .001) were *Rhincalanus nasutus*, *Subeucalanus subtenuis*, *Temora discaudata*, *Nannocalanus minor*, and *Mesocalanus tenuicornis*. *R. nasutus* (Figure 9) has its maximum mean abundance in this area (Table 4); it was present in all but one station in 1968. The distribution of this species partially explains the shape of area B in both seasons.

Area C shows the largest amount of geographical variability between cruises. The species correlated by abundance and occurrence in this area are *Undinula vulgaris*, *Pareucalanus attenuatus*, *Centropages gracilis*, and *Neocalanus robustior*.

DISCUSSION

The results demonstrate that groups of species were indeed related to the hydrography of the system. Ward's cluster analysis provided evidence that stations grouped by similarities in species and abundances encompassed coherent geographical areas affected by different circulation systems. Relative mean abundance and frequency analysis showed consistent patterns in the areas formed by the cluster analysis for both cruises, as seen in Tables 4 and 5. Pearson's correlation coefficients indicated highly significant positive correlations between pairs of species. With the positive correlations arranged along the diagonal axis in Figure 26, the species became ordered in such a manner that there is a trend from cool-water to warm-water species.

The numerically important filter-feeding calanoid copepod species in the Eastern Equatorial Pacific, as seen in Table 1, are *Nannocalanus minor* (Figure 7), *Subeucalanus subtenuis* (Figure 8), and *Cosmocalanus* spp. (Figure 10). The species best defining the limits of biologically different water masses of the region are *Calanus chilensis* (Figure 5 and 6), *Rhincalanus nasutus* (Figure 9), and *Neocalanus robustior* (Figure 24); these are likely indicator species for areas affected by different water masses of the EEP. *C. chilensis* indicates the northernmost influence of the Peru Current in area A; *R. nasutus* is most abundant in the transition zone (area B) and is apparently supported by equatorial upwelling; and *N. robustior*, although extremely low in abundance, appears to be an indicator of equatorial warm waters.

Area A is related to the Peru Current with hydrographic characteristics of low temperature and high salinity. The area is identified by the numerically dominating occurrence of *C. chilenis* (Figures 5 and 6) and *Eucalanus inermis* (Figure 14). The seasonal variation in shape and size of this area can be explained by the strength of the Peru Current's flow, shown by the altered extent of the low surface temperatures off the Gulf of Guayaquil (Figure 2). The presence of this area has been shown to be associated with several species of euphausiids (Antezana and Cornejo de Gonzáles 1979) and with high values of zooplankton biomass (Cajas 1982). Fleminger (1975) indicates a sharp break in the distribution of neritic calanoids at the south of the Gulf of Guayaquil.

Area C is related to warm tropical waters. It shows high geographical variation between cruises, probably in response to a breakdown of the circulation during February-April 1968. In 1967, the species grouping representing this area appears to originate from and be maintained by the North Equatorial Countercurrent as it contributes to the South Equatorial Current moving to the west. Weakening of the westward flow, and dominance of equatorial waters flowing to the east along the equator (Tsuchiya 1970; Lukas 1981) allowed warm waters found only in the north in 1967 to be present west and south in the sampled area in 1968.

The populations of neritic species *Temora discaudata* (Figure 11), *Centropages furcatus* (Figure 12), and *Undinula vulgaris* (Figure 18)—in the judgment of Jones (1962) and Fleminger and Hulsemann (1973)—are probably supported offshore by high standing stocks of phytoplankton and by the shallow mixed layer found in the area during the two periods of this study (Blackburn et al. 1970). An example of offshore maintenance of a neritic fine-particle feeding copepod population related to food supply is given by Checkley (1980a,b). He studied *Paracalanus parvus* in the California Current system and found that its offshore distribution and breeding was associated with high concentrations of chlorophyll *a*. Neritic copepods extending into the EEP in general originate from the coasts of Panama, Ecuador, and Colombia. The consistent presence of these species north of the equator and towards the continent in both years could be associated with the flow to the west. In February-April 1968, intermediate to high numbers of individuals of the same neritic species were found in the southwestern stations (Figures 11, 12, and 18). High numbers of individuals of the neritic copepod *Canthocalanus pauper* were also found in those stations but not in surrounding waters. This suggests that the populations of neritic copepods offshore southwest of the Galápagos in 1968 were independent of those north of the equator and that the southern populations may originate far west of the Galápagos (e.g., the Marquesas Islands) and be transported by an eastward surface flow. Eldin (1983) has called attention to the South Equatorial Countercurrent located between latitudes 7° and 14°S moving at <10 cm/sec and passing through the Marquesas Islands. Jones (1962) showed the presence of *U. vulgaris* 180 km downstream of the Marquesas Islands. He related its presence to enhanced productivity associated with the wake of the islands. There is also evidence of a weak eastward flow along about 10°S from 112°W to 90°W in February-March 1967 and February-April 1968, as discussed by Tsuchiya (1974). This flow is too far south to account for the occurrence of *U. vulgaris* east of the Marquesas.

Area B, having intermediate values of temperature and salinity, is transitional between the two previously discussed groupings. It also is an area of biotic transition between species supported by the Peru Current and those of the central and equatorial waters to the east; an increase in the EC in 1968 is suggested by the westward reduction in the distribution of *R. nasutus* in 1968 (Figure 9). The populations maintained in this region, including neritic species, could be supported by high phytoplankton productivity resulting from equatorial upwelling. Vingradov and Voronina (1963) observed maximum concentrations of zooplankton along the equator in the Central Pacific associated with upwelling events. From the Eastropac atlases one can observe that in both seasons covered by this study the higher values of zooplankton standing stocks are related to areas A and B where the main upwellings occur. This agrees with Fleminger's (in press) findings in the Indo-Australian region. He describes *R. nasutus* as an upwelling species related to low surface temperatures and high displacement volumes of zooplankton biomass.

ACKNOWLEDGMENTS

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LIFE CYCLE OF THE MARINE CALANOID COPEPOD *ACARTIA CALIFORNIENSIS* TRINAST REARED UNDER LABORATORY CONDITIONS

ANTONIO TRUJILLO-ORTIZ
Centro de Investigaciones de Quintana Roo, A.C. (CIQRO)
Apartado Postal 886
Cancún, Quintana Roo
77500-México

ABSTRACT

For the first time the entire life cycle of 6 naupliar and 5 copepodid stages and 1 adult stage of the marine calanoid copepod *Acartia californiensis* Trinast is described and illustrated. The account includes setation and segmentation for all stages. Specimens from Estero de Punta Banda, Baja California, México, were reared under laboratory conditions (17°C ± 1°C and 35 ‰).

The sexual differences found in the structure of appendages, in the urosome, fifth swimming legs, and first antenna were only in the sixth copepodid stage (adult). Comparative anatomical measurements such as total length and prosome/urosome ratio were also recorded.

RESUMEN

Se describe, por primera vez, el ciclo de vida completo del copépodo calanoídeo marino *Acartia californiensis* Trinast, a partir de especímenes cultivados bajo condiciones de laboratorio (17°C ± 1°C y 35 ‰) provenientes del Estero de Punta Banda, Baja California, México. La descripción incluye la setación y segmentación de todos los estadíos de desarrollo.

En base a los resultados de la descripción, las diferencias sexuales en la estructuración de los apéndices, en el urosoma, quinta pata natatoria y anténula, sólo fueron encontradas en el estadío adulto (C-VI). También se registraron datos anatómicos comparativos como longitud total y razón prosoma/urosoma.

INTRODUCTION

In most investigations of copepod population dynamics, a production estimate has been approached through study of the populations' life cycles, for example, cohort analysis (Landry 1976). For the sake of simplicity, however, naupliar stages (Yablonskaya 1962; Heinle 1966; Parsons et al. 1969) and copepodid stages (Greze and Baldina 1964) have often been grouped as single units.

Several authors have observed that naupliar larvae of marine copepods belonging to the same genus are remarkably similar, and sometimes identical. Examples are *Acartia longiremis* Lilljeborg, *A. bifilosa* Giesbrecht, and *A. clausi* Giesbrecht (Oberg 1906; Gurney 1932), and *A. tonsa* Dana and *A. californiensis* Trinast (Trinast 1976; Pace 1978; Johnson 1981).

According to Johnson (1934) there are two main reasons for studying the life cycle of copepods. First, from a taxonomic point of view, knowing larval development will help reveal the natural relationships among adult organisms. Second, in order to better understand their importance in the ocean's economy, it is necessary to know the organisms accurately, to distinguish all their developmental stages, and to ascertain the habits and requirements of each.

Life cycles have been described for at least 106 copepod species, but almost all of the descriptions are incomplete. Björnberg (1972) also described the partial life cycles of 21 more species. The descriptions are incomplete because it is difficult to collect all developmental stages of copepods in nature and to keep them in culture.

Acartia, the only genus in the family Acartiidae, contains about 79 described species belonging to the 8 subgenera proposed by Steuer (1923); undoubtedly, new species are yet to be described. This genus is widely distributed and recorded in all oceans (Subbaraju 1967). It occurs in coastal waters, especially estuaries (Uye 1982). However, larvae of only 13 of the 79 species have been described.

Acartia californiensis Trinast (subgenus *Acanthacartia:* group Rostrata of Steuer 1923) was described by Trinast (1976). It is endemic to the northeastern Pacific and apparently restricted to estuaries and coastal lagoons (Figure 1). According to Johnson (1981), *A. californiensis* extends north to Yaquina Bay, Oregon. On the California coast, this species has been recorded from San Francisco Bay (Johnson 1981), Elkhorn Slough in Monterey Bay (Pace 1978), Newport Bay in Los Angeles (Trinast 1976), and Laguna Peñasquitos and Mission Bay in San Diego (Fleminger, pers. comm.). It has also been observed in abundance at Estero de Punta Banda in Bahía de Todos Santos in Ensenada, Baja California (Trujillo-Ortíz, unpublished data), Laguna de Guerrero Negro, Baja California Sur (Fleminger, pers. comm.), and Laguna

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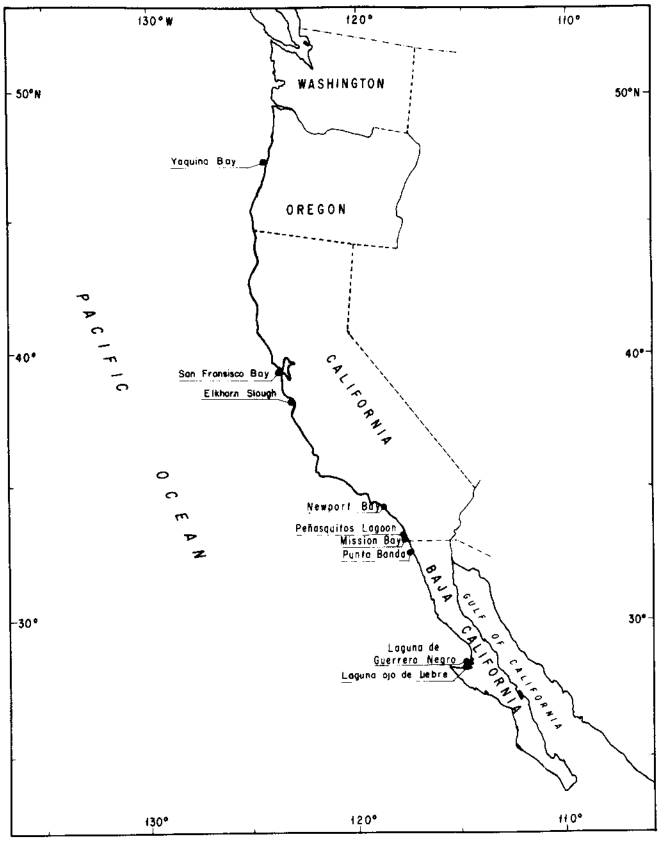

Figure 1. Known geographical distribution of *Acartia californiensis.*

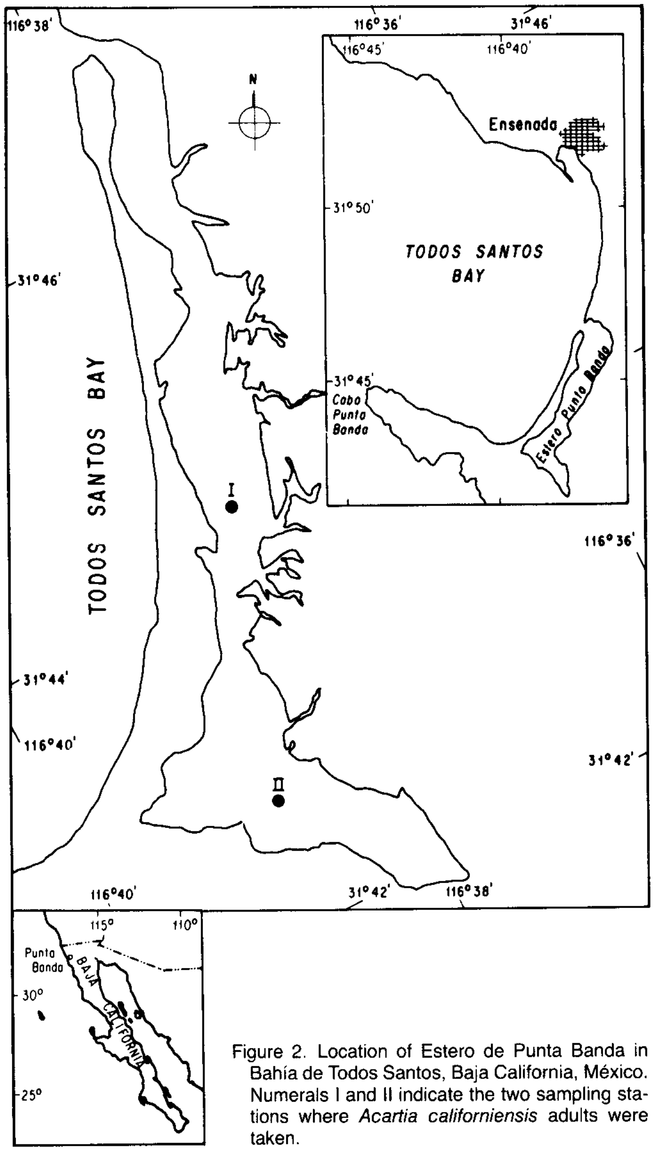

Figure 2. Location of Estero de Punta Banda in Bahía de Todos Santos, Baja California, México. Numerals I and II indicate the two sampling stations where *Acartia californiensis* adults were taken.

Ojo de Liebre, Baja California Sur (Trujillo-Ortíz, unpublished data).

The biology of *Acartia californiensis* is practically unknown. Pace (1978) studied its distribution, abundance, and rates of fecundity and growth in Elkhorn Slough in Monterey Bay; Johnson (1980) studied the effects of temperature and salinity on production and hatching of dormant eggs in Yaquina Bay; and Johnson (1981) studied population dynamics and cohort persistence in Yaquina Bay. Zimmerman (1972), Frolander et al. (1973), Johnson (1974), Johnson and Miller (1974), and Miller et al. (1977) had already worked with *A. californiensis,* but because of its close resemblance to *A. tonsa,* and because it had not yet been described as a separate species, they mistook it for *A. tonsa.* They considered it a smaller ecophenotypic variant of the larger offshore *A. tonsa,* present in the northerly Davidson Current during the winter. In other studies Trinast (1975) called it *Acartia* n. sp., and Uye and Fleminger (1976) *Acartia* sp. I.

MATERIALS AND METHODS

Sampling Site

Adult specimens of both sexes were collected from populations in the inner and middle regions of Estero de Punta Banda (Figure 2). Estero de Punta Banda is a coastal lagoon located between 31°42'–31°47'N and 116°37'–116°40'W in the southwestern end of Bahía de Todos Santos about 13 km south of the city of Ensenada on the Pacific coast of Baja California.

Collection of Samples

Zooplankton sampling was done with a 0.5-m-diameter standard plankton net of Nitex 202-μm-mesh monofilament screen cloth (nylon) hauled obliquely for 3 minutes at 1-2 knots at the two stations in Estero de Punta Banda. Hauls were circular, with the net beside the boat in order to avoid water disturbance caused by the propeller. Sampling depth varied according to bottom topography.

Two hauls were performed at each station: I kept one sample alive, and preserved the other with 5% formaldehyde buffered with sodium borate (borax) for subsequent analysis.

The live samples were deposited in ice chests containing water from the site. I added 37 mg•l^{-1} EDTA (Bernhard 1957; Carrillo Barros-Gómez et al. 1974; Azcárate-Capriles 1980) and 6.25 mg•l $^{-1}$ G-penicillin (Neunes and Pongolini 1965; Azcárate-Capriles 1980) to the water samples in order to keep the copepods healthy during transport to the laboratory.

Precipitated material (feces and dead phytoplankton and zooplankton) was siphoned out. Oxygen was provided through a controlled air system. After 5 hours, I transferred samples from the ice chests into 500-ml beakers. Because *Acartia californiensis* is positively photoactive to light, I used a lamp to concentrate the organisms for separation. I took aliquots with Pasteur pipettes and transferred them to glass Petri dishes. To facilitate the identification of adults of *A. californiensis*, I added a few drops of 0.1% MS-222 marine solution to the dishes to anesthetize the copepods and stop their movement.

I placed selected specimens of *A. californiensis* into 1000-ml beakers containing seawater previously filtered in 3-, 5-, and 10-μm polypropylene Kuno cartridges and UV-sterilized. To this water I added 37 mg•l^{-1} of EDTA.

Culturing Method

I selected 600 *A. californiensis* individuals in a ratio of 3 males per female to enhance fecundity. I transferred these organisms to two culture towers (10-liter polyethylene bags, 65 cm tall and 17 cm in diameter). Each tower contained 29 individuals per liter, or one individual per 35 ml, of water (Urry 1965; Corkett and Urry 1968). Each tower (Figure 3) had a simple conical drain valve at the bottom, an opening mechanism in the top for adding food, and an oxygen-supply line extending into the top 10 cm of the water column.

Every 5 days I added food consisting of an equal mixture of the chrysomonid *Isochrysis tahitiana* and the microflagellate *Tetraselmis* sp. kept in the "f/2" culturing medium of Guillard (1975), concentrated at 75 x 10^{3} cells per ml. A Fushs-Rosenthal hemocytometer was used to count the cells to maintain the desired concentration, after the method of Corkett and Urry (1968).

I used Houde's (1978) method to maintain the phytoplankton concentration. Water was changed weekly through a PVC cylinder (11.5 cm in diameter and 12.5 cm long) provided with a Nytex 40-μm monofilament screen cloth (nylon) attached to the end.

Laboratory temperature was kept constant at 17°C ± 1°C; the air conditioning system was equipped with an electrostatic filter. Twelve 75W fluorescent cool-white tubes were arranged horizontally 10 cm from the towers to provide light. Water salinity was 35‰.

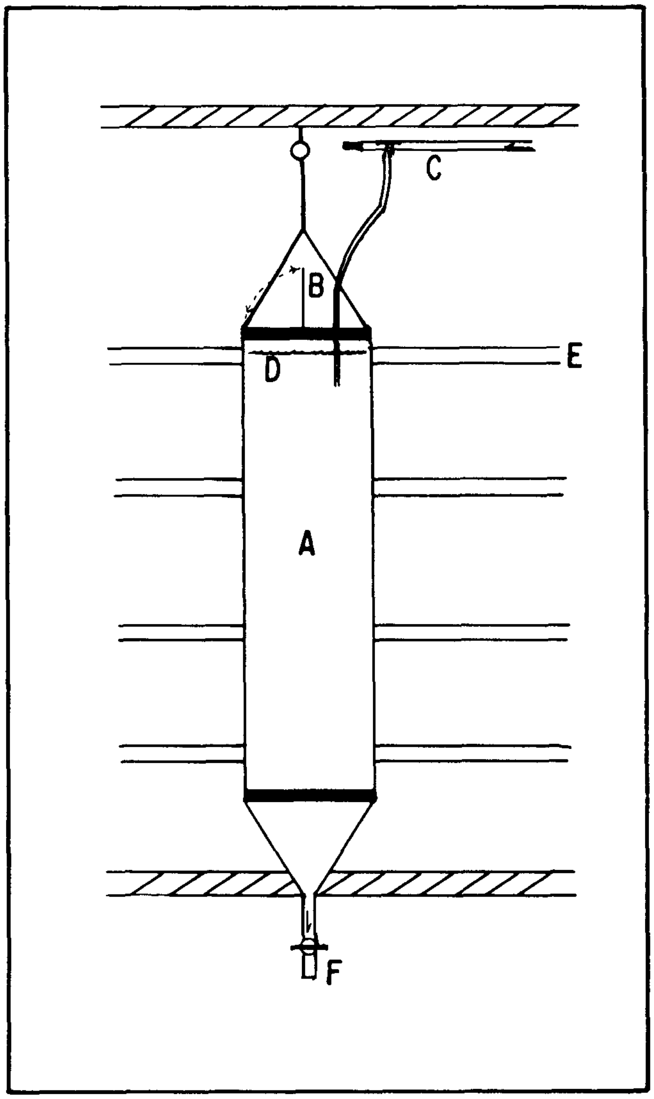

Figure 3. Culturing device: *A*, polyethylene bag (tower); *B*, opening mechanism; *C*, air-supply line; *D*, water level; *E*, fluorescent cool-white tube; *F*, conical drain valve.

Taxonomic Considerations

The characteristics chosen to identify the different naupliar stages in cultivated and preserved samples include: number of setae in the segments of the antennule; number and pattern of spines in the caudal armature; presence of other appendages such as maxillule, maxilla, maxilliped, buds of swimming legs (pereiopods); and body size. I used an ocular micrometer to measure 30 specimens dorsally and laterally from the anterior end of the cephalosome (head) to the end of the caudal armature. I chose a subsample of 10 specimens for dissection. These were cleared with 100% lactic acid for a week. I made naupliar dissections directly in a drop of lactic acid under a dissecting microscope at magnifications of 50 and 100 ×.

In the copepodid stages, I counted the abdominal segments (urosome) and number of swimming legs; the urosome also served for sex determination. The measurements in these stages were the same as in the naupliar stages, except that the furcal setae were not included in the body length. Prosome (cephalosome and metasome or thorax) and urosome length, and prosome/urosome ratios were also recorded. The number of copepodids measured varied from 43 (copepodid V, female) to 83 (copepodid I).

I used a 70% alcoholic chlorazol black E (CBE) solution to stain copepodids (10 of each stage) from preserved samples, in the depressions of a Boerer chamber. The sequence was as follows: (1) 2 baths of distilled water, 2-3 minutes each to eliminate excess formaldehyde; (2) a 35% alcohol solution bath for 2-3 minutes to dehydrate partially; (3) a 70% alcohol solution bath for 3 minutes to complete dehydration; (4) a bath of CBE in 70% alcohol for 1-2 minutes; (5) the same steps in reverse order (without the fourth); (6) microdissection in a glycerin drop on microscope slide. This procedure is my modification of that of Omori and Fleminger (1976).

I made microdissections of the copepodid stages in drops of glycerin under a dissecting microscope at magnifications of 25 and 50 ×. I used sharpened 000 entomological needles for all dissections. As the appendages were dissected off, I arranged them in natural sequence in glycerin drops on microscope slides and covered them with no. 1 round cover slips. For additional information on this method, refer to Pantin (1964), Griffiths et al. (1976), and Omori and Fleminger (1976).

All drawings were made with the aid of a camera lucida mounted in a compound microscope. I observed naupliar stages and their appendages at 400 ×. For the copepodid stages, I observed complete specimens at 250 ×, and their appendages at 400 ×.

RESULTS

Egg

The egg of *Acartia californiensis* (Figure 4a) is spherical, 0.075 ± 0.002 mm in diameter, $n = 30$ eggs, range 0.069-0.083 mm, SD ± 0.01 mm. The eggs are granular and clear yellow-brown or yellow-green. Three concentric membranes can be clearly distinguished. The outer membrane is thin, has no fuzz, and usually bears protuberances that make it appear irregular. In fertile eggs, cell differentation is often visible. When hatching, the nauplius emerges, and the remainder of the egg tends to remain spherical. The middle membrane is also thin and flexible, and sometimes it partially collapses toward the outer membrane, causing the inner space between them to vary as embryonic development progresses. The inner membrane covers and protects the first naupliar stage during its development.

The newly laid eggs are small and capsular. They immediately sink to the bottom and gradually swell until they become completely spherical.

Naupliar Stages

During postembryonic development, six naupliar stages are evident. Average naupliar length is about 2.1 times its width. The body is not significantly curved laterally. All naupliar stages are oval anteriorly, and narrow toward the caudal armature. There is an anteroventral pigment spot, generally red, also known as the naupliar eye. The posterior-inner part is tan, and the body is generally clear and translucent but slightly yellow-green. A small internal lipid body is usually present posteroventrally in most of the naupliar stages, and is clearly visible. In lateral view (Figure 5), the labrum is clearly evident in all naupliar stages; in addition, there are short, thin setules in the labrum's inferior margin.

The most important distinguishing characters of the naupliar stages of *Acartia californiensis* are as follows.

Nauplius I (Table 1; Figures 4b, 5a, 6a, 7a, 8a). Average length of 30 specimens was 0.095 ± 0.004 mm, range 0.081-0.113 mm, SD ± 0.01 mm. Caudal armature has 2 terminal sensory setae and transverse row of setules. First nauplius only slightly resembles adult, except for oval-shaped labrum bearing setules at bottom margin, and rudimentary antennule, antenna, and mandible.

After the first molt, the nauplii enlarge slightly, and the antennule, antenna, and mandible become more specialized.

Nauplius II (Table 1; Figures 4c, 5b, 6b, 7b, 8b). Average length of 30 specimens was 0.116 ± 0.002 mm, range 0.111-0.123 mm, SD ± 0.004. Body is egg-shaped. The 2 terminal sensory setae of the caudal armature (Figures 4c, 5b) are longer than in the previous stage; one is ventral, the other dorsal. The labrum is oval, with setules in the lower margin. Posteroventrally the body has a transverse row of fine setae.

Nauplius III (Table 1; Figures 4d, 5c, 6c, 7c, 8c). Average length of 30 specimens was 0.137 ± 0.003 mm, range 0.127-0.147 mm, SD ± 0.007. The body remains egg-shaped. The caudal armature now consists of 2 ventral spines with slightly toothed margins (saw-type), 2 sensorial setae that have the same appearance as in the previous stage, and a transverse row of fine setae. Posteroventrally the body has 2 transverse rows of setae.

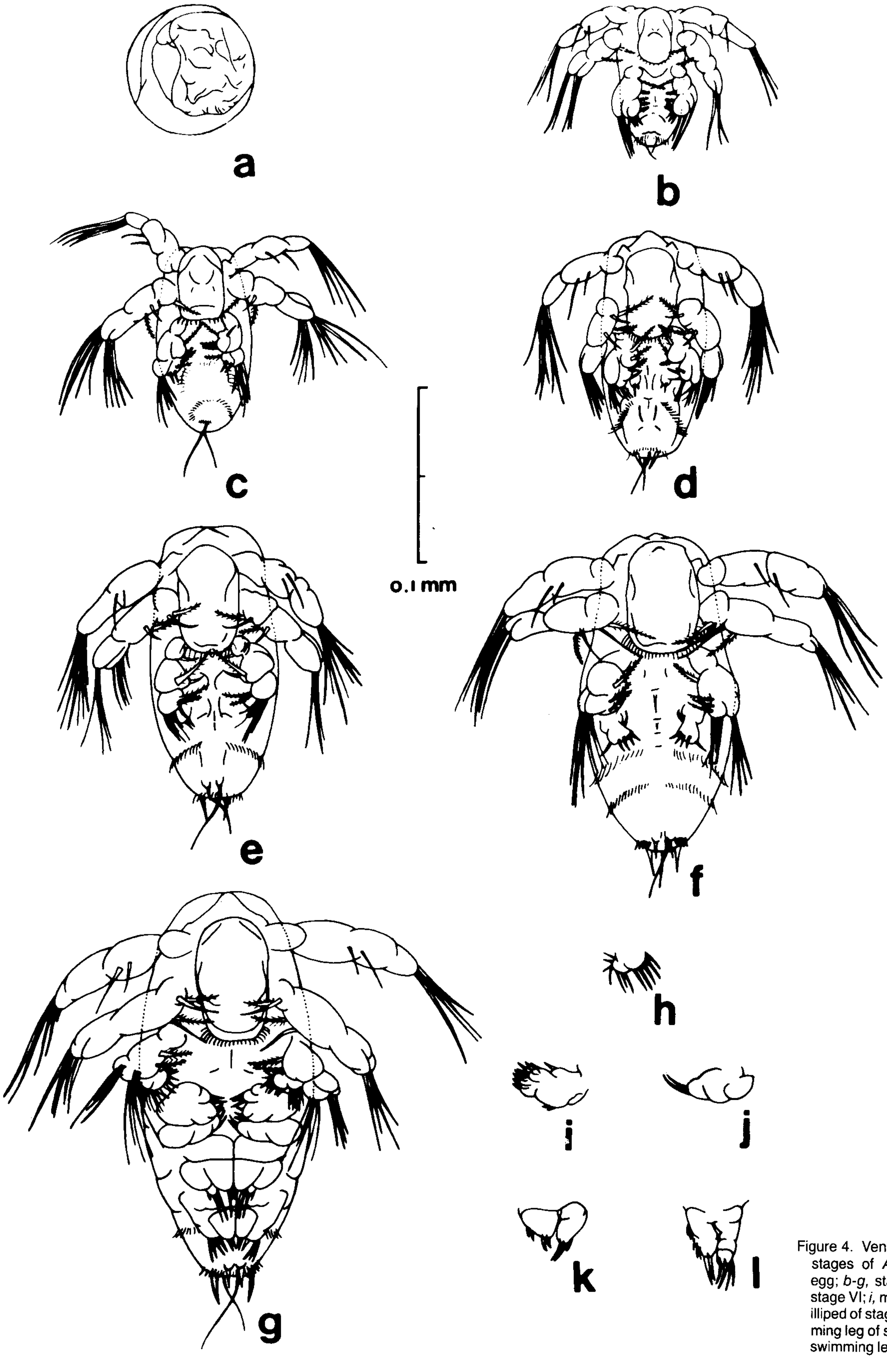

Figure 4. Ventral views of the naupliar stages of *Acartia californiensis*: *a*, egg; *b-g*, stages I-VI; *h*, maxillule of stage VI; *i*, maxilla of stage VI; *j*, maxilliped of stage VI; *k*, bud of first swimming leg of stage VI; *l*, bud of second swimming leg of stage VI.

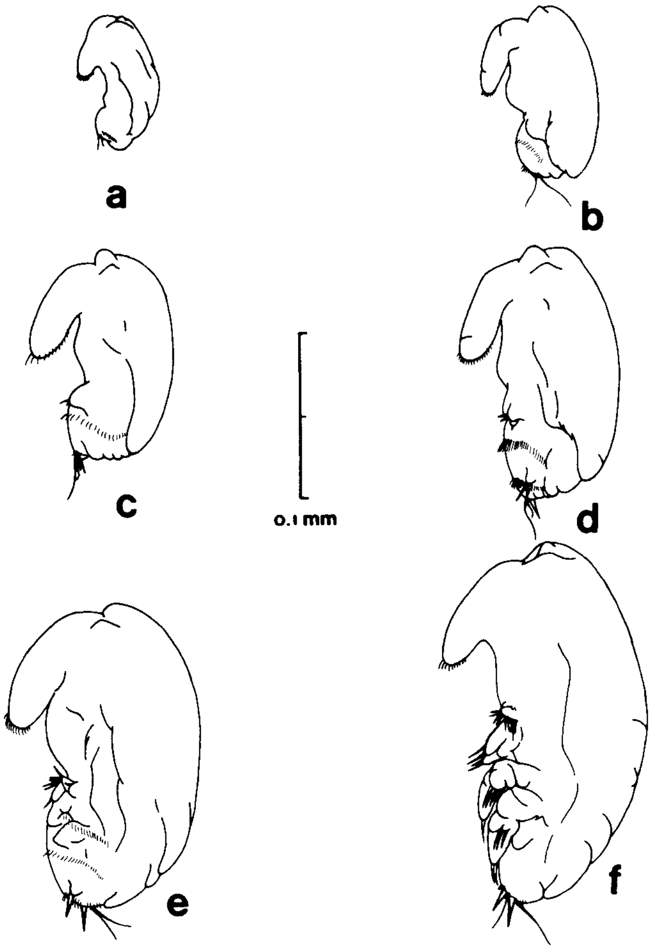

Figure 5. Lateral views of naupliar stages I-VI of *Acartia califoriensis.*

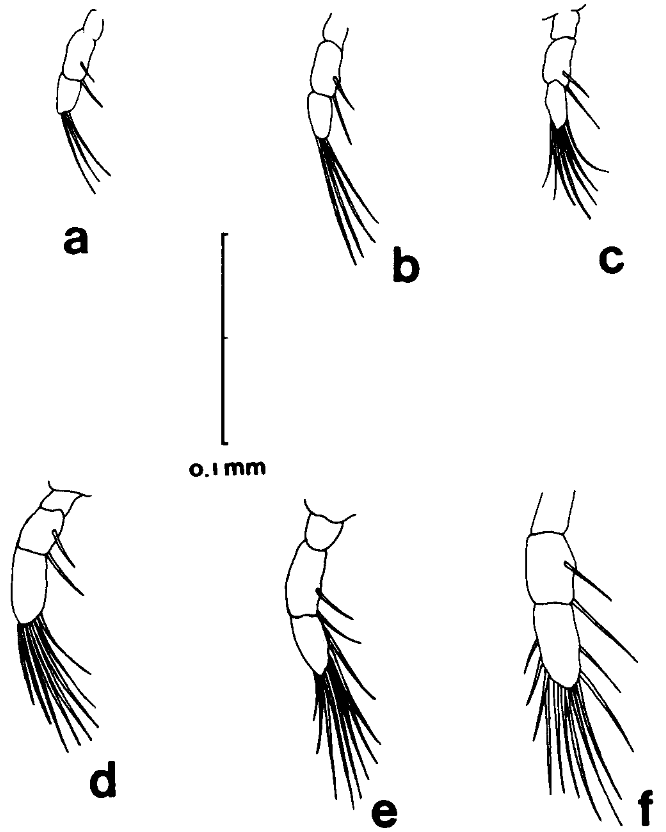

Figure 6. Antennules of naupliar stages I-VI of *Acartia californiensis.*

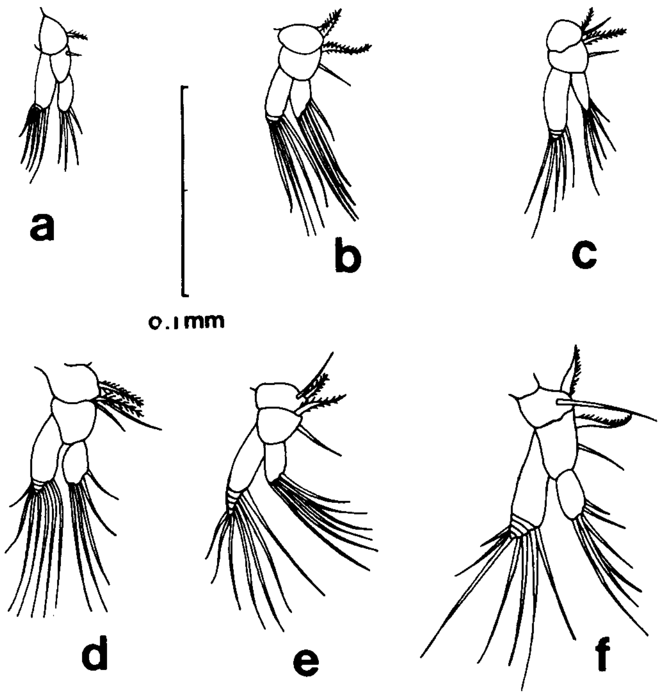

Figure 7. Antennae of naupliar stages I-VI of *Acartia californiensis.*

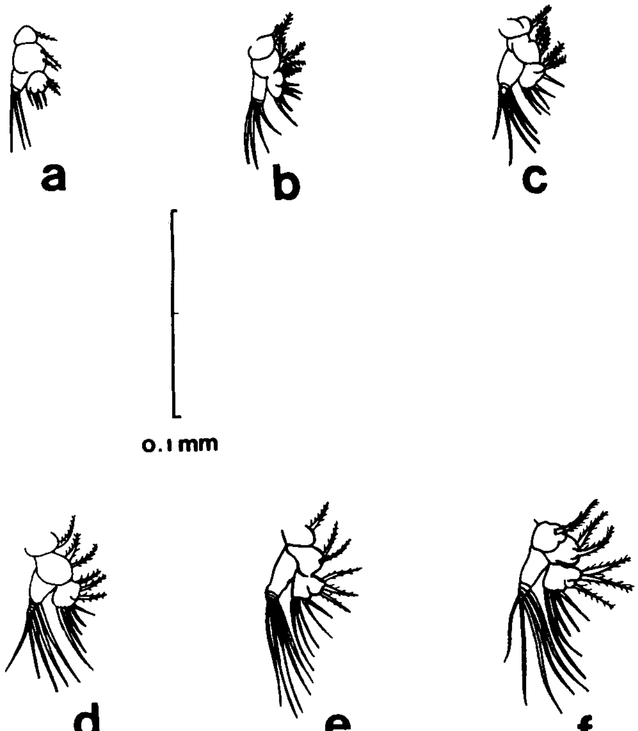

Figure 8. Mandibles of naupliar stages I-VI of *Acartia californiensis.*

TABLE 1
Setae, Spines, and Masticatory Processes on Appendages of Naupliar Stages of *Acartia californiensis*

Stage	N I	N II	N III	N IV	N V	N VI
Total average length (mm)	0.095 ± 0.004	0.116 ± 0.002	0.137 ± 0.003	0.167 ± 0.003	0.198 ± 0.003	0.229 ± 0.003
Range (mm)	0.081–0.113	0.111–0.123	0.127–0.147	0.157–0.176	0.189–0.208	0.218–0.240
Antennule (Fig. 6)						
No. segments	3	3	3	3	3	3
No. setae	5	6	8-9	9-10	10-11	12-13
Proximal segment	0	0	0	0	0	0
Medial segment	2	2	2	2	2	2
Distal segment	3	4	6-7	7-8	8-9	10-11
Antenna (Fig. 7)						
Coxopod	1sp	1sp	1 + 1sp	1 + 1sp	1 + 1sp	1 + 1sp
Basiopod	1	1 + 1sp	1 + 1sp	1 + 1sp	1 + 1sp	1 + 1sp
Endopod	4	5	5	5	6	6
Exopod	5	5	5	7	7	7
Mandible (Fig. 8)						
Coxopod	1pm	1pm	1pm	1pm	1pm	1pm
Basiopod	2pm	2pm	2pm	2pm	2pm	2pm
Endopod	2pm:4	2pm:5	2pm:5	3pm:5	2pm:1pm:5	2pm:1pm:5
Exopod	3	4	5	5	5	5
Maxillule (Figs. 4,5)						
External lobe I			1	1	1	5
External lobe II			0	0	0	0
Exopod			0	0	0	0
Internal lobe I			1	2	1	2
Internal lobe II			0	0	4	5
Internal lobe III						
Basiopod						
Endopod						
Maxilla (Figs. 4,5)						
Lobe I						0
Lobe II						2
Lobe III						4
Lobe IV						4
Lobe V						1
Endopod						0
Maxilliped (Figs. 4,5)						
Coxopod						2
Lobe I						0
Lobe II						0
Lobe III						0
Basiopod						0
Endopod						0
Caudal armature (Figs. 4,5)						
Sensory setae	2	2	2	2	2	2
Dorsal terminal spines	0	0	0	2	2	2
Ventral terminal spines	0	0	2	2	2	2
Bristles	1	1	1	1	1	1
Leg I (Figs. 4,5)						
Coxopod						0
Basiopod						0
Endopod 1						2S + 2
2						0
3						0
Exopod 1						2S
2						0
3						0

TABLE 1 (continued)
Setae, Spines, and Masticatory Processes on Appendages of Naupliar Stages of *Acartia californiensis*

Stage	N I	N II	N III	N IV	N V	N VI
Total average length (mm)	0.095 ± 0.004	0.116 ± 0.002	0.137 ± 0.003	0.167 ± 0.003	0.198 ± 0.003	0.229 ± 0.003
Range (mm)	0.081–0.113	0.111–0.123	0.127–0.147	0.157–0.176	0.189–0.208	0.218–0.240
Leg II (Figs. 4,5)						
Coxopod						0
Basiopod						0
Endopod 1						2S + 5
2						0
3						0
Exopod 1						2S + 5
2						0
3						0

Main designations are according to Owre and Foyo (1967) and Björnberg (1972). Special designations of appendage armature are: arabic numerals = setae, sp = plumose seta, S = spine, pm = masticatory process.

Nauplius IV (Table 1; Figures 4e, 5d, 6d, 7d, 8d). Average length of 30 specimens was 0.167±0.003 mm, range 0.157-0.176 mm, SD±0.007. Body is oval. The caudal armature is larger than in naupliar stage III, and has 2 terminal spines with toothed margins, 2 anterior sensory setae, a new pair of ventral spines, and a fine, transverse row of setules.

Nauplius V (Table 1; Figures 4f, 5e, 6e, 7e, 8e). Average length of 30 specimens was 0.198±0.003 mm, range 0.189-0.208 mm, SD±0.007. The caudal armature is a small transverse row of small setae: 4 spines remain as in naupliar stage IV (2 ventral strong and small, 2 large dorsal, terminally toothed); there are also 2 sensorial setae. Oval labrum has an inferior margin with setules.

Nauplius VI (Table 1; Figures 4g-l, 5f, 6f, 7f, 8f). Average length of 30 specimens was 0.229±0.003 mm, range 0.218-0.240 mm, SD±0.008. Until this last naupliar stage the body remains oval. In lateral view (Figure 5f), there is a clear differentiation of 5 segments that are well delimited. The oval labrum has setules on its inferior margin. The caudal armature is the same as in nauplius stage V.

Copepodid and Adult Stages

The final naupliar stage metamorphoses into the first of six copepodids. When the individual reaches copepodid stage I, as the direct result of a drastic change in structure, it is a miniature adult, except that it has only two pairs of functional swimming legs. A new pair of legs is added in each successive molt until copepodid IV. From that stage until the adult form (copepodid VI), no new swimming legs are added; instead, the sexually modified fifth pair of legs develops in the adult form.

During the copepodid stages, males increase 2.23 times in average body length to reach the adult stage; females increase 2.62 times. From copepodid IV on, the sex of each individual is evident.

The most important characters of the copepodid stages of *Acartia californiensis* are as follows:

Copepodid I (Table 2; Figures 9a, 10a, 11a, 12a, 13a, 14a, 15a, 16a, 17a, 18a). Average length of 83 specimens (including caudal furca, omitting furcal setae here and in all subsequent copepodid stages) was 0.385±0.004 mm, range 0.347-0.443 mm, SD±0.017, average prosome/urosome ratio 3.75:1. The cephalosome occupies about 60% of the prosome length. The metasome has 4 segments: the first two have functional swimming legs; the third, in some cases, has biramous buds of the third pair of swimming legs; and the fourth lacks appendages. The urosome has one segment. In the caudal furca each ramus is longer than it is wide (1:0.76) and has 4 plumose setae, of which the inner one is shortest. The appendages, in general, are very similar to each other but not identical to those of the adult. With maturation, the appendages enlarge and specialize by acquiring such ornamental structures as setae and spines. The rostrum bears two filaments.

Copepodid II (Table 2; Figures 9b, 10b, 11b, 12b, 13b, 14b, 15b, 16b, 17b, 18b, 19a). Average length of 82 specimens (including caudal furca) was 0.469±0.003 mm, range 0.424-0.500 mm, SD±0.017, average prosome/urosome ratio 4.02:1. The cephalosome occupies 54% of prosome length; it has 2 rostral filaments. The metasome has 4 segments, of which the first 3 have functional swimming legs and the fourth lacks appendages. The urosome has 2 segments. Each ramus of caudal furca has 5 plumose setae; both the outer and inner setae are short. In some cases buds of the fourth biramous legs are present.

Copepodid III (Table 2; Figures 9c, 10c, 11c, 12c, 13c, 14c, 15c, 16c, 17c, 18c, 19b, 20a). Average length

TABLE 2
Anatomical Characteristics of Copepodid Stages of *Acartia californiensis*

Stage	C I	C II	C III	C IV	
				Male	Female
Total average length (mm)	0.385 ± 0.004	0.469 ± 0.003	0.577 ± 0.005	0.656 ± 0.005	0.700 ± 0.007
Range (mm)	0.347–0.443	0.424–0.500	0.519–0.635	0.597–0.674	0.635–0.751
Prosome/urosome ratio	3.75:1	4.02:1	4.03:1	3.99:1	3.54:1
Antennule (Fig. 11)					
No. segments	11	14	16	17	17
Antenna (Fig. 12)					
Coxopod	1sp	1sp	1sp	1sp	
Basiopod	4	5	6	7	
Endopod	7(2+5)	8	11	11(6+5)	
Exopod	8	8	8	8(5+3)	
Mandible (Fig. 13)					
Coxopod: gnathobase	6t	7t	8t	8t	
Basiopod	1+sm	1+sm	1+sm	1+sm	
Endopod	2:6	2:7	2:7	2:8	
Exopod	6	6	6	6	
Maxillule (Fig. 14)					
External lobe I	4	6	8	9	
External lobe II	1	1	1	1	
Exopod	2	2	2	2	
Internal lobe I	7	7	7	7	
Internal lobe II	3	3	3	3	
Internal lobe III	1	1	1	1	
Basiopod	sm	sm	sm	sm	
Endopod	5	5	5	5	
Maxilla (Fig. 15)					
Lobe I	2	2	2	2	
Lobe II	1	1	1	2	
Lobe III	1	1	1	1	
Lobe IV	1	2	2	2	
Lobe V	1	1	2	1	
Endopod	4	4	4	5	
Maxilliped (Fig. 16)					
Coxopod	0	0	0	0	
Lobe I	1	1	1	1	
Lobe II	2	3	3	3	
Lobe III	1	1	1	1	
Basiopod	0	1	1	1	
Endopod	3	4	4(1:1:2)	5(1:1:1:2)	

Main designations are according to Owre and Foyo (1967). Special designations of appendage armature are: arabic numerals = setae, sp = plumose seta, t = tooth, sm = micro setule, S = spine, Se = external spine, St = terminal (apical) spine.

of 71 specimens (including caudal furca) was 0.577±0.005 mm, range 0.519-0.635 mm, SD±0.02, average prosome/urosome ratio 4.03:1. The cephalosome occupies nearly 52% of the total length of the prosome. Metasome has 4 segments, each with a pair of functional swimming legs. The caudal furca has 6 setae; the same number occurs in the following copepodid stages. Forehead has 2 rostral filaments.

Copepodid IV, male (Table 2; Figures 9d, 10d, 11d, 12d, 13d, 14d, 15d, 16d, 17d, 18d, 19c, 20b, 21a). Average length of 75 specimens (including caudal furca) was 0.656±0.005 mm, range 0.597-0.674 mm, SD±0.02, average prosome/urosome ratio 3.99:1. From this stage on, sexes are easily distinguishable. The cephalosome occupies nearly 51% of the total length of the prosome. Each of the 4 metasomal segments has a pair of swimming legs; the posteriormost segment also has the two-jointed fifth pair of legs, which is symmetrical. The urosome has 3 abdominal segments. The caudal furca has 2 furcal rami with 6 plumose setae each, as in the previous copepodid stage. The innermost seta is the shortest. The species has two rostral filaments.

C V		C VI	
Male	Female	Male	Female
0.759 ± 0.009	0.818 ± 0.016	0.859 ± 0.008	1.008 ± 0.009
0.693-0.809	0.712-0.924	0.770-0.924	0.924-1.097
3.13:1	3.3:1	2.93:1	3.35:1
17	17	17	17
1sp		1sp	
9		9	
13(6+7)		14(3:4:7)	
8(5+3)		8	
9t		10t	
1+sm		1+sm	
2:8		2:9	
6(1:1:1:3)		6	
9		9	
1		1	
2		2	
7		7	
3		3	
1		1	
sm		sm	
5		5	
2		3	
2		2	
1		2	
2		1	
1		1	
5		4	
0		0	
1		1	
3		3	
1		1	
1		1	
5(1:1:1:2)		6(1:1:1:3)	

Table 2 continued on next page.

Copepodid IV, female (Table 2; Figures 9e, 10e, 11e, 13e, 14e, 15e, 16e, 17e, 18e, 19d, 20c, 21b). Average length of 66 specimens (including caudal furca) was 0.700±0.007 mm, range 0.635-0.751 mm, SD±0.027, average prosome/urosome ratio 3.54:1. Female has the same general characteristics as the corresponding male stage, except that the urosome has 2 segments. The fifth pair of legs is symmetrical.

Copepodid V, male (Table 2; Figures 9f, 10f, 11f, 12f, 13f, 14f, 15f, 16f, 17f, 18f, 19e, 20d, 21c). Average length of 59 specimens (including caudal furca) was 0.759±0.009 mm, range 0.693-0.809 mm,

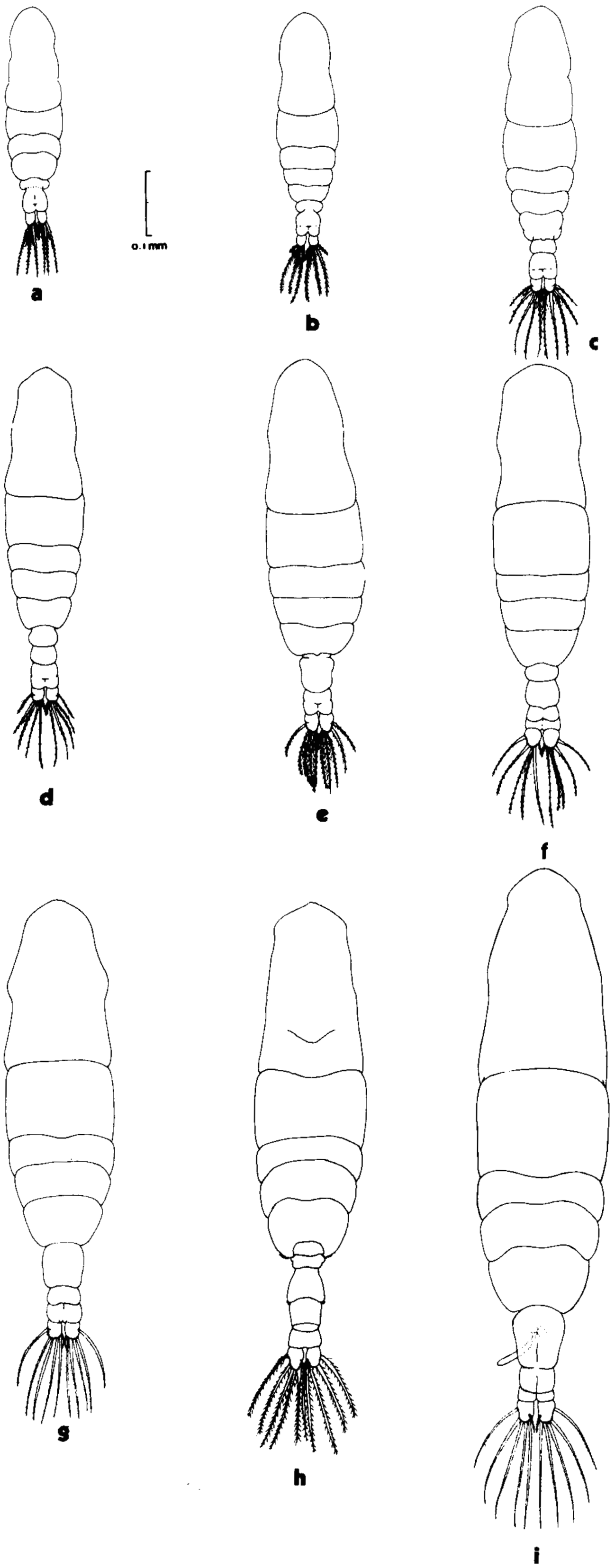

Figure 9. Dorsal views of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female, with spermatophore.

TABLE 2 (continued)
Anatomical Characteristics of Copepodid Stages of *Acartia californiensis*

Stage	C I	C II	C III	C IV	
				Male	Female
Total average length (mm)	0.385 ± 0.004	0.469 ± 0.003	0.577 ± 0.005	0.656 ± 0.005	0.700 ± 0.007
Range (mm)	0.347–0.443	0.424–0.500	0.519–0.635	0.597–0.674	0.635–0.751
Prosome/urosome ratio	3.75:1	4.02:1	4.03:1	3.99:1	3.54:1
Leg I (Fig. 17)					
Coxopod					
Basiopod					
Endopod 1	1	1	1	1	
2	6	6	6	6	
3	0	0	0	0	
Exopod 1	1	1	2	2	
2	0*	0*	0*	0*	
3	2+1Se+1+1St+3	2+1Se+1+1St+4	2+1Se+1+1St+4	2+1Se+1+1St+4	
Leg II (Fig. 18)					
Coxopod					
Basiopod					
Endopod 1	1	1	2	2	
2	5	5	5	6	
3	0	0	0	0	
Exopod 1	1Se+1	1Se+1	1Se+1	1Se+1	
2	0*	0*	1Se+1	1Se+1	
3	1Se+1St+3	1Se+1St+4	1Se+1St+4	1Se+1St+4	
Leg III (Fig. 19)					
Coxopod					
Basiopod					
Endopod 1	0	1	2	2	
2	0	4	5	6	
3	0	0	0	0	
Exopod 1	0	1Se	1Se	1Se+1	
2	0	0*	0*	1Se+1	
3	0	1Se+1St+3	1Se+1St+4	1Se+1St+4	
Leg IV (Fig. 20)					
Coxopod					
Basiopod					
Endopod 1			1	2	
2			4	5	
3			0	0	
Exopod 1			1Se	1Se	
2			0*	1Se+1	
3			1Se+1St+3	1Se+1St+4	
Leg V (Fig. 21)					
Coxopod				1	0
Basiopod				0	0
Right leg				1:1+1S	1:0
Left leg				1:1+1S	1:0

Main designations are according to Owre and Foyo (1967). Special designations of appendage armature are: arabic numerals = setae, sp = plumose seta, t = tooth, sm = micro setule, S = spine, Se = external spine, St = terminal (apical) spine, * = segment not defined.

SD±0.035, average prosome/urosome ratio 3.13:1. The cephalosome occupies nearly 46% of the prosome's length. The metasome has 4 segments; each one has a pair of swimming legs; the posteriormost segment also bears the two-jointed fifth pair of swimming legs, which is asymmetrical. The urosome has 4 segments. Each furcal ramus has 6 plumose setae; the innermost is shortest. This stage has 2 rostral filaments.

Copepodid V, female (Table 2; Figures 9g, 10g, 11g, 12g, 13g, 14g, 15g, 16g, 17g, 18g, 19f, 20e, 21d). Average length of 43 specimens (including caudal furca) was 0.818±0.016 mm, range 0.712-0.924 mm, SD±0.053, average prosome/urosome ratio 3.3:1.

C V		C VI	
Male	Female	Male	Female
0.759 ± 0.009	0.818 ± 0.016	0.859 ± 0.008	1.008 ± 0.009
0.693–0.809	0.712–0.924	0.770–0.924	0.924–1.097
3.13:1	3.3:1	2.93:1	3.35:1
1		1	
6		6	
0		0	
2		2	
2*		2	
1 + 1Se + 1 + 1St + 4		1 + 1Se + 1 + 1St + 4	
2		2	
6		7	
0		0	
1Se + 1		1Se + 1	
1Se + 1		1Se + 1	
1Se + 1St + 5		1Se + 1St + 5	
2		2	
7		7	
0		0	
1Se + 1		1Se + 1	
1Se + 1		1Se + 1	
1Se + 1St + 5		1Se + 1St + 5	
3		3	
6		6	
0		0	
1Se + 1		1Se + 1	
1Se + 1		1Se + 1	
1Se + 1St + 5		1Se + 1St + 5	
1sp	0	0	0
0	0	1sp	0
2s:1S	1:1St	1S:1S:2-3	1sp:1St
0:1S	1:1St	0:0:2S	1sp:1St

The female is larger than corresponding stage of male (mean ratio 1:0.87). The cephalosome is approximately 46% as long as the prosome, and has 2 rostral filaments. In general, the female has the same characteristics as the male, except that urosome has 3 segments, of which the first is larger. The fifth swimming legs are symmetrical.

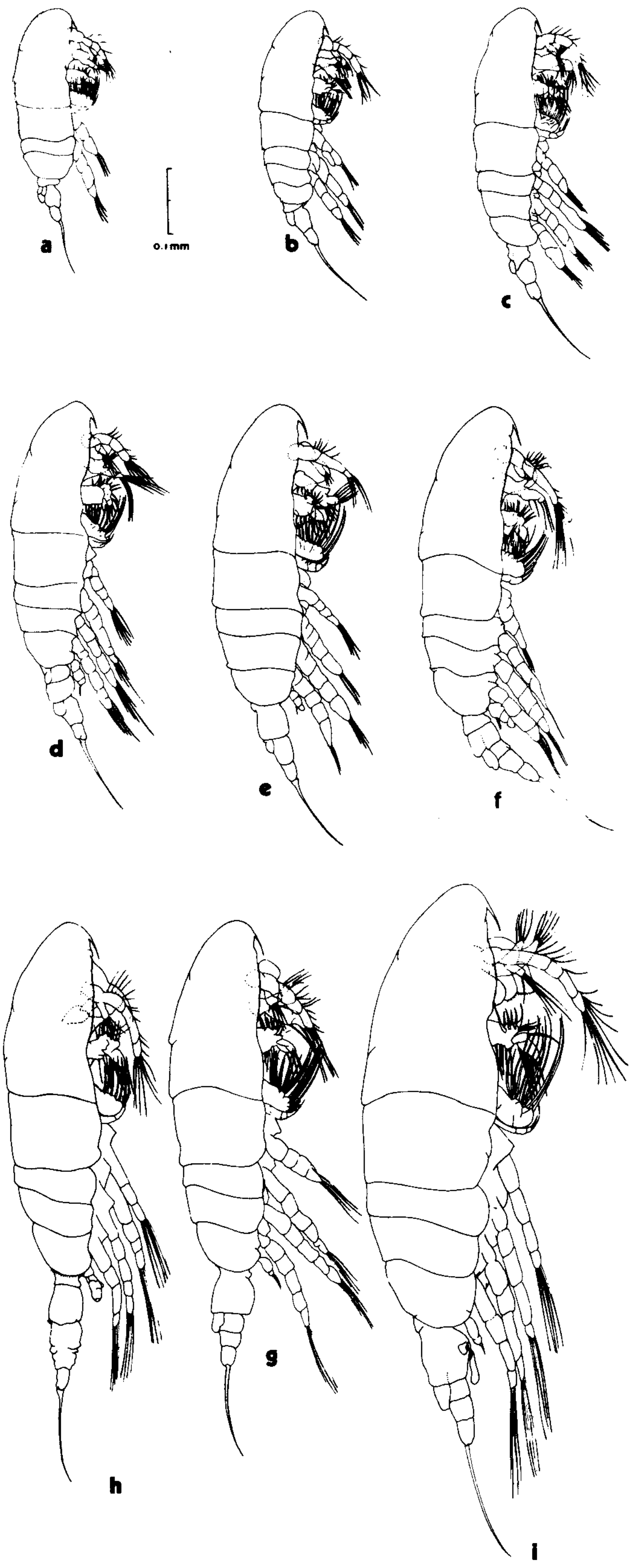

Figure 10. Lateral views of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female, with spermatophore.

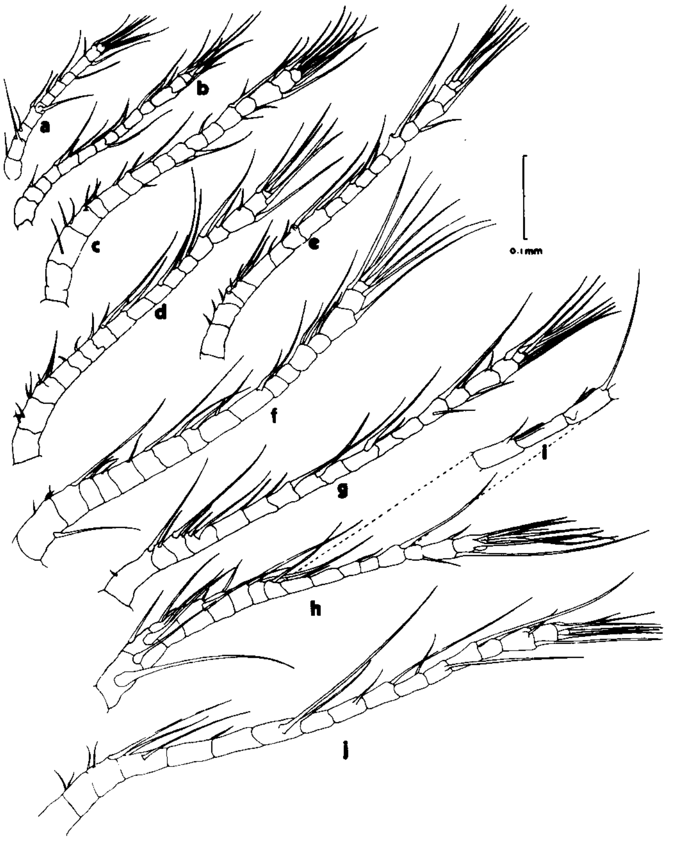

Figure 11. Antennules of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male left; *(i)* stage VI, male right; *(j)* stage VI, female.

Copepodid VI, male (Table 2; Figures 9h, 10h, 11h, 12h, 13h, 14h, 15h, 16h-i, 17h, 18h, 19g, 20f, 21e). Average length of 59 specimens (including caudal furca) was 0.859 ± 0.008 mm, range 0.770-0.924 mm, SD ± 0.036, average prosome/urosome ratio 2.93:1. The prosome has 6 segments. The cephalosome is approximately 50% as long as the prosome; it has 2 rostral filaments. The metasome has 4 segments. The urosome has 5 abdominal segments. Furcal rami have 6 plumose setae (the innermost is the smallest). The fifth legs are uniramous and asymmetrical.

Copepodid VI, female (Table 2; Figures 9i, 10i, 11i, 12i, 13i, 14i, 15i, 16i, 17i, 18i, 19h, 20g, 21f). Average length of 73 specimens (including caudal furca) was 1.008 ± 0.009 mm, range 0.924-1.097 mm, SD ± 0.04, average prosome/urosome ratio 3.35:1. The female is longer than the same male stage (average ratio 1:0.82). The cephalosome is nearly 46% as long as the prosome; it has 2 rostral filaments. This stage has the same general characteristics as the corresponding male stage, except that the urosome has 3 segments: the first one (genital) is longer than it is wide, and the third one (anal) is shorter and lacks spines and setae. The caudal furcal rami are longer than they are wide. The fifth legs are uniramous and symmetrical.

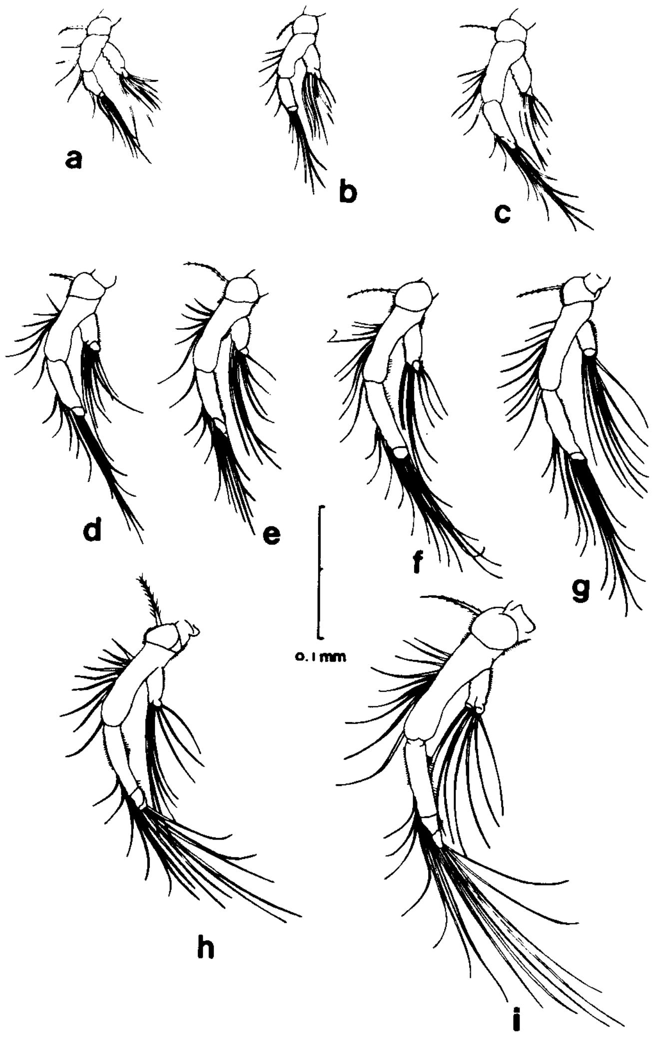

Figure 12. Antennae of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

DISCUSSION

This work describes for the first time the life cycle of the marine calanoid copepod *Acartia californiensis* Trinast from specimens reared in the laboratory. The life cycles of only 13 species of the genus *Acartia* have been described previously, and most of these descriptions are incomplete. There is a close morphological similarity between *A. californiensis* and *A. tonsa* Dana, especially in the adult stage, as well as, to a lesser extent, with *A. clausi* Giesbrecht, *A. bifilosa* Giesbrecht, and *A. iseana* Ito. It is possible that the juvenile stages of the latter four species are very similar to those of *A. californiensis*. However, published descriptions of their life cycles (except for *A. iseana*) are inadequate for further comparison and discussion of possible relationships.

Changes occurring during naupliar development of *Acartia californiensis* are: an increase in body length;

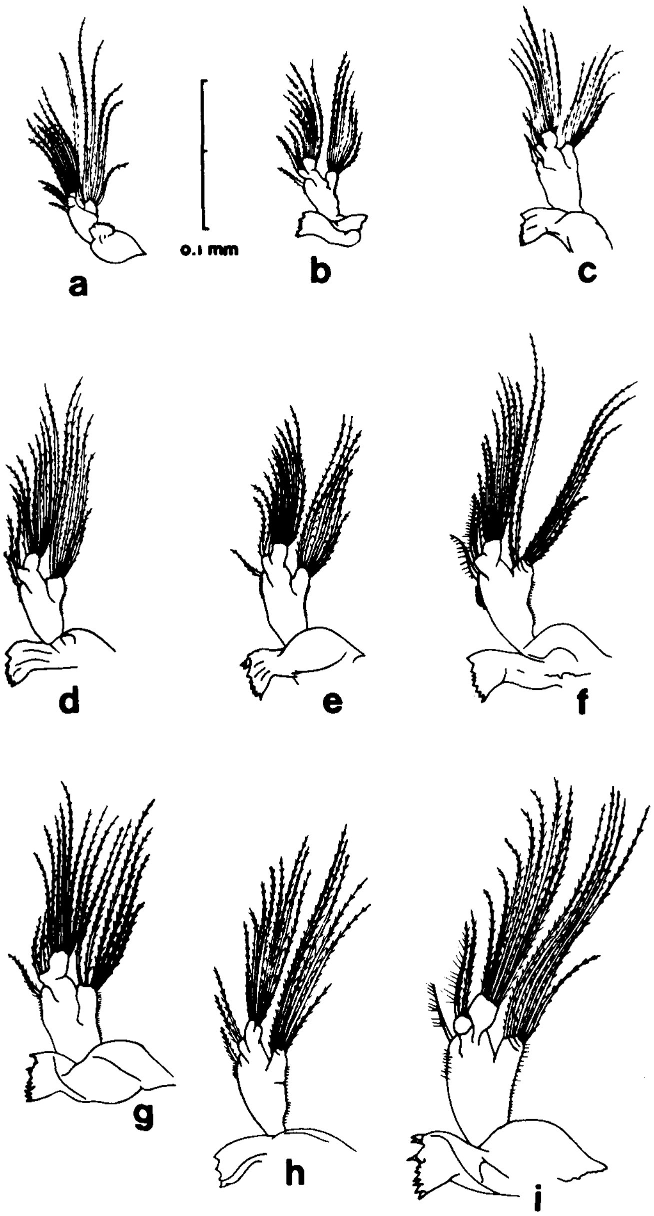

Figure 13. Mandibles of copepodid stages of *Acartia californiensis:* *(a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

an increase in the number of setae of the distal segment of the antennule; an increase in the setation of the antenna and mandible; and an increase in the number of elements in the caudal armature until naupliar stage IV. The next stages (V and VI), remain the same except for the addition of new pairs of appendages, as follows: maxillule during naupliar stage III; maxilla and maxilliped (buds) during naupliar stage V; and first and second pairs (buds) of swimming legs during naupliar stage VI.

In the copepodid development stages, which are morphologically different from the naupliar stages and essentially miniature versions of the adult stages, body size increases until copepodid stage III. At this stage it becomes possible to differentiate sexes, either by size or number of urosome segments, as well as by the presence and structure of the fifth pair of swimming legs. The female always increases more in size than the male.

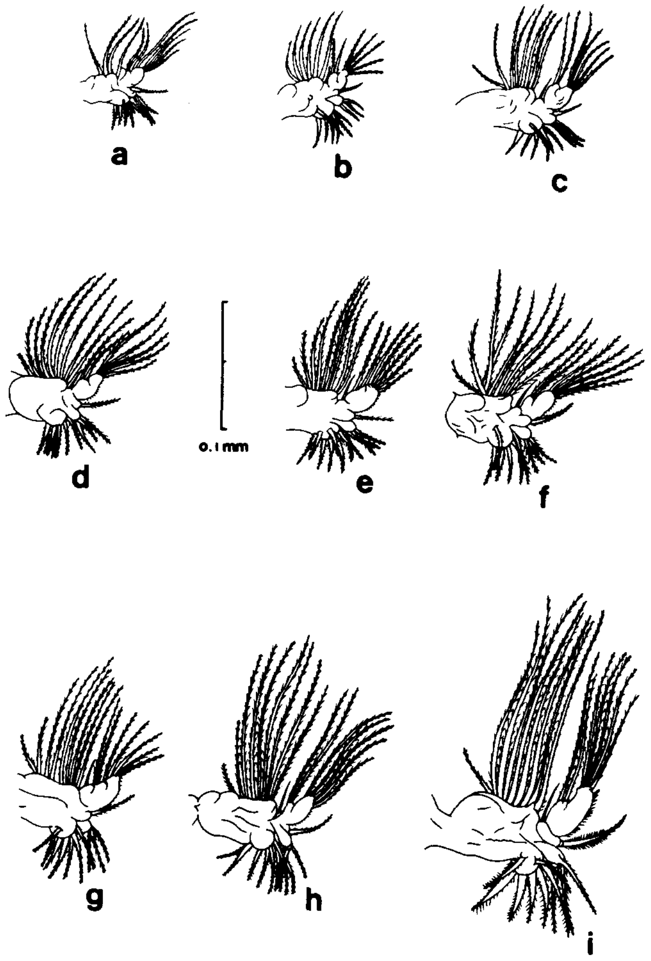

Figure 14. Maxillules of copepodid stages of *Acartia californiensis:* *(a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

At first, there are two pairs of swimming legs. Then, in each successive copepodid stage until stage IV, a new pair of swimming legs is added. Copepodid stages V and VI do not add swimming legs.

Acartia californiensis—like other neritic-estuarine species of the genus *Acartia,* such as *A. tonsa* (Zillioux and Wilson 1966; Zillioux 1969; Heinle 1969, 1970), *A. clausi* (Corkett 1968; Zillioux 1969), and *A. grani* (Vilela 1972)—proved able to live and breed for several generations under simple laboratory culturing conditions.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of the late Martin Wiggo Johnson (Sept. 30, 1893–Nov. 28,

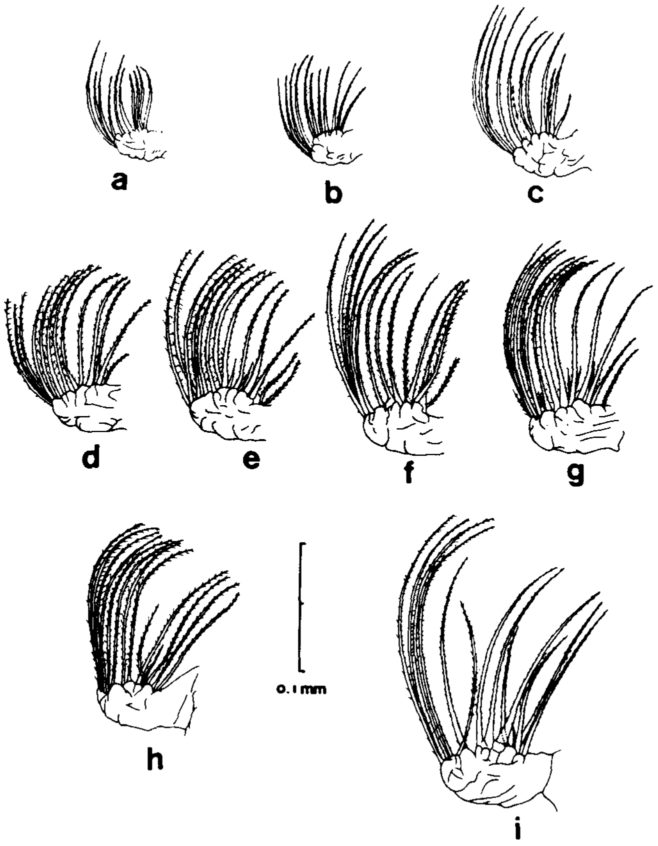

Figure 15. Maxillae of copepodid of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

1984), whose accomplishments in marine biology focused on the distribution and life history of marine crustaceans and planktonic organisms.

I thank Abraham Fleminger, Mark E. Huntley, José R. Lara-Lara, Alejandro Chagoya-Guzmán, and Alberto Carvacho-Bravo for their useful discussions and suggestions on this work. Also I thank José R. Campoy-Favela for his help with the illustrations. I am grateful to Carlos Rodríguez for his aid with the final pictures, and to Myra Pamplona-Salazar, Daniel Navarro, Hans Herrmann, and Carlos Yruretagoyena for their help with a first English version. Special thanks are also due to John C. Markham for his help in the final English version.

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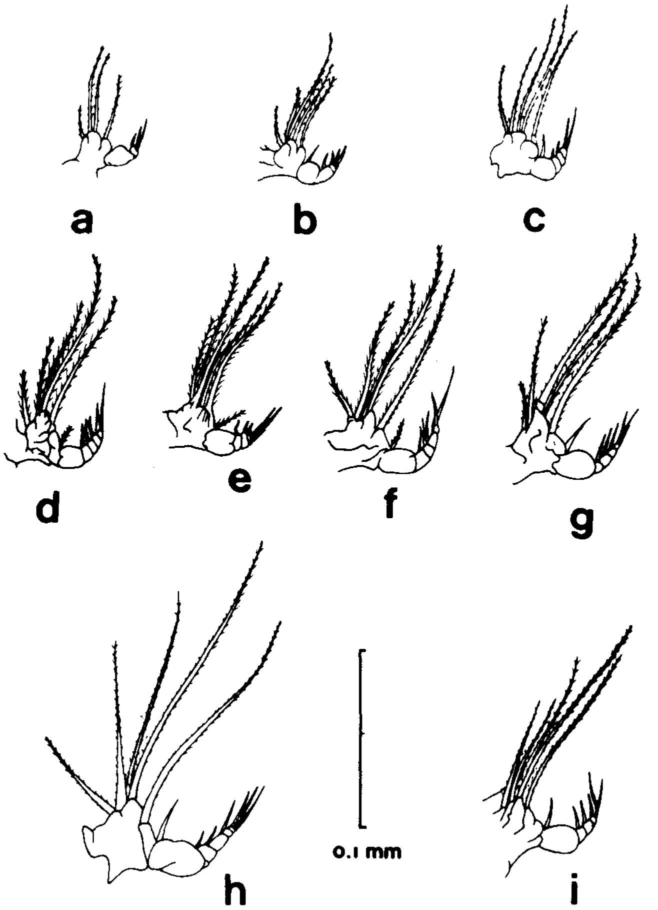

Figure 16. Maxillipeds of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

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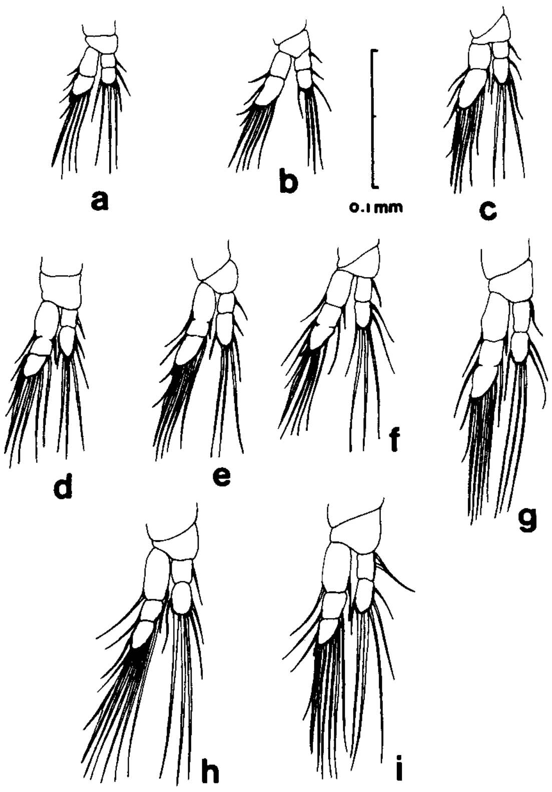

Figure 17. Leg I of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

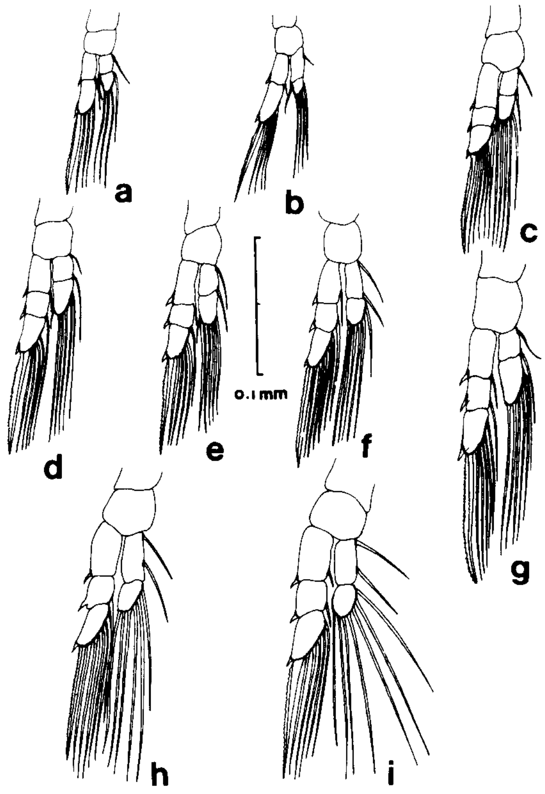

Figure 18. Leg II of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

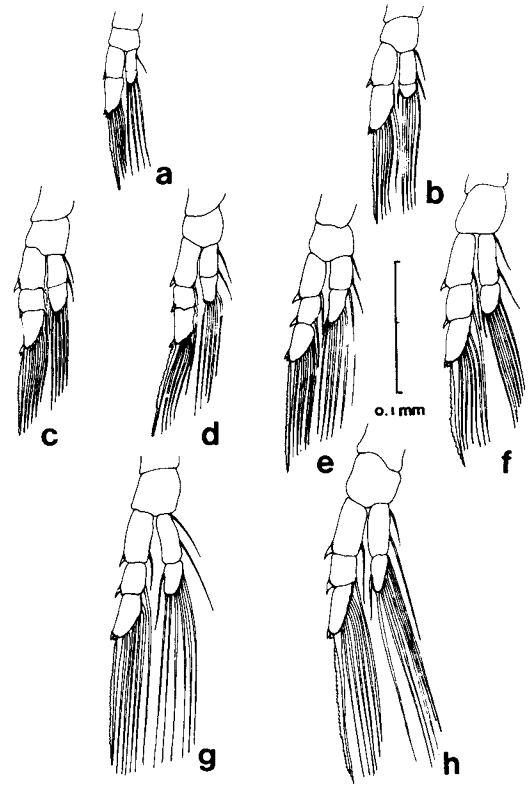

Figure 19. Leg III of copepodid stages of *Acartia californiensis: (a-b)* stages II-III; *(c)* stage IV, male; *(d)* stage IV, female; *(e)* stage V, male; *(f)* stage V, female; *(g)* stage VI, male; *(h)* stage VI, female.

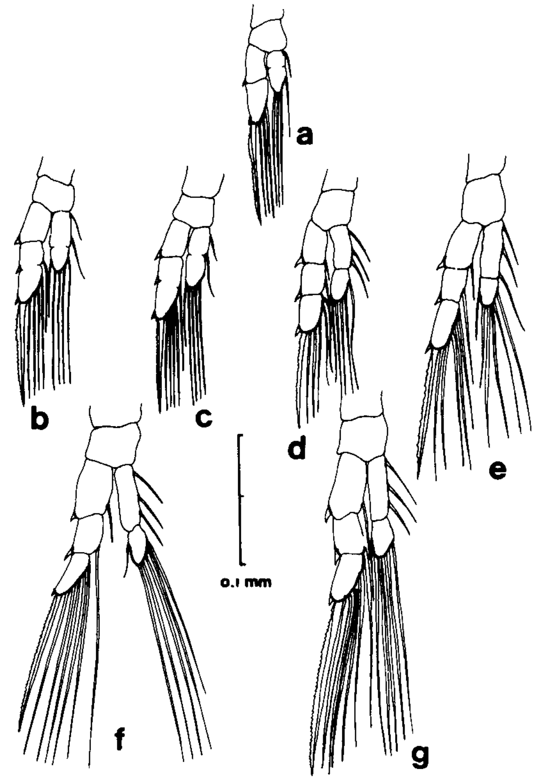

Figure 20. Leg IV of copepodid stages of *Acartia californiensis: (a)* stage III; *(b)* stage IV, male; *(c)* stage IV, female; *(d)* stage V, male; *(e)* stage V, female; *(f)* stage VI, male; *(g)* stage VI, female.

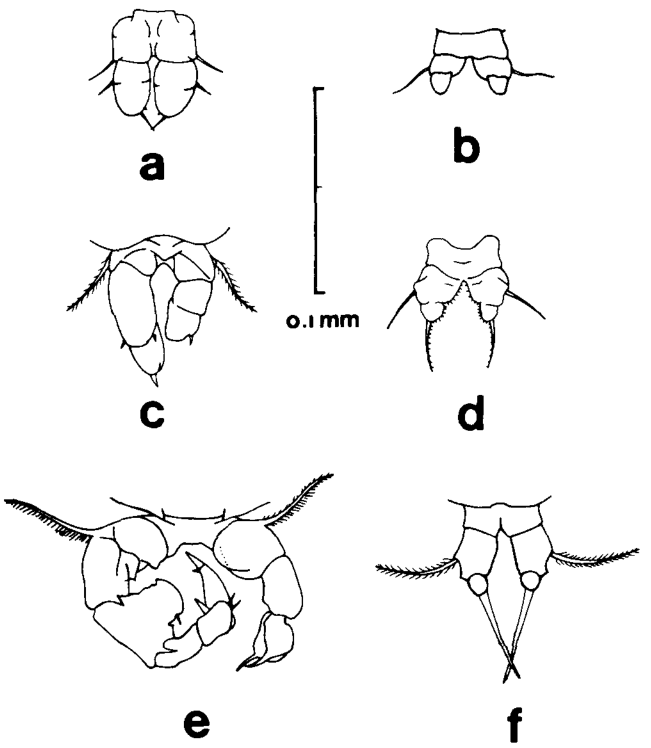

Figure 21. Leg V of copepodid stages of *Acartia californiensis: (a)* stage IV, male; *(b)* stage IV, female; *(c)* stage V, male; *(d)* stage V, female; *(e)* stage VI, male; *(f)* stage VI, female.

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THE VERTICAL DISTRIBUTION OF SOME PELAGIC COPEPODS IN THE EASTERN TROPICAL PACIFIC

YA-QU CHEN
East China Sea Fisheries Research Institute
300 Jun Gong Road
Shanghai, China

ABSTRACT

This study was based on zooplankton samples collected with standard, opening-closing bongo nets through eight depth intervals to 600 m or 800 m at 10 stations along a transect from 23°N to 3°S in the eastern tropical Pacific during May-June 1974. The investigation covered four environments: (1) the mouth of the Gulf of California, where some California Current species occurred at their southern limits: (2) the oxygen-deficient region ($0_2 < 0.1$ ml/l^{-1}); (3) the North Equatorial Countercurrent; and (4) the Equatorial Undercurrent. More than 60 species of calanoid copepods were identified and counted. The numerically dominant species—*Eucalanus subtenuis, Eucalanus subcrassus*, and *Rhincalanus nasutus*—constituted respectively 33.5%, 12.8%, and 9.5% of the total numbers. The quantitative, geographical, and vertical distributions of the most common and abundant species are described. Most of the species are subtropical or tropical, and oceanic in habitat. The ranges of vertical distribution of the abundant copepods are divided into several patterns: 0 to 200 m, 0 or 50 to 300 m, 200 or 300 to 400 m, and 400 to 800 m. The relationship between the distributions of copepods and current regimes is discussed.

RESUMEN

Este estudio está basado en las muestras de zooplancton colectadas con redes bongo estándares, a ocho profundidades, entre la superficie y 600 u 800 m de profundidad, en 10 estaciones ubicadas a lo largo de un corte entre 23°N y 3°S en el Pacífico Este tropical, en mayo-junio de 1974. Se cubrieron cuatro ambientes: (1) la boca del Golfo de California, la cual corresponde al límite Sur de distribución para algunas especies típicas de la corriente de California; (2) la región con bajas concentraciones de oxígeno ($0_2<0.1$ ml/l); (3) la Contracorriente Norecuatorial; y (4) la Corriente Ecuatorial Subsperficial. Más de 60 especies de copépodos calanoídeos fueron identificadas y contadas. Las especies numéricamente dominantes—*Eucalanus subtenuis, E. subcrassus*, y *Rhincalanus nasutus*—constituyeron 33.5%, 12.8%, y 9.5% respecitivamente del total. Se describen las distribuciones cuantitativas, geográficas, y verticales de las especies más abundantes y comunes. La mayoría de las especies es subtropical o tropical y de habitat oceánico. Los rangos de distribución vertical de aquellos copépodos abundantes muestran ciertos patrones; 0 a 200 m, 0 ó 50 a 300 m, 200 ó 300 a 400 m, y 400 a 800 m. Se discute la relación entre las distribuciones de copépodos y los regímenes de corrientes.

INTRODUCTION

Copepods are an important component of the zooplankton in the tropical Pacific (Vinogradov and Voronina 1964). The general character of the tropical plankton's vertical distribution, and the peculiarities of distribution and migration of individual species have been studied by several authors (e.g., Vinogradov and Voronina 1962, 1963). The vertical distribution of some species of copepods in some areas of the tropical Pacific Ocean was also studied by King and Hida (1954, 1957), Motoda and Anraku (1955a, b), and Heinrich (1960, 1961). The data for individual species, however, were procured mainly from east and southeast of Japan (Motoda and Anraku 1955a, b; Heinrich 1961). This study uses zooplankton samples collected on the Krill Expedition (May-June 1974) to describe the composition and vertical distribution of copepods in the eastern tropical Pacific (ETP) and their relationship to its currents.

Past studies of the ETP's copepods are sporadic and incomplete. Giesbrecht (1895) presented a taxonomic report dealing with a few species found between the Galápagos Islands and the west coast of Mexico. Additional lists and descriptions of ETP copepods may be found in Wilson (1942), Grice (1961), Lang (1964), Heinrich (1960, 1973), Fleminger (1964a, 1964b, 1967a, 1967b, 1973), Fleminger and Hulsemann (1973, 1974), and Manrique (1977), but all deal with a few select species or represent limited localities within the region. There are no general references on the relation of copepod species and their horizontal and vertical distribution to ETP currents and water masses.

Tsuchiya (1974) detailed the currents and water masses of the ETP, each with unique physical and chemical features: (1) the California Current, (2) the North Equatorial Countercurrent, and (3) the Equatorial Undercurrent. Brinton (1979) presented an extensive review of the physical, chemical, and biological environments of the ETP. The California Current off

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central and southern California, 38°N to 33°N, supports zooplankton species with temperate affinities, notably *Euphausia pacifica* and the copepod *Calanus pacificus californicus* Brodskii. Their dominance diminishes southward, where their distributions are compressed shoreward along Baja California. At the western edge of the current, the temperate fauna is replaced by species of the subtropical Central Pacific Gyre. The central water species range eastward at 30°–33°N toward southern California and northern Baja California in a large meander and then drift westward off the Punta Eugenia upwelling center (e.g., Brinton 1962, Figure 118). Immediately to the north of the ETP, off Baja California, production is largely a consequence of coastal upwelling (Blackburn 1969). Within the ETP, high concentration of nutrients in the euphotic zone is associated with the shallow thermocline (Blackburn et al. 1970).

During late May-June west of the tip of Baja California near 23°30′N, part of the California Current turns westward in a series of temporally and spatially irregular anticyclonic eddies, and eventually joins the North Equatorial Current. Another part continues southward, though it is inconsistent in direction and speed while exchanging water with the Gulf of California (Roden 1958; Wyllie 1966). In the vicinity of the gulf, the California Current loses its faunistic and hydrographic identity. It is replaced by water containing the ETP assemblage of species. Sverdrup et al. (1942) designated this water "equatorial" because of its low oxygen content and its distinctive oceanic water mass indicative of local formation. The data presented here suggest that this boundary is less abrupt than that described by Brinton (1979). Brandhorst (1958), Wooster and Cromwell (1958), Cromwell and Bennett (1959), Austin (1960), Wyrtki (1965, 1966, 1967), Tsuchiya (1968, 1970, 1974), and Love (1971, 1972, 1973) also presented physical, chemical, and meteorological characteristics of the ETP.

The objective of this study is to investigate interrelationships between the distribution of calanoid species, the equatorial currents, and the steep hydrographic gradients of oxygen and temperature characterizing the ETP. The study covers a transect of 16 stations from 23°N to 3°S (northern Mexico to the coast of Equador; Figure 1).

MATERIALS AND METHODS

Zooplankton and hydrographic data were collected in May and June 1974 during the Krill Expedition on RV *Alexander Agassiz* of Scripps Institution of Oceanography. All but one of the samples reported on here (ten stations) were collected with 0.7-m-diameter, opening-closing bongo nets (Brown and McGowan 1966); at one station an open, 1-m-diameter net was used. Mesh size of both nets was 0.33 mm, and of the cod ends 0.22 mm. The volume of water strained, measured by flow meters, varied from 500 to 1000 m^3; estimates of plankton abundance were standardized to 1000 m^3 of water strained. Bongo net tows were made with four net pairs in series, which sampled depth increments of about 40 m in the 0-160-m layer, about 80 m in the 160-500-to-600-m layer, and about 80 m in the 600-800-m layer. The separation of about 10 m between the shallow and deep series minimized the possibility of overlap. Open-water net tows were oblique hauls to about 200-m depth. Separate day and night series were made at each station; the time of day of sampling was not consistent among stations. The deep, night series failed at station 12. Actual depths of the nets were estimated from a Benthos time-depth recorder attached to the bottom net. When the recorder failed, depths were calculated from meters of wire out and the mean wire angle. The bongo nets were opened by messenger at maximum depth, towed obliquely upward while the ship steamed at 1 to 15 m/sec, and closed by messenger at minimum depth. Temperature, salinity, oxygen, phosphate, nitrate, and nitrite were measured to 1000-m depth at all stations.

In the laboratory, one of the paired samples collected by the bongo nets from each depth interval was randomly selected for analysis. Aliquots of one percent by volume were removed with a 10-cc piston pipette and counted. Males, females, and late juveniles were tallied individually for numerically dominant species. Sufficient aliquots were counted to reach at least 100 individuals for commoner species. For rarer species, 10 aliquots were counted.

Brinton et al. (1986) reviewed the species of copepods reported from the Gulf of California and considered their biogeographical affinities and distributional characteristics. Brinton et al. recognized three categories: (1) temperate, (2) broadly tropical or tropical to subtropical, Indo-Pacific or cosmopolitan, and (3) narrowly tropical and endemic. They also assigned the species to habitat categories—estuarine waters, coastal waters, neritic waters, and oceanic waters. The biogeographical and habitat assignments have been used in the notes on individual species that follow.

RESULTS

Species Composition of Copepods

About 140 species of calanoid copepods have been reported for the ETP area. In this investigation 63 species of copepods were identified and counted (Table 1). The average abundance of all individuals of the ten numerically dominant species varied from 1.5% to 33.5% of copepods in the sample. Two species, *Eucal-*

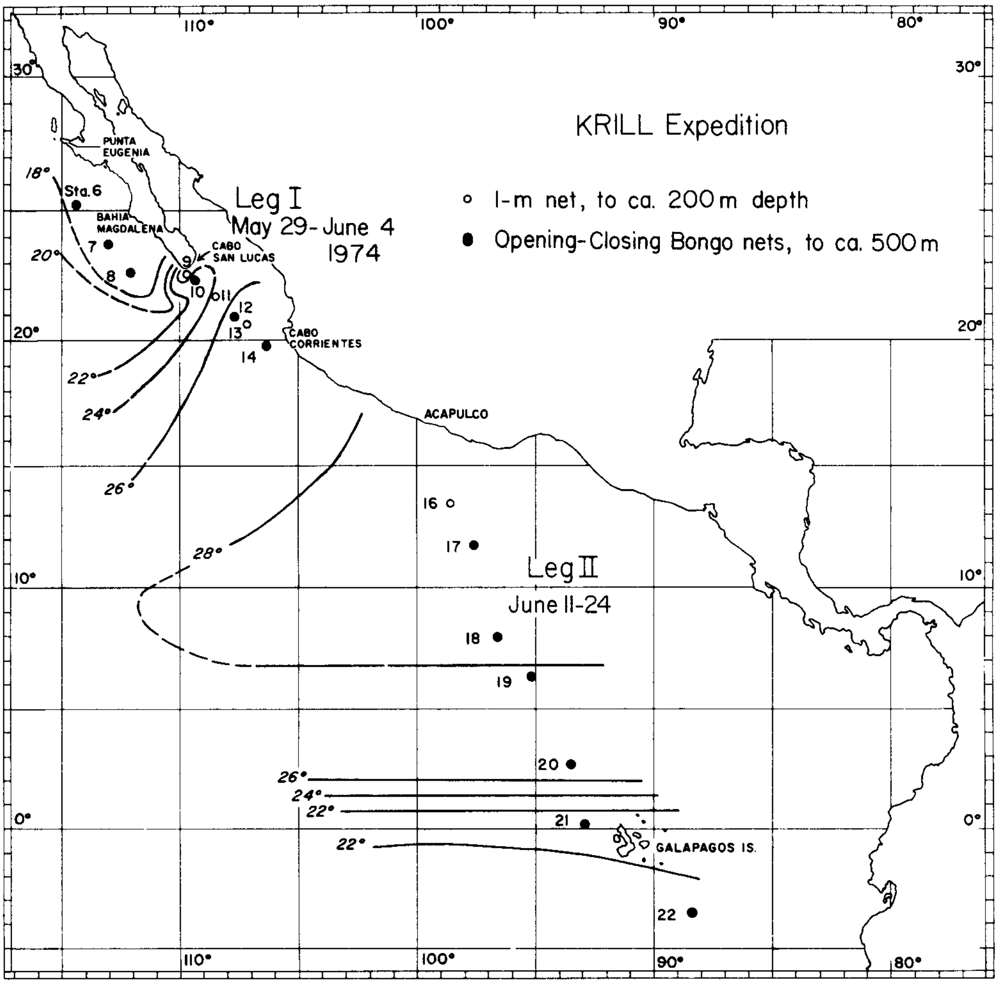

Figure 1. Localities occupied for plankton and hydrographic observations. Positions of surface isotherms beyond transect are generalized from published reports. From Brinton (1979).

anus subtenuis and *Eucalanus subcrassus*, produced the highest percentage (33.5% and 12.8%). Another 11 species were common, averaging 1.6% to 0.625% of all copepods, and 42 species were rare (< 0.5%). Two species averaged greater than 10%; 2 species from 5% to 10%; 11 species from 1% to 5%; and 6 species from 0.5% to 1% (Table 1). In general, frequencies were higher in night samples than in day samples.

Most of the copepods were tropical, oceanic species occurring throughout most of the tropical Pacific. Some species are endemic to the ETP; others are widespread in tropical latitudes.

Distribution of the Numerically Dominant Species

Eucalanus subtenuis. This species was the most abundant copepod sampled, constituting 33.5% of the total catch in combined day and night samples. It was more numerous in day samples—56.5% of the total daytime catch—and, in agreement with Timonin and Voronina's (1977) results, maximum numbers by day exceeded those of night samples. The distribution of this species was marked by large concentrations. Greatest numbers extended from 25 to 175 m, and adults were concentrated at 50-100 m at stations 17 and 19. In the daytime the maximum densities of females were 175,000 per 1000 m^3 (station 17, 0-150 m) and 11,700 per 1000 m^3 (station 19, 50 m). The maximum number of females between 0 and 100 m at station 17 was 183,000 individuals per 1000 m^3. Adults and juveniles together ranged from 25 to 50 m at stations 10 and 19. Their maximum densities in night samples, 44,400 and 483,000 individuals per 1000 m^3, were similar to those of day sampling. Maximum numbers of females, concentrated at stations 18 and 12, were 21,600 and 5,460 individuals per 1000 m^3, respectively. The number of males and of juveniles was less than that of females. Diel vertical migration was not apparent. The overall range of vertical distribution extended from the surface to 630 m (Figure 2).

Eucalanus subcrassus. This was the second most abundant species in the Krill Expedition's zooplankton samples. Its horizontal distribution was irregular; the species appeared at stations 10-14 (20°-23°N) and stations 18-22 (8°N-4°S) (Figure 3). The trend of vertical distribution was similar to that of *E. subtenuis*, occurring mainly above 200 m, but the overall vertical range

TABLE 1
Abundance of Copepod Species Observed in Bongo Net Samples from Krill Expedition

Species	Mean Percentage		
	Day	Night	Combined
1. *Eucalanus subtenuis*	56.5	10.5	33.5
2. *Rhincalanus nasutus*	5.9	13.2	9.6
3. *Eucalanus inermis*	5.9	7.2	6.6
4. *Eucalanus subcrassus*	5.4	20.1	12.8
5. *Nannocalanus minor*	4.7	1.3	3.0
6. *Eucalanus attenuatus* s.l.	2.9	2.2	2.6
7. *Cosmocalanus darwini* s.l.	2.8	4.5	3.7
8. *Rhincalanus rostrifrons*	1.6	1.6	1.6
9. *Pleuromamma gracilis*	1.4	2.1	1.5
10. *Euchaeta media* and *acuta*	0.8	5.0	2.9
11. *Lucicutia flavicornis*	0.8	1.5	1.2
12. *Pleuromamma abdominalis*	0.8	1.3	1.1
13. *Temora discaudata*	0.7	1.0	0.9
14. *Haloptilus longicornis*	0.7	1.1	0.9
15. *Pleuromamma indica*	0.6	3.0	1.8
16. *Aetideus pacifica*	0.5	1.4	0.9
17. *Centropages furcatus*	0.2	2.2	1.1
18. *Haloptilus orientalis*	0.2	1.1	0.6
19. *Scolecithrix danae*	0.1	1.3	0.7
20. *Euchaeta rimana*	0.1	4.9	2.4
21. *Canthocalanus pauper*	0.1	1.0	0.6

The following species all occurred at abundances less than 0.5%.
Calanus chilensis
Calanus pacificus californicus
Candacia bipinnata
Candacia curta
Candacia pachydactyla
Candacia truncata
Clausocalanus spp.
Clytemnestra rostrata (Harpacticoid)
Euaetideus acutus and *giesbrechti*
Eucalanus hyalinus
Euchaeta longicornis
Euchaeta spinosa
Euchirella maxima
Euchirella sp.
Gaetanus minor
Haloptilus bradyi
Haloptilus ornatus
Haloptilus oxycephalus
Heterorhabdus papilliger
Heterostylites major
Labidocera acuta
Labidocera sp.
Lophothrix sp.
Lucicutia clausi
Lucicutia ovalis
Metridia sp.
Neocalanus gracilis
Neocalanus robustior
Pachyptilus sp.
Parauchaeta sp.
Phaenna spinifera
Phyllopus integer
Pleuromamma xiphias
Pontellina plumata
Pontellina sobrina and *morii*
Scaphocalanus minuta
Scaphocalanus sp.
Scolecithricella abyssalis
Scolecithricella ctenopus
Scolecithricella nicobarica
Scolecithrix bradyi
Undinula vulgaris

was deeper. Diel vertical migration was not indicated in a comparison of day and night samples (Figure 3). The vertical range of males was shallower than that of females and extended to 250 m in day samples and 150 m in night samples.

Eucalanus attenuatus s.l. This category includes *E. attenuatus* s.s. and *E. sewelli* s.s., which were not counted separately. They were distributed mainly between 25 and 100 m (Figure 4). Their vertical distribution was mainly confined to depths above 100 m at stations 14-16. They appeared only in the surface between 18°N and 20°N. The distribution of males and females was similar, but the females were more numerous, and the number of juveniles was less than that of males. At the mouth of the Gulf of California they were found only between 25 and 75 m at station 10. The maximum concentration was 30,700 individuals/1000 m^3. Numbers were higher in night samples. Diel vertical migration was not obvious. Generally, the species were distributed above 100 m. At stations 10 and 12 abundance was highest above 50 m, and the maximum number was 26,500 individuals/1000 m^3. Female numbers were higher in night samples. The species were not observed in samples from the oxygen-deficient layer or from stations near Mexico.

Eucalanus inermis. This was one of the most numerically important species in the ETP. Its vertical distribution ranged from the surface to the deepest layer sampled. Adults occurred mainly at three stations: 17, 18, and 19; thus its principal horizontal distribution extended from 6°N to 11°N with greatest abundances from 300 to 600 m. Females were more abundant than males, being concentrated mainly from 500 to 800 m in the day samples. The trend of vertical distribution of juveniles was similar to that of the females, whereas males occurred at shallower depths. Adults were less frequent at the surface (Figure 5), especially at stations 12, 14, 16, 17, and 20-22. At stations influenced by the California Current, *E. inermis* was found at the surface. The distribution of juveniles differed from that of the adults: juveniles occurred mainly near the surface at stations 14 and 16 and at mid- and deep depths at stations 17 and 18. Juveniles appeared below 500 m at stations 19-21. At station 22, which was located south of the equator, adults and juveniles were found in large numbers.

Rhincalanus nasutus. Although *R. nasutus* is distributed widely in tropical latitudes, its distribution in the ETP is restricted to the middle and maximum depths sampled. South of 8°N its distribution appears to have been influenced by the Equatorial Countercurrent (Figure 6). The maximum concentration occurred between 500 and 600 m. At station 21, the maximum number of females was 11,100 individuals/1000 m^3 at about 500 m. From 20°N to near the equator, *R. nasutus* was not present from middle depths to the surface. Numbers of females were higher than those of the male, and diel vertical migration was not apparent.

Rhincalanus rostrifrons. This species was less abundant than *R. nasutus*, but its distribution was more extensive. In day samples, *R. rostrifrons* occurred mainly beneath 50 m south of 11°N. In general, both females and males were concentrated above 400 m. The highest densities reached 5000 individuals/1000 m^3 (Figure 7). The species occurred in lower numbers and at fewer depths at stations 12 and 14. Diel vertical migration was not apparent. *R. rostrifrons* appears to be better adapted to the ETP than *R. nasutus*.

Cosmocalanus darwini s.l. This category includes *C. darwini* s.s. and *C. caroli* s.s., which were not counted separately. They constituted about 3.65% of the total number of copepods and occurred mainly from 3°N to 4°S above 200 m at stations 20-22. The maximum number of females (17,900 individuals/1000 m^3) was concentrated between 100 and 150 m (Figure 8). Apart from this, there were other high concentrations above 120 m at stations 14, 12, and 10 between 23° and 20°N. Although diel vertical migration was not apparent, the numbers at night were much higher than the numbers in day samples. The species were concentrated between 50 m and the surface. Female numbers were higher than those of males.

Pleuromamma indica. The numbers of this species were the highest for the genus *Pleuromamma* in the ETP. The species was found at most of the stations occupied (Figure 9). Females occurred primarily between 250 m and 600 m during the day. The depths of maximum concentrations were from 350 to 400 m between 6°N and 8°N. Maximum numbers were 2800 individuals/1000 m^3. Female vertical distribution at night was from 150 to 300 m between 20°N and 3°N. It appears that vertical distribution was shallower north of 12°N than south of this latitude. The data suggest that the species undergoes diel vertical migration.

Pleuromamma gracilis. The numbers of this species were less than that of *Pleuromamma indica*. *P. gracilis* was distributed at most of the stations occupied except stations 16 and 17. Females occurred mainly from 200 to 600 m between 5°S and 8°N in day samples. The depths of maximum concentrations were from 300 to 450 m. Females occurred only above 200 m between 20°N and 22°N. Maximum numbers were 11,600 individuals/1000 m^3. Most males occurred mostly above 200 m in night samples (Figure 10).

Pleuromamma abdominalis. The numbers of this species were the lowest for the genus in the ETP. Females were distributed at most of the stations except stations 16 and 17. Females usually occurred between 200 and 600 m, but at stations 18-20 they occurred at depths below 400 m in day samples. The ranges of vertical distribution of females and males were similar. The maximum concentration was 1000 individuals/1000 m^3 and was found between 300 and 450 m. The shallow depths of females and males in night samples suggest pronounced diel vertical migrations over an extensive vertical range (Figure 11).

Euchaeta rimana. *E. rimana* was confused with *E. marina* until it was separated by Bradford (1974). Its number (2.42%) occupied ninth position among copepods of the ETP area. It was found in lower numbers in day samples than in night samples. Its vertical distribution extended from the surface to 600 m, but in general it was concentrated above 100 m. The maximum number was 35,600 males, 13,800 females, and 62,400 juveniles per 1000 m^3. The species occurred in low numbers (130-800 individuals/1000 m^3) below 200 m.

Euchaeta acuta and *media*. *E. acuta* and *E. media* were not distinguished from one another in the present study. Together they constituted the most abundant category of *Euchaeta* in the ETP. They were less frequent in day samples than in night samples. Their horizontal distribution was vast, extending from the California coast to the southernmost stations. Their vertical distribution was from the surface to the deepest depths. They were not found at the surface or subsurface in the oxygen-deficient area north of 6°N.

Nannocalanus minor. Although this is a tropical to subtropical, oceanic species, *N. minor* was found mainly at station 10, which was dominated by hydrographic conditions indicative of the California Current. The maximum number of females reached 11,900 individuals/1000 m^3 in day samples and 119,000 individuals/1000 m^3 in night samples. It also was found at station 22 (about 4°S), where it was concentrated mainly above 200 m in day samples. Elsewhere *N. minor* occurred mainly above 100 m. Its overall depth distribution tended to coincide with the depth of the thermocline.

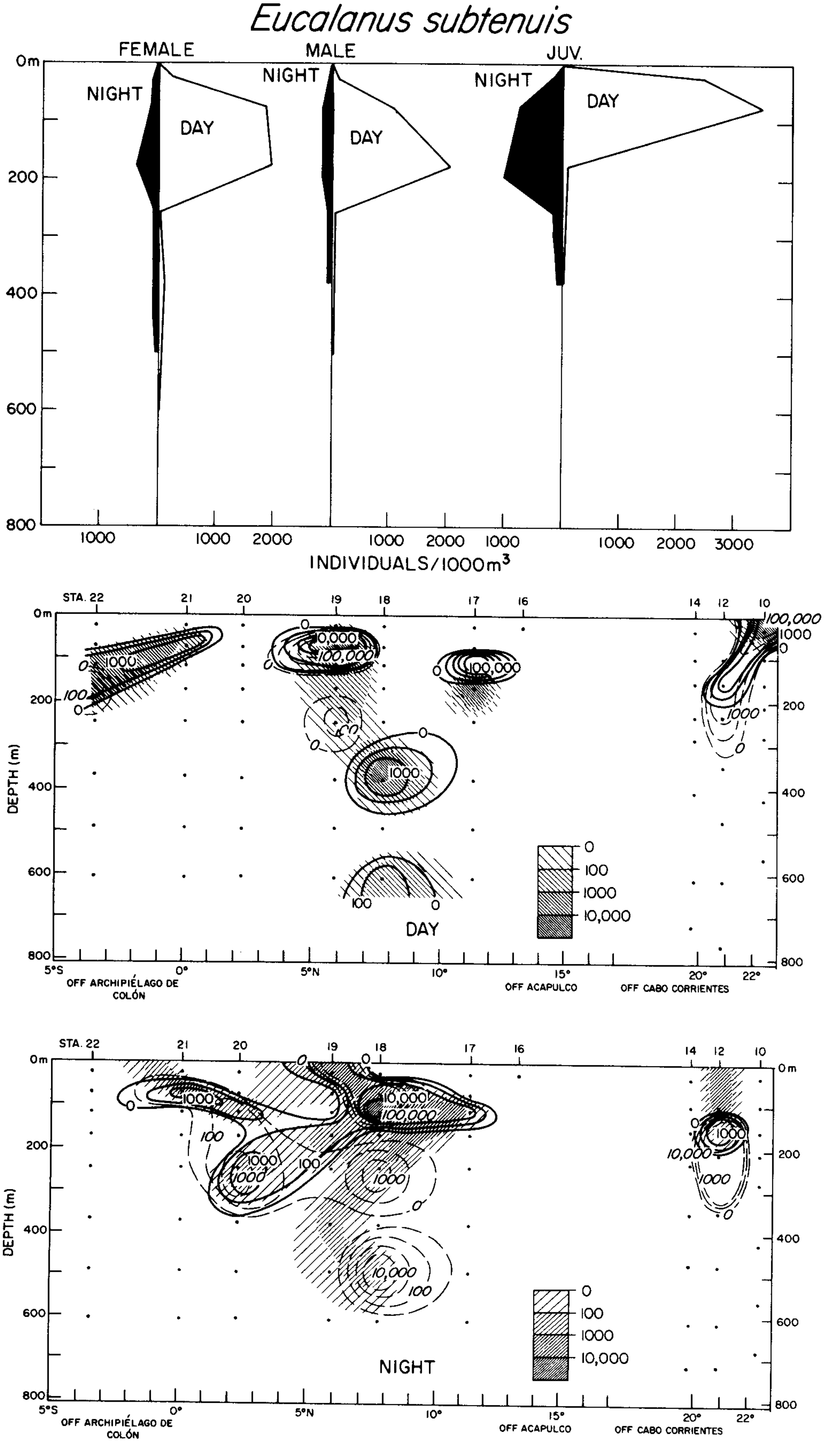

Figure 2. *Eucalanus subtenuis. Top panel:* Vertical profile of mean abundance (no./1000 m^3) of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. Night values to left, day values to right. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Sampling stations are shown across top, latitudes across bottom, and vertical depth scale along sides of middle and bottom panels. Dots represent midpoints of oblique tows.

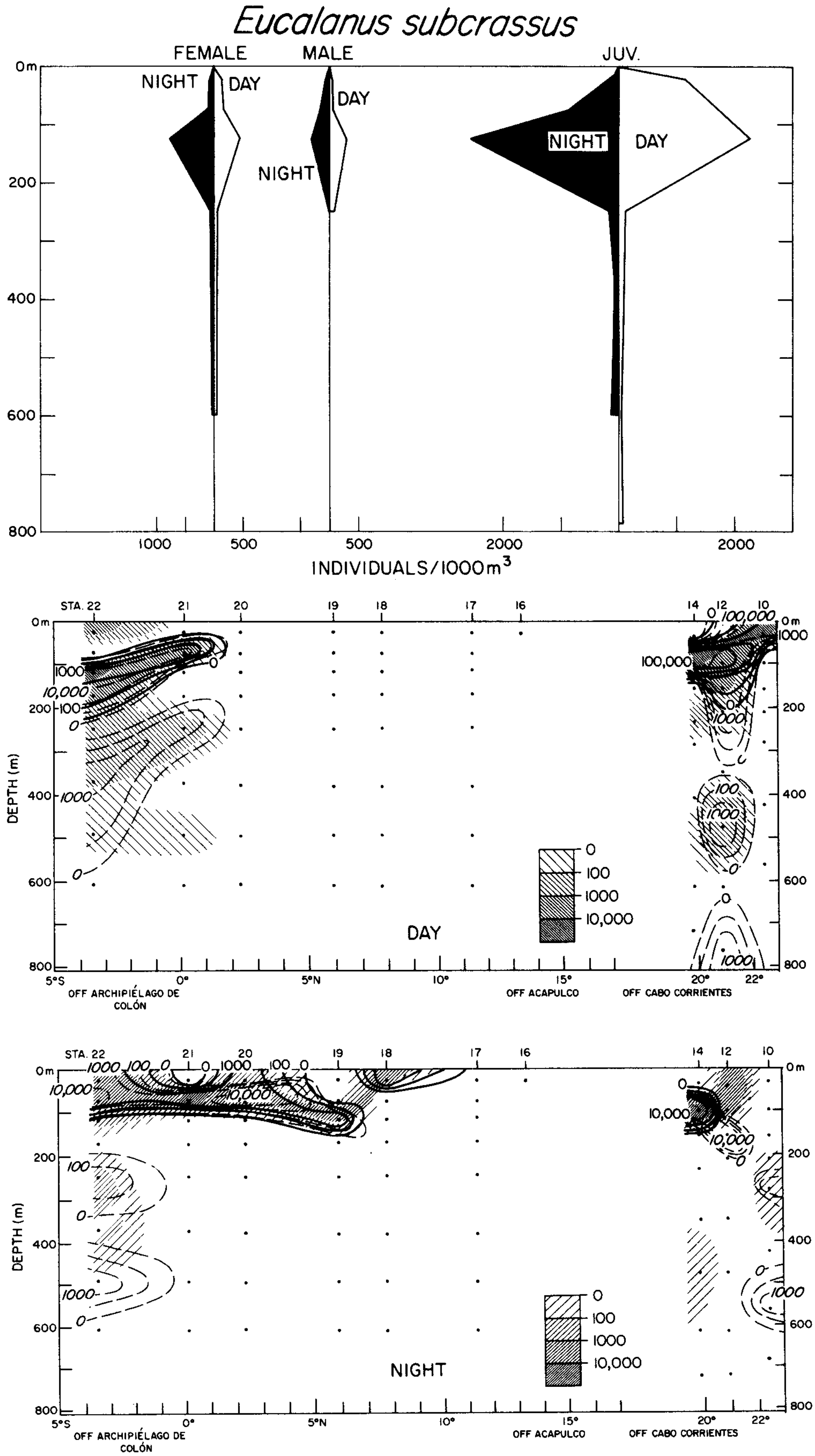

Figure 3. *Eucalanus subcrassus. Top panel:* Vertical profile of mean abundance of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Dots represent midpoints of oblique tows.

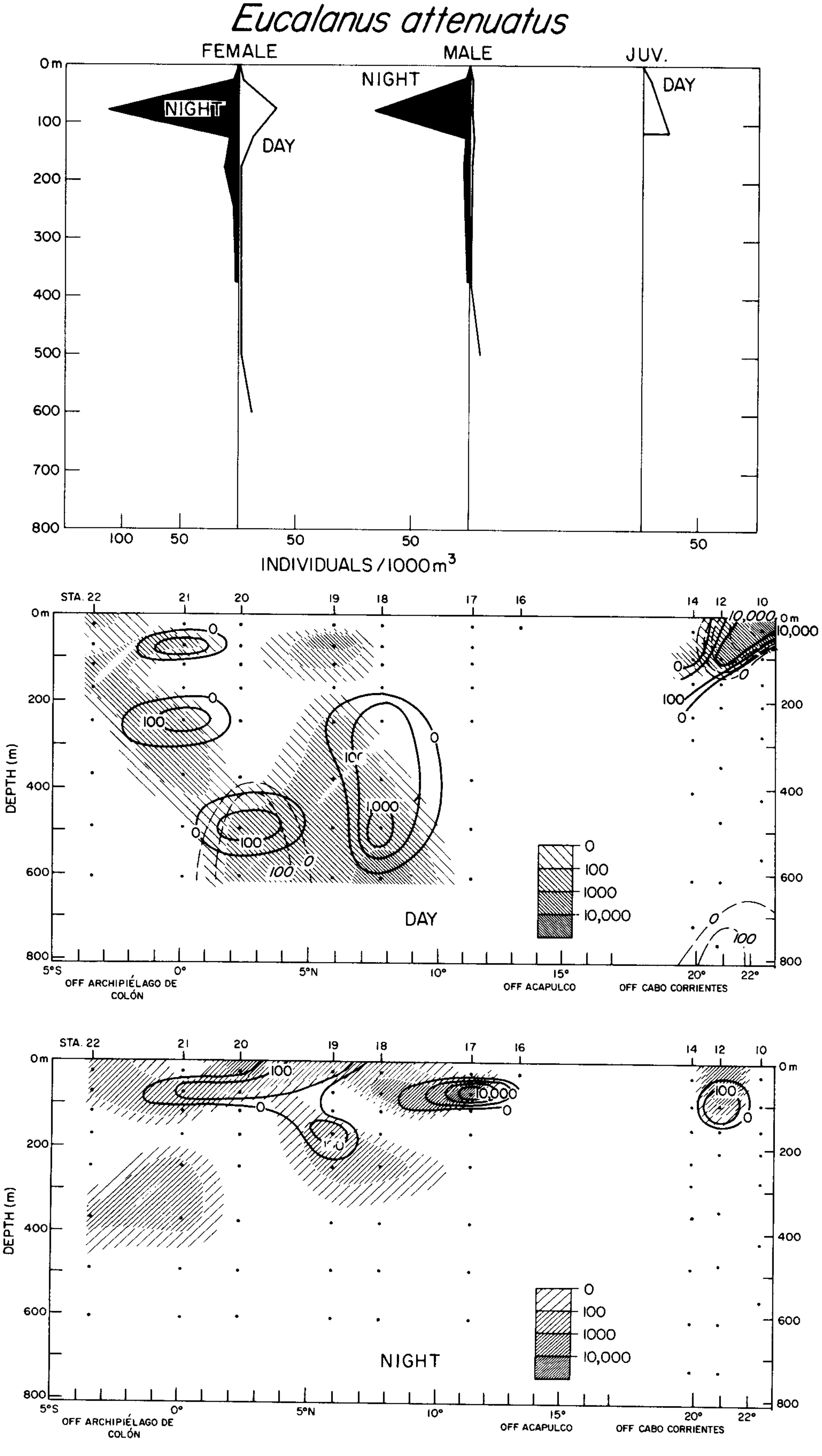

Figure 4. *Eucalanus attenuatus* s.l. *Top panel:* Vertical profile of mean abundance of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Dots represent midpoints of oblique tows.

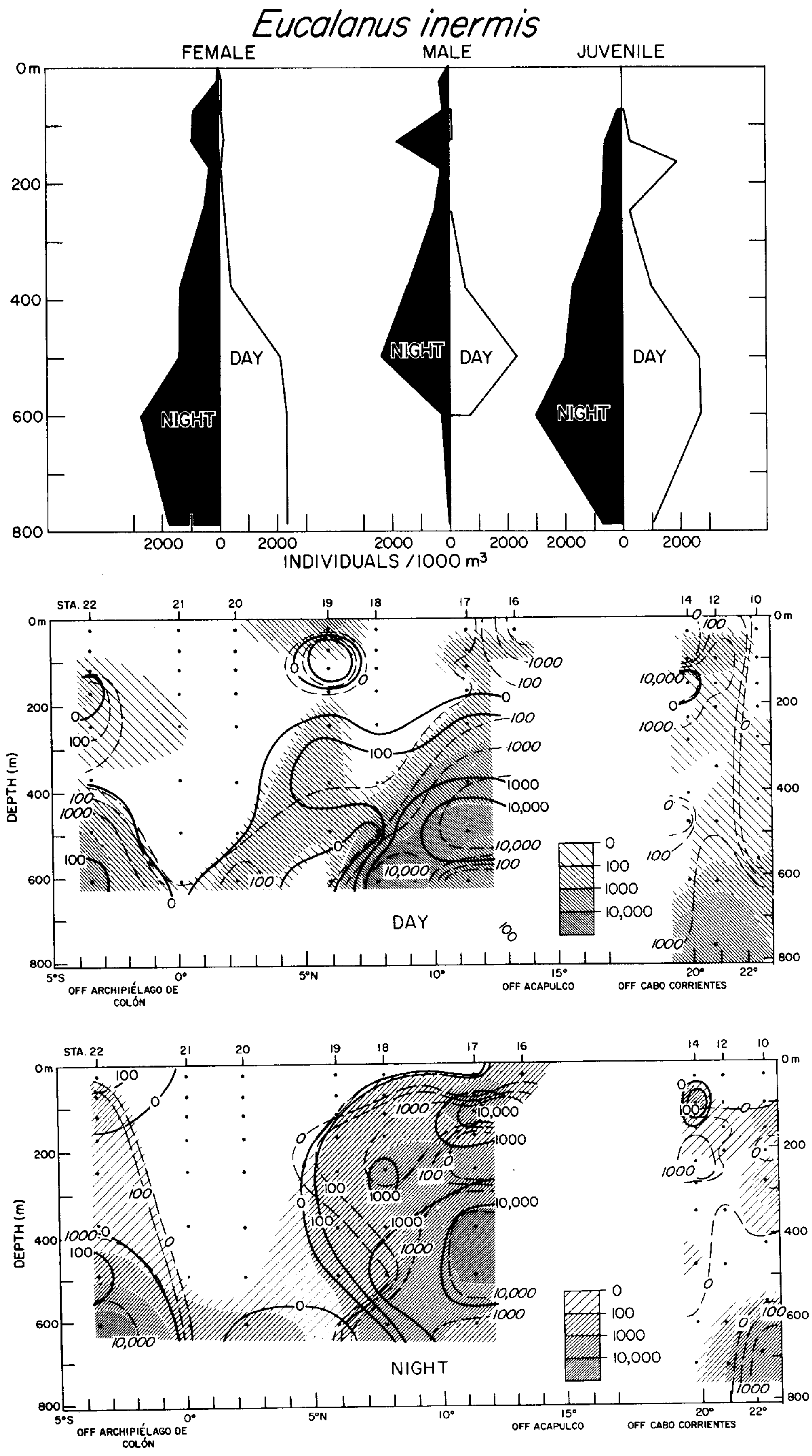

Figure 5. *Eucalanus inermis*. *Top panel:* Vertical profile of mean abundance of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Dots represent midpoints of oblique tows.

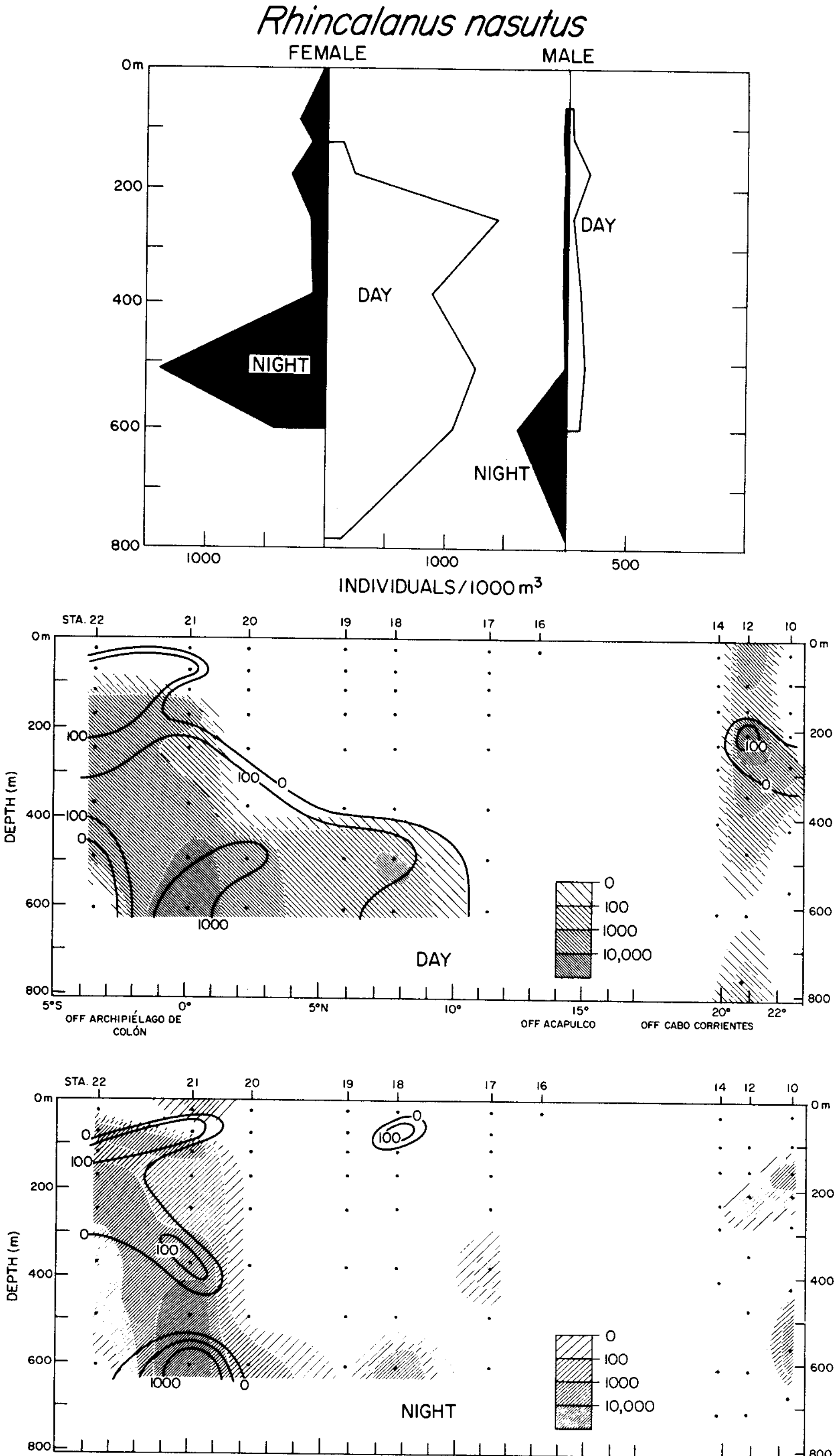

Figure 6. *Rhincalanus nasutus. Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of males (continuous line) and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of males (continuous line) and females (crosshatching). Dots represent midpoints of oblique tows.

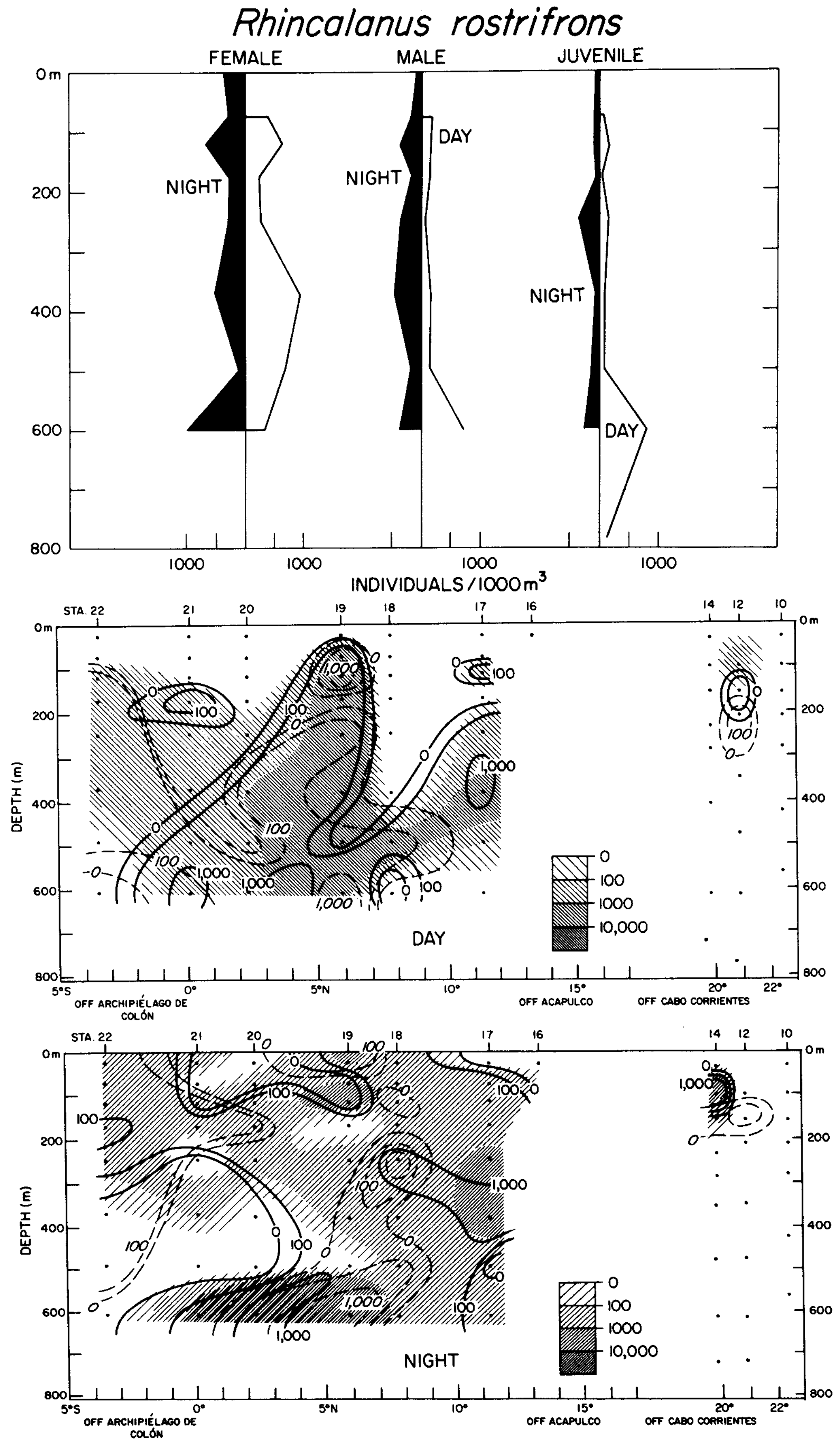

Figure 7. *Rhincalanus rostrifrons*. *Top panel:* Vertical profile of mean abundance of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m³) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Dots represent midpoints of oblique tows.

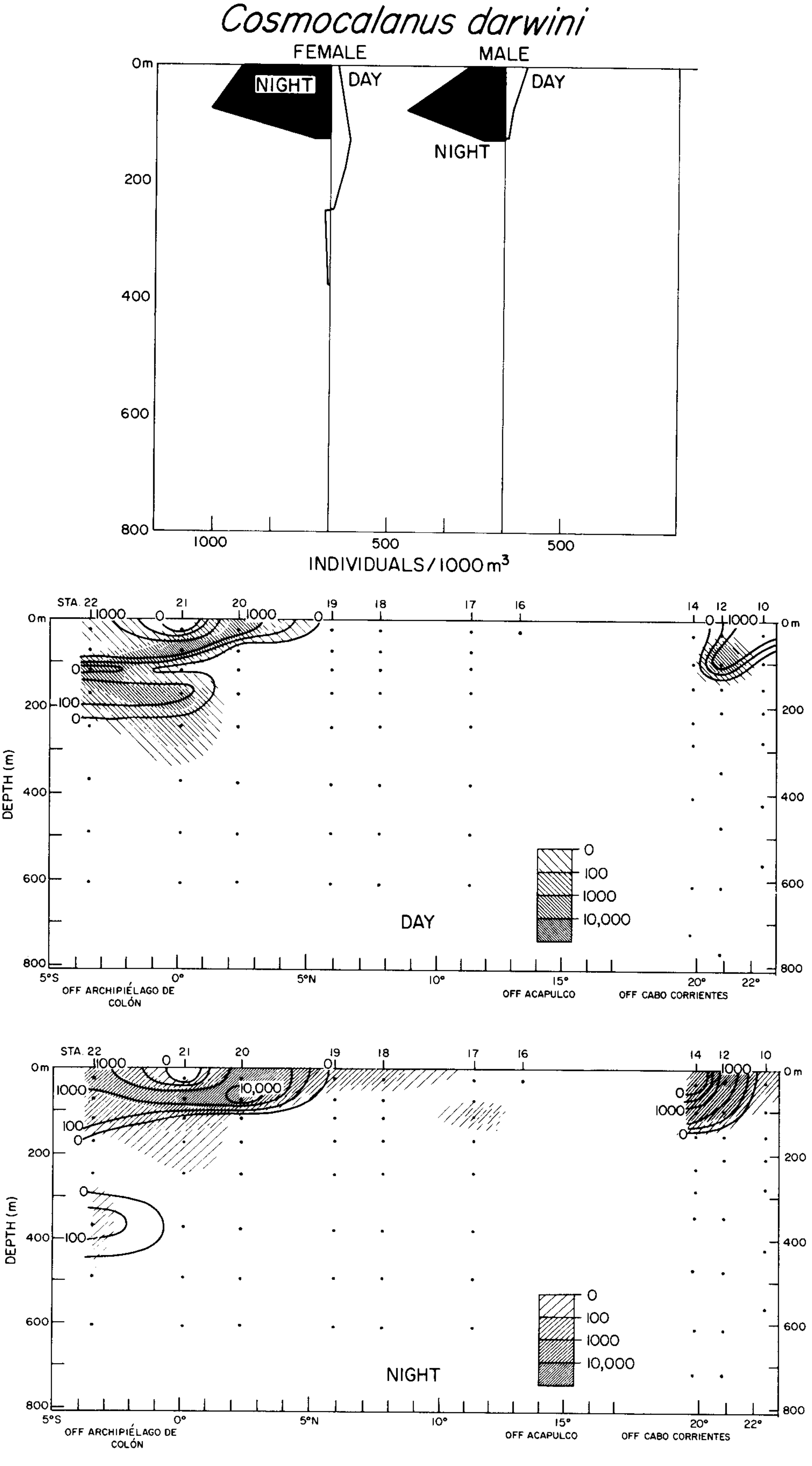

Figure 8. *Cosmocalanus darwini* s.l. *Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of males (continuous line) and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of males (continuous line) and females (crosshatching). Dots represent midpoints of oblique tows.

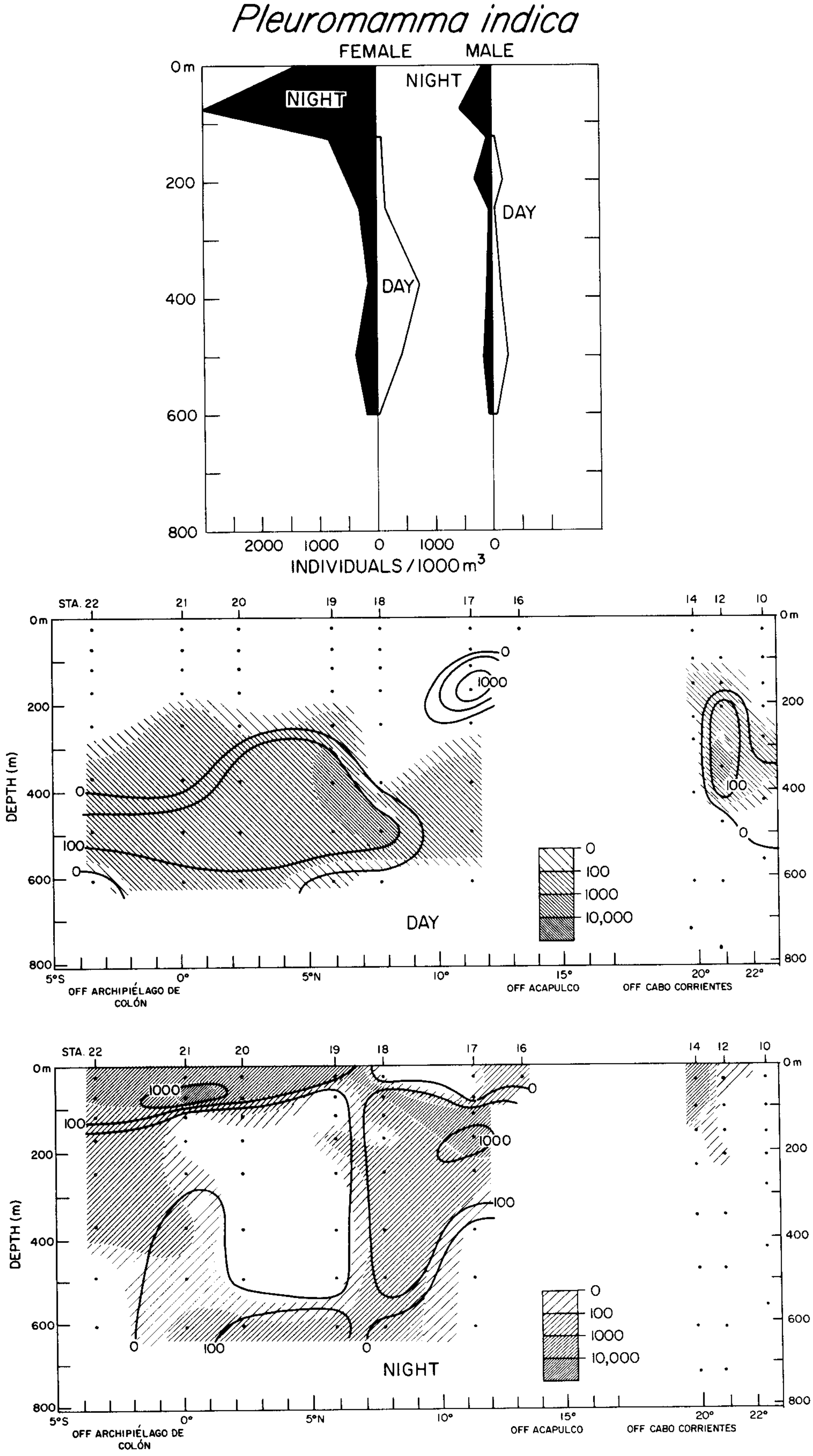

Figure 9. *Pleuromamma indica. Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of males (continuous line) and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of males (continuous line) and females (crosshatching). Dots represent midpoints of oblique tows.

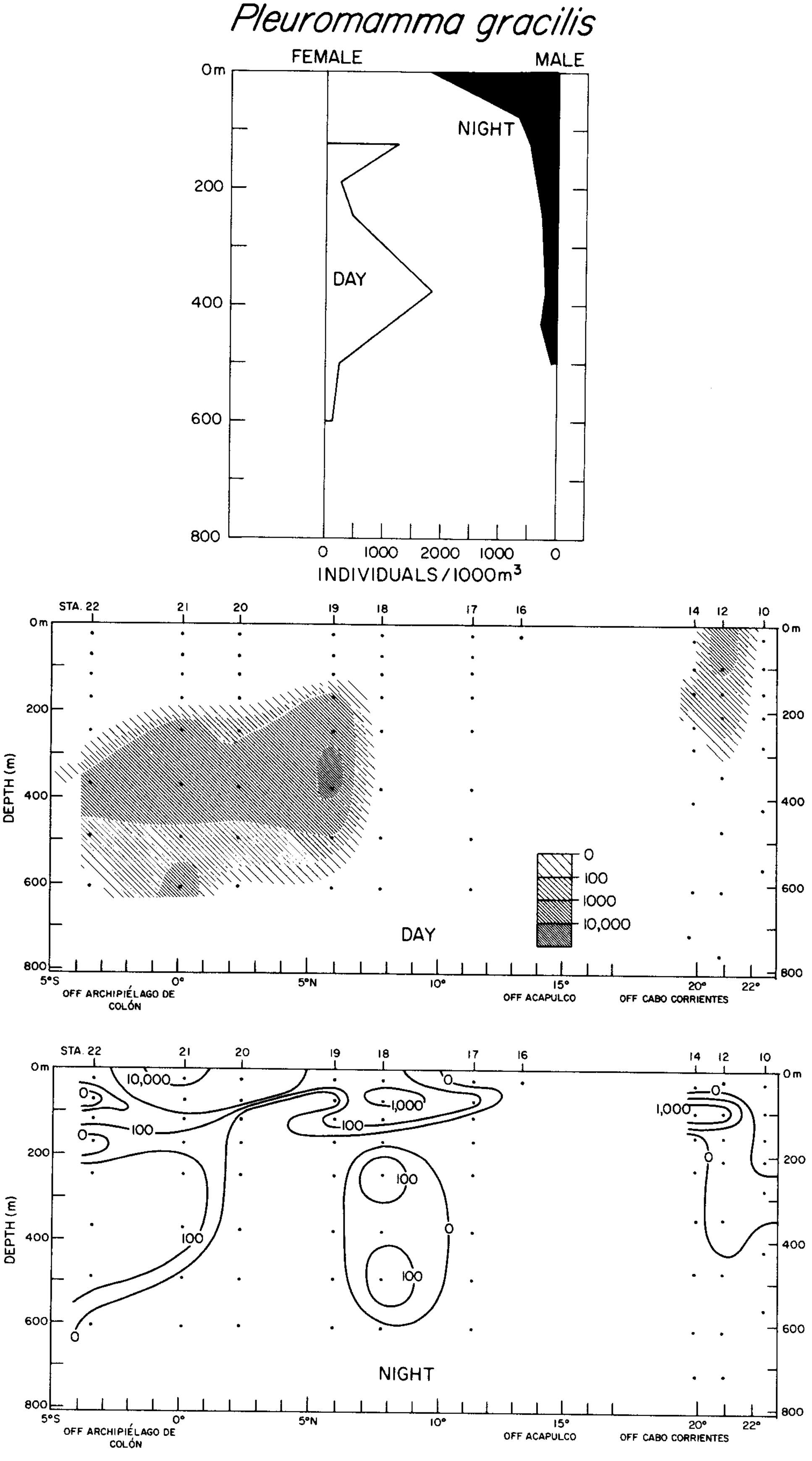

Figure 10. *Pleuromamma gracilis. Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of females. *Bottom panel:* Vertical profile of contoured abundance in night samples of males. Dots represent midpoints of oblique tows.

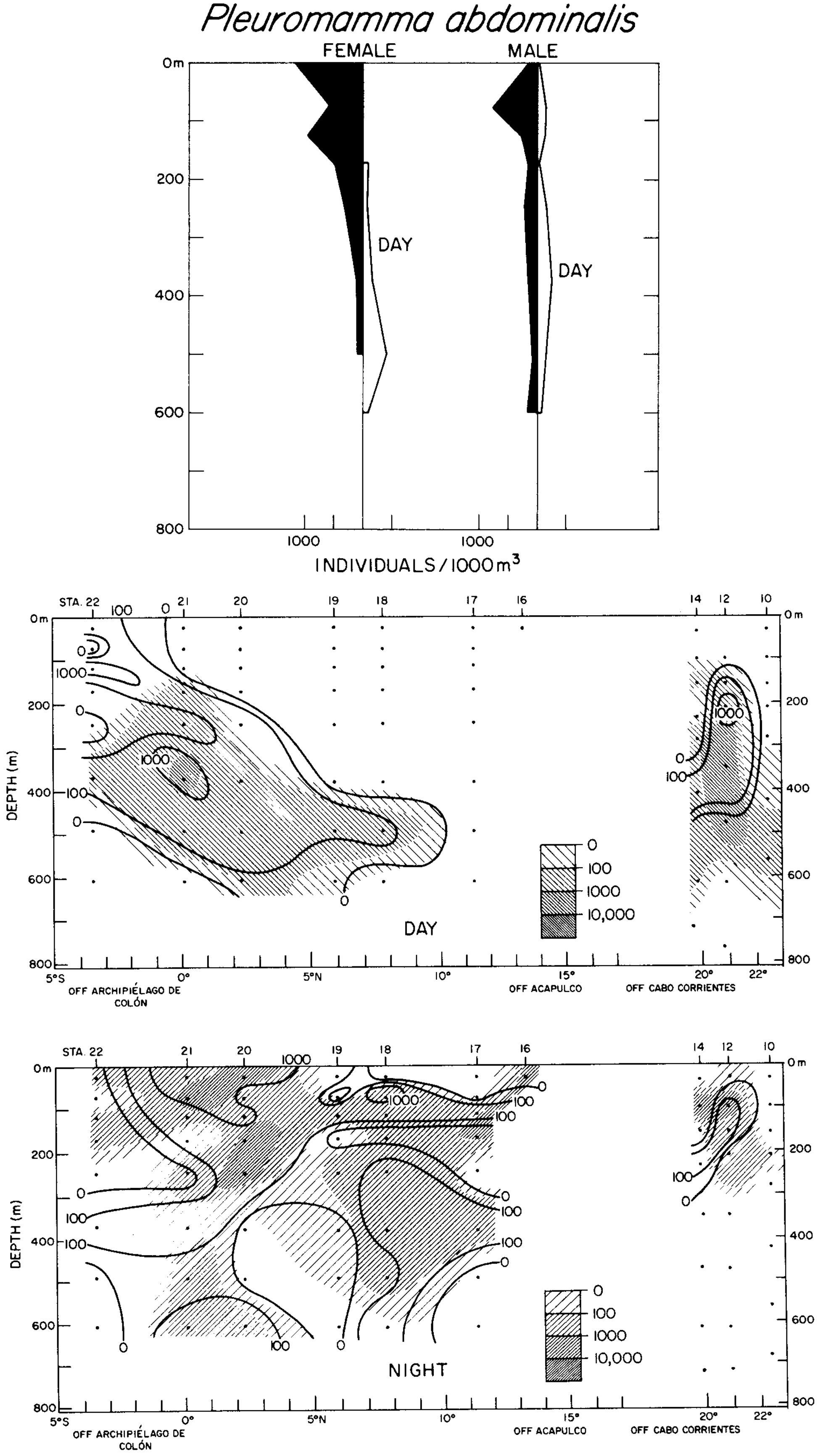

Figure 11. *Pleuromamma abdominalis. Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. Night values to left, day values to right. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of males (continuous line) and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of males (continuous line) and females (crosshatching). Dots represent midpoints of oblique tows.

Scolecithrix danae. This broadly tropical oceanic species was found everywhere except in the oxygen-deficient area of the ETP. The main concentrations occurred above 150 m, especially in night samples. The maximum numbers were 300-1500 individuals/1000 m^3 at station 14 from 0 to 100 m. In day samples the total numbers were lower, but female numbers were higher. Vertical distribution tended to coincide with the thermocline. Abundance declined from north to south.

Aetideus pacifica. This species occurred mainly below 100 m. In general, it ranged from 100 to 350 m at abundances varying from 200 to 500 individuals/1000 m^3. The maximum female concentration was 8160 individuals/1000 m^3. Female numbers were higher than those of males and juveniles. In night samples *A. pacifica* was found in the uppermost 100 m. A maximum of 13,600 individuals/1000 m^3 was observed between 0 and 100 m at station 14; the species also occurred at 600 m. It was not found in the oxygen-deficient area.

Temora discaudata. This species is found commonly in coastal waters of tropical to warm-temperate areas. It occurred mainly above 400 m over the entire area of investigation, except for the oxygen-deficient region. Its main concentrations were found between 50 to 100 m. Its maximum concentration (11,000 individuals/1000 m^3) was in a day sample from 0 to 50 m at station 10, although numbers were usually higher in night samples than in day samples.

Neocalanus gracilis. This species was found mainly in mid-depth to surface samples taken south of 10°N (stations 18-22). The greatest depth of occurrence was 500 m, where the number (142 individuals/1000 m^3) was less than that at 50 m. In night samples the species was found, in greater numbers than in day samples, between 0 and 350 m. The maximum number was 1020 individuals/1000 m^3 in 0-50 m at station 21. *N. gracilis* was not present in the oxygen-deficient area.

DISCUSSION

Hydrographic Conditions

To understand the distributions indicated above, it is necessary to review oceanographic environmental conditions along the Krill Expedition's cruise track. These conditions were originally described by Brinton (1979).

Between stations 10 and 11, flow appeared easterly, as indicated by the slope of the σ_t surface and the surface temperatures of 23.8° and 24.9°C (Figures 12 and 13). At station 12, near 21°N off the middle of the mouth of the gulf, subsurface influence of the California Current was evident from the higher oxygen content (Figure 13b) and from the presence of northern euphausiid species, although surface temperatures were > 24°C (Figure 13a). Stations 13 and 14 were south of 21°N, lying in waters considerably warmer at all depths than those to the north, and showed fully developed characteristics of the ETP, evidently associated with northerly or easterly flow toward the gulf.

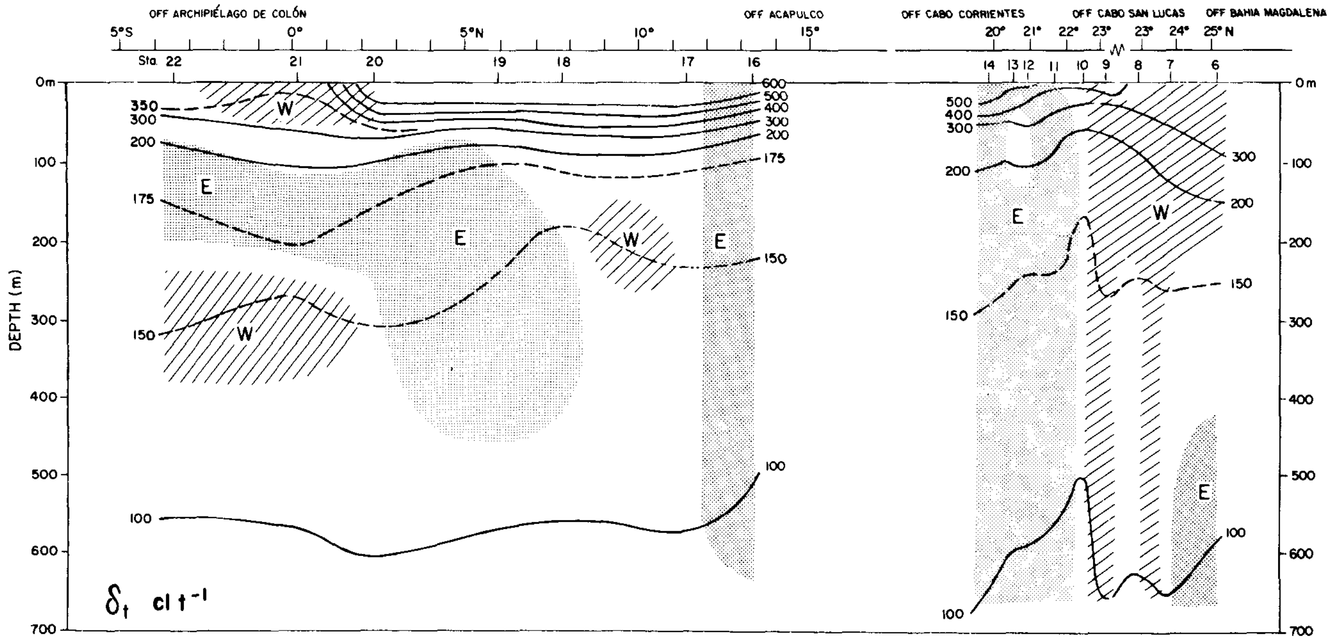

Figure 12. Vertical distribution of thermosteric anomaly σ_t (cl$_t^{-1}$). Direction of zonal components of flow is inferred from slopes of isopleths; inferences within about 2° of the equator are least reliable. From Brinton (1979).

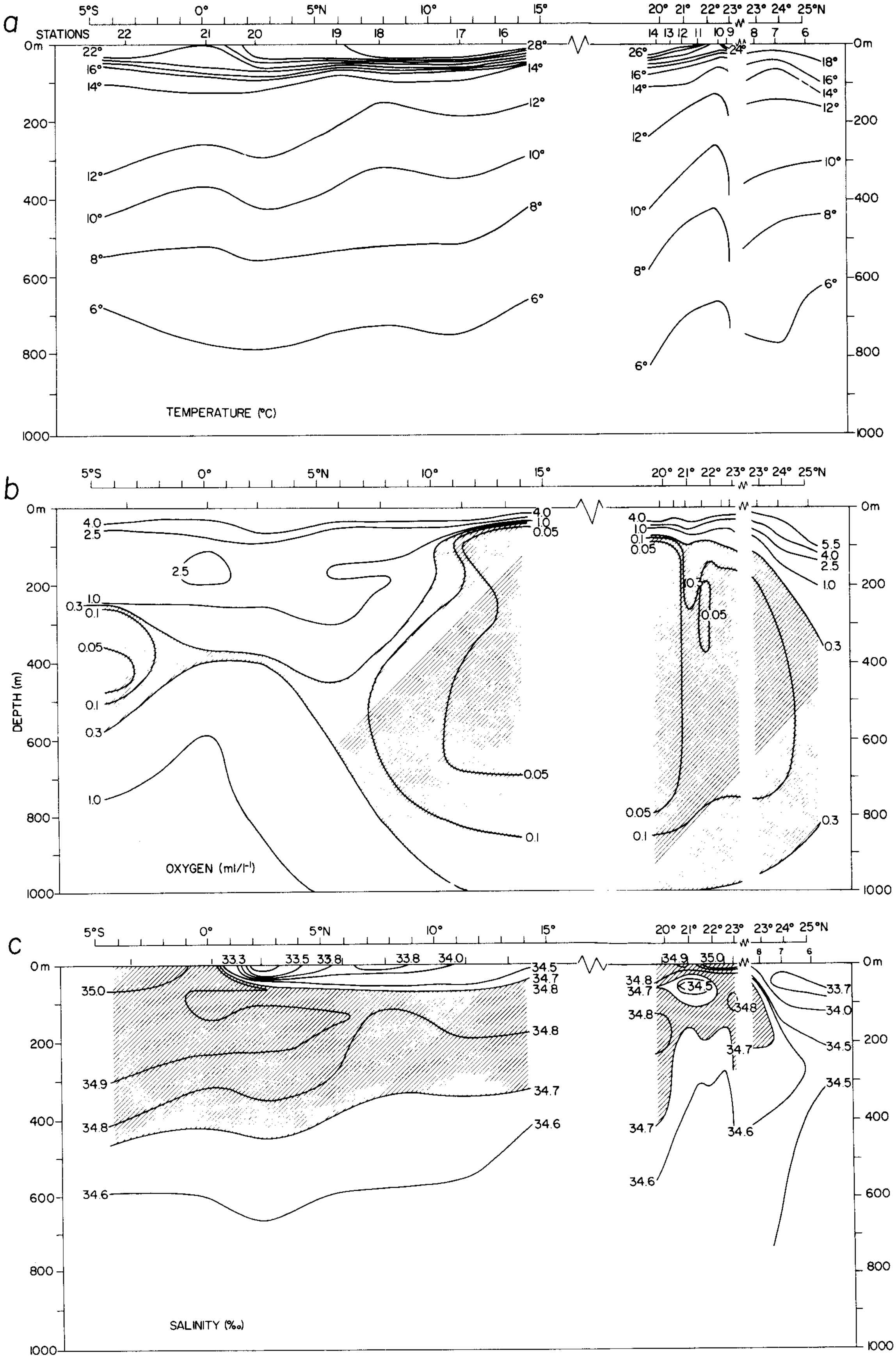

Figure 13. Profiles of *(a)* temperature, *(b)* dissolved oxygen, with depths having < 0.3 ml/l⁻¹ crosshatched, and *(c)* salinity, with depths having >34.7‰ crosshatched. From Brinton (1979).

Along the Krill Expedition's cruise track, the weak thermocline at 50-100 m off Baja California gave way to the strong ETP thermocline between 25 and 60 m off the gulf (Figures 12 and 13a).

The distribution of oxygen (Figure 13b) also showed strengthening of ETP characteristics along the southerly track, as oxygen values in the minimum layer progressively decreased south of 25°N, where the lowest measurable value (< 0.05 ml/l^{-1}) was first encountered. This low value was uniformly distributed in a thick, oxygen-deficient layer between 11°N and 21°N (Figure 13b). Extremely low oxygen concentrations (< 0.05 ml/l^{-1}) were also present at some depths at stations 11 and 22.

Salinity (Figure 13c) was $< 34‰$ above 100-m depth off Baja California, indicating water of northern origin. The core of the flow appeared in the 33.7‰ southerly tongue at 50-100 m. The axis of the deep countercurrent of the California Current (Reid et al. 1958) was evident at 200-400 m, where water having salinity in excess of 34.5‰ extended northward. To the south, ETP salinities were high (34.6-35.0‰), except for a localized subsurface patch off the mid-gulf (station 12), where salinity was lower (34.5‰) and associated with an increase in oxygen above 300 m and with plankton species indicative of California Current influence.

The Krill Expedition's transect (stations 16-22) across the ETP was between the 88°W and 98°W meridians. Tsuchiya's (1974) April-May 1967 chart of flow above 500-m depth showed flow varying between easterly and westerly in the area where stations 16 and 17 were situated (ca. 13°N and 11°N off southern Mexico). On the Krill Expedition's transect, the slope of σ_t surface (Figure 12) indicated an easterly component of flow at all observed depths between stations 16 and 17; however, south of station 17 there was a westerly component centered near 200-m depth. In these latitudes the characteristic ETP oxygen minimum was highly developed beneath 70 m, indicating little dilution by other water masses (Figure 13b). High temperature (> 28°C) and low salinity ($< 34‰$) were found in the 50-m-thick mixed layer (Figure 13a,c). Stations 18 and 19 were occupied between 6°N and 8°N, typically the zone of the North Equatorial Countercurrent. Tsuchiya (1974) showed easterly flow across 97°E between 4°N and 6°N during April and May 1967, and Love (1971) reported easterly flow between 4°N and 8°N during July 1967. Wyrtki and Kendall (1967) provided evidence that eastward geographic flow in the countercurrent is maximal from March through June, overlapping the time of the present observations. Brinton (1979) reported finding considerable faunistic evidence of the countercurrent's influence in this zone.

At station 20 (2°41′N), extremely low surface salinity ($< 33.3‰$) indicated westerly flow in the mixed layer. However, the presence here of 13°C water (Jones 1973) and a secondary oxygen maximum at 100-200 m indicated a contribution from the easterly Equatorial Undercurrent, which mixed with ETP water beneath and lateral to the undercurrent's core. At equatorial station 21, 0°19′N, stronger evidence of the undercurrent's activity was seen between 100- and 225-m depth in the 13°C water, the secondary oxygen maximum in excess of 2.5 ml/l^{-1}, and the secondary salinity maximum. Station 22, south of the Galápagos Islands, was also in water of high surface salinity, again indicating little or no contribution of westerly water by the South Equatorial Current. Salinity was homogeneous between 60 and 275 m, but an oxygen maximum near 150 m intercepting the generally oxygen-deficient water beneath the mixed layer indicated penetration by water from a direction other than the east. Faunistically, this locality was mixed, but without the easterly intrusions found at the equator (Brinton 1979).

Patterns of Vertical Distribution of Copepods in the ETP

Vertical distribution of copepods in the Krill Expeditions transect varied, probably because of the different environmental conditions encountered along the cruise track. It is necessary to consider the variations in vertical distribution among the species in order to understand relationships within the ETP.

Table 2 shows that patterns of vertical distribution of ETP copepods can be divided as follows:

From the surface to 200 m. Sixteen species occurred between the surface and 200 m. They constituted about 28% of the total calanoid numbers identified and were mainly tropical and oceanic. Environmental conditions were rather different above than below 200 m. The thermocline layer extended from 50 to 80 m, and the temperature gradient tended to be very steep. The range of temperature differed in different areas; thus it was 14°-28°C south of 15°N, while north of 20°N it was 12°-26°C. Salinity ranged from 33.3 to 34.9‰ above 200 m. The low salinity suggests the possible influence of neritic waters, and the zooplankton included some broadly neritic species such as *Centropages furcatus* and *Temora discaudata*.

From the surface or 50 m to 320 m. The range of vertical distribution of five ETP copepods was from the surface to 300 m. *Phaenna spinifera* was distributed between 200 m and 320 m in day samples and between the surface and 200 m in night samples. *Lophothrix* sp. was rare and occurred only from 200 to 320 m where hydrographic conditions are relatively stable (12°-14°C, 34.0-34.8‰).

TABLE 2
Maximum Depth Range of More Abundant Copepod Species in Day (▭) and Night (■) Samples

Species	Distribution layer (m)								
	0-50	50-100	100-150	150-200	200-319	319-438	438-557	557-676	676-800
Lucicutia ovalis	■								
Candacia truncata	■								
Scolecithricella ctenopus		▭ ■							
Scolecithricella abyssalis		▭							
Candacia pachydactyla	■	▭							
Clausocalanus sp.		■							
Euaetideus giesbrechti		▭							
Neocalanus robustior			▭						
Eucalanus hyalinus			▭						
Calanus pacificus californicus	▭	▭	▭	■					
Temora discaudata	▭ ■	▭ ■	■	■					
Pontellina plumata		▭		▭					
Pontellina morii	■			▭					
Candacia bipinnata		■	▭	■					
Candacia curta	▭		▭	▭					
Heterostylites major				▭					
Eucalanus subcrassus		▭			▭				
Undinula vulgaris	■	■	■		■				
Phaenna spinifera	■	▭ ■	■	■	▭				
Scaphocalanus minuta				■	■				
Lophothrix sp.					■				
Nannocalanus minor	▭ ■	▭ ■	▭		■	▭			
Cosmocalanus spp.	▭ ■	▭ ■	▭ ■	▭	▭	■			
Calanus chilensis			▭ ■	▭	▭	▭			
Euchaeta longicornis	▭ ■	▭ ■	▭ ■	▭ ■	▭ ■	▭ ■			
Euchaeta spinosa	▭	▭	▭ ■	▭ ■	■	■			
Euchaeta rimana	▭ ■	▭ ■	▭ ■	■	▭ ■	■			
Haloptilis longicornis		▭ ■	▭ ■	▭ ■	▭ ■	▭ ■	▭ ■		
Lucicutia clausi				■	▭ ■	▭ ■	▭		

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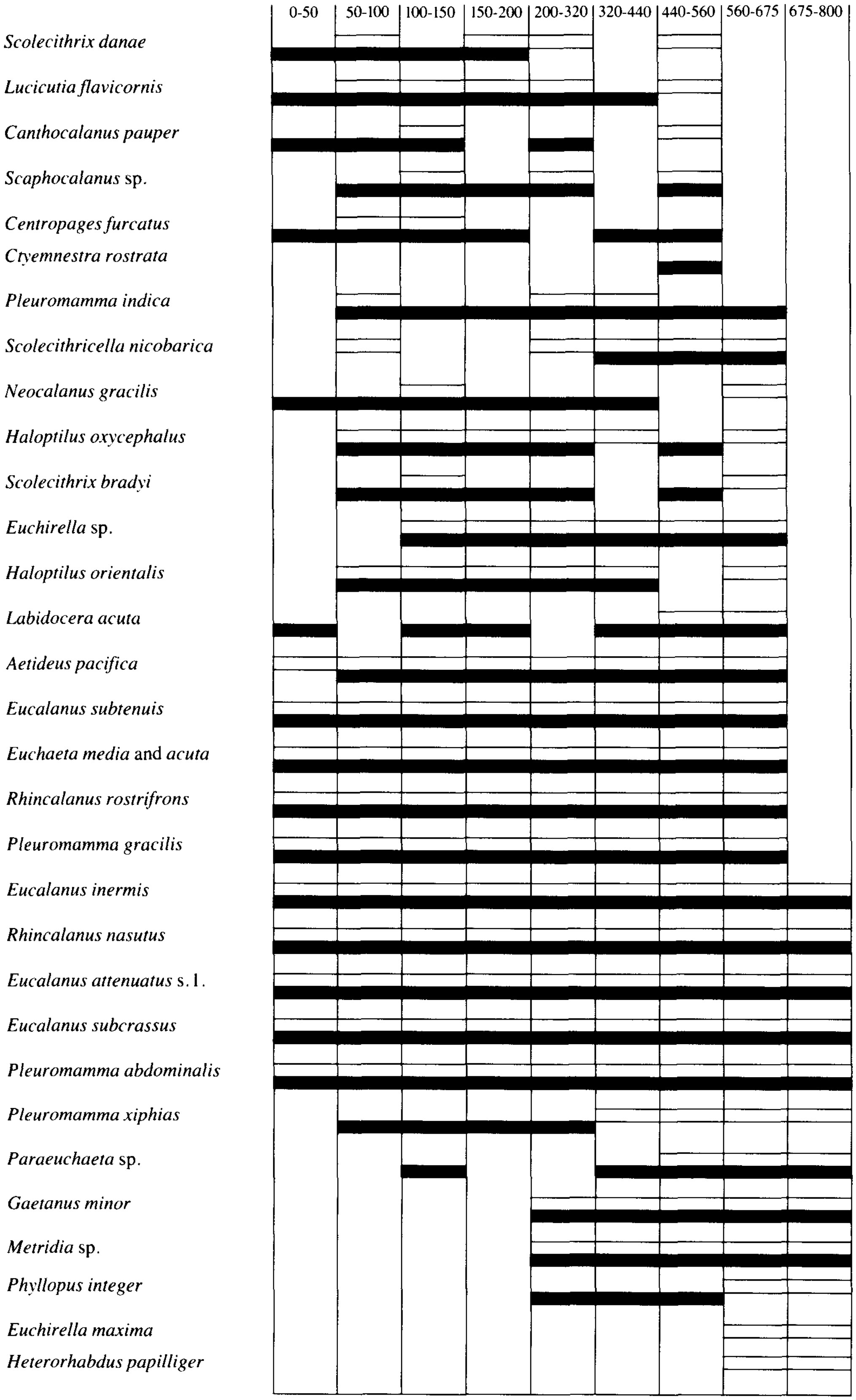
TABLE 2—*Continued*

Maximum Depth Range of More Abundant Copepod Species in Day (____) and Night (▬) Samples



From the surface to 440 m. Six species were restricted to depths above 440 m in the ETP.

From 440 to 800 m. Thirty-two species, or about half of the total species list, were found in samples taken between 440 and 800 m. These species can be subdivided into several subgroups on the basis of vertical ranges as follows:

1. Distribution above 560 m. *Lucicutia clausi, Canthocalanus pauper, Scolecithrix danae,* and *Lucicutia flavicornis* reached this depth in day samples, but they occurred in shallow water (above 150 m) in night samples.
2. Distribution above 680 m. Thirteen species occurred above 676 m. Twelve species were found in day samples and nine species in night samples. The vertical range of five species (*Eucalanus subtenuis, Rhincalanus rostrifrons, Euchaeta media* and *acuta, Pleuromamma gracilis*) extended from the surface to 680 m in both day and night samples.
3. Distribution to 800 m. Twelve species occurred in the samples obtained from 800 m. Five of these species were distributed from the surface to 800 m in both day and night samples. They were numerically dominant species in the ETP. The range of vertical distribution of three species (*Gaetanus minor, Metridia* sp., and *Phyllopus integer*) was from 200 to 800 m. *Euchirella maxima* and *Heterorhabdus papilliger* were found only below 560 m.

Relationship between Currents and the Distribution of Copepods in the ETP

Brinton (1979) described four environments in the ETP that differ in physical and chemical conditions as well as in their euphausiid species. He reported that stations from 25°N to 21°N were located in a transition between the California Current and the ETP, merging a coastal upwelling regime with strongly stratified tropical water. The copepods in this sector were characterized by temperate species of the California Current region. In California Current water (23°N-25°N) above 200 m, the temperature was 12°-18°C. South of 23°N the temperature above 100 m increased, varying from 14° to 26°C, and the temperature gradient increased (Figure 13a).

Station 10 was located at a transition from California Current water to Gulf of California water. The zooplankton obtained at this station was a mixture of the two biogeographically different regions. Numerically dominant ETP species included *E. subtenuis, E. attenuatus* s.l., and *E. subcrassus.* The numerically dominant California Current species was *Calanus pacificus californicus.* All occurred in high concentrations in the mixed waters above 70 m, where the temperature ranged from 18° to 24°C.

The oxygen-deficient region of the ETP between 21°N and 10°N has tropical water forming a shallow surface layer (Brinton 1979). At the bottom of the shallow oxycline, oxygen was < 0.05 ml/l^{-1}, and temperatures were compressed in a steep gradient ranging from 28° to 14°C (Figure 13a). The vertical distribution of the oxygen-deficient layer extended from 25 m to as deep as 600 m. The changes in depth reflect the influence of the Equatorial Countercurrent.

According to Brinton (1979), euphausiids have adapted to the oxygen minimum in two ways. First, one group of species has a vertical distribution that is limited to all or part of the mixed layer, day and night. Second, a group of strongly migrating species tolerates oxygen-deficient waters in their daytime depths of 200-400 m and moves up into the oxygenated mixed layer at night. Comparing the distribution of ETP copepods with euphausiids (Brinton 1979) in the oxygen-minimum layer of the ETP, the patterns of vertical distribution of the former can be divided as follows:

First pattern. About 15 species (e.g., *Eucalanus subcrassus, E. attenuatus* s.l., *E. crassus, E. subtenuis,* and *Cosmocalanus darwini* s.l.) resided in the mixed layer above the oxygen-deficient layer at station 14 or 17.

Second pattern. Some dominant or common species are distributed in both shallow and deep layers, ranging from the surface to 630 m. *Eucalanus inermis* was a typical example of this pattern. Some species in this category also migrated into shallower depths at night. *Pleuromamma indica* and *Pleuromamma gracilis* were found deeper than 300 m in daytime samples but occurred between 100 and 150 m in night samples

Third pattern. Some species occurred in the deepest layers in both day and night samples. Representative species in this pattern were *Euchaeta acuta* and *media, Gaetanus minor, Heterorhabdus papilliger, Haloptilus orientalis,* and *Haloptilus oxycephalus.*

Copepods of the North Equatorial Countercurrent

The copepods residing within middle depths (100-400 m) north of the equator, a zone approximately from 0° to 10°N, were characterized by species considered tropical and oceanic. Stations 18 and 19 (ca. 6°N-8°N) were located in the North Equatorial Countercurrent. Tsuchiya (1974) showed easterly flow across 97°E between 4°N and 6°N during April and May 1967. Wyrtki and Kendall (1967) provided evidence that eastward geostrophic flow in the countercurrent is at a maximum during June. Evidence of the countercurrent's influence on the copepods of this zone was found at stations 18 and 19. Twenty-five species were found in the North Equatorial Countercurrent flow. The representative species were *Eucalanus at-*

tenuatus s.l., *Rhincalanus rostrifrons*, *Aetideus pacifica*, *Gaetanus minor*, *Heterorhabdus papilliger*, and *Euchaeta acuta* and *media*. Most of them are tropical oceanic species abounding in the central equatorial Pacific (Timonin and Voronina 1977) and living in or above the thermocline where oxygen values exceed 1 ml/l. Some of these species appeared to show diel vertical migration. A few neritic species, such as *Eucalanus subcrassus*, were also found in the North Equatorial Countercurrent. *Euchirella* sp., distributed in middle-layer waters at all stations but station 10, seemed endemic to the ETP.

The Equatorial Undercurrent Species

Station 21, located at the equator, lies within the Equatorial Undercurrent (Brinton 1979), and 13°C water at this station implies strong evidence of undercurrent activity (Figure 13a). The westerly South Equatorial Current occupies the surface layer at the equator and extends to greater depths on each side of it. The easterly Equatorial Undercurrent (Cromwell Current) is about 160 km wide in the eastern Pacific (Jones 1969), and the velocity core is consistently at 50-150 m (Taft and Jones 1973).

The range of vertical distribution and migration of copepods in equatorial waters can be divided into different categories as follows:

a. Three species (*Pleuromamma indica*, *P. abdomnalis*, *P. gracilis*) resided mainly below the 200-m layer in day samples and ascended to above 100 m at night. This vertical range could have allowed these species to maintain substantial east-west equilibrium. Easterly transport by the undercurrent during the day, balanced by usually westerly surface transport at night establishes the possibility of locally resident stocks' using opposite-flowing currents of the equatorial system to maintain a relatively fixed geographical position, if current speeds are similar. This vertical range of copepod migration was similar to that of some euphausiids such as *Euphausia eximia* and *Euphausia distinguenda* (Brinton1979).

b. *Scolecithrix danae*, *Euchaeta longicornis*, and *Eucalanus subtenuis*—like *Stylocheiron carinatum*, a euphausiid—had shorter spans of vertical range and nighttime levels even more surface-linked. This was also reported by Timonin and Voronina (1977) and Vinogradov (1970).

c. The vertical distribution exceeded 200 m during the day and 300-500 m or deeper at night. Species showing this distribution include *Metridia* sp., *Scaphocalanus minuta*, *Gaetanus minor*, and *Haloptilus longicornis*. They occurred beneath the thermocline and undercurrent, where horizontal flow is presumed much weaker.

d. *Eucalanus attenuatus* s.l. and *Cosmocalanus darwini* s.l. occurred at and beneath the thermocline at depths of the undercurrent. They appeared to be nonmigrating at the equator and seemed to be entrained within the undercurrent, which would ensure easterly drift toward unsuitable waters. In comparison with the data of Timonin and Voronina (1977), *Eucalanus attenuatus* s.l. was distributed deeper at the equator in this investigation.

It is necessary to note that the higher surface salinity at station 22, located near the Galápagos Islands, indicates that this locality was not strongly influenced by westward flow from the South Equatorial Current. The presence of *Calanus chilensis* at stations 21 and 22 indicated mixing of several different water currents, including an intrusion of the Peru Current, which may account for the oxygen-deficient water beneath the mixed surface waters.

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THE TEMPERATE AND TROPICAL PLANKTONIC BIOTAS OF THE GULF OF CALIFORNIA

EDWARD BRINTON, ABRAHAM FLEMINGER
Marine Life Research Group, A-001
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093

DOUGLAS SIEGEL-CAUSEY
2423 Morningside Drive
Lawrence, Kansas 66044

ABSTRACT

Studies examining composition and distribution of the planktonic flora and fauna of the Gulf of California have been few. Several are thorough in geographical coverage, though time-change has received little attention. Published species lists and distributional records are now particularly complete for phytoplankton, Foraminifera, Medusae, Siphonophorae, Chaetognatha, and Euphausiacea. New lists of Copepoda and Amphipoda are included in this paper; we also detail biogeographical affinities of these species. All available records of planktonic species are cited (including some not generally available), and faunistic zonation of the gulf is examined in a general way. Studies describing direct (*in situ*) observations of gulf zooplankton are discussed.

RESUMEN

El número de publicaciones sobre composición y distribución de la flora y fauna planctónica en el Golfo de California es bajo. Varios estudios son de extenso y detallado alcance geográfico aunque la variabilidad temporal presente en dicha cobertura ha recibido poca atención. Las listas de especies y registros de distribución actualmente publicados están completos, especialmente en el caso de fitoplanction, Foraminifera, Medusae, Siphonophorae, Chaetognatha, y Euphausiacea. Se incluyen nuevas listas para Copepoda y Amphipoda en este trabajo; ademas, se detallan las afinidades biogeográficas de estas especies. Todos los registros disponibles de especies planctónicas son citados y la zonación faunística del golfo es examinada en forma general. Algunos trabajos que describen observaciones directas (*in situ*) de zooplancton del golfo son revisados.

INTRODUCTION

The Gulf of California is known to harbor an abundance of plankton (e.g., Osorio-Tafall 1943; Zeitzschel 1969). How productive the gulf is, and the nature of regional and seasonal change in its biological properties, remain largely to be determined. The many hues of the "Vermilion Sea" intrigued navigators for centuries before Streets (1878) found milky-red water at Bahía Mulege to be thick with the dinoflagellate *Noctiluca mirabilis*, and red-tinged water off Isla Cerralvo to be caused by another "flagellated infusoria."

The gulf extends from 32°N within the zone of the warm-temperate Californian Transition Zone (e.g., Newman 1979) to its mouth in contact with the Panamic Province near the Tropic of Cancer, 23°27′N (Figure 1). Little attention has yet been paid to ways in which the gulf's semienclosed planktonic populations range along its 1,000-km length. On the basis of fish fauna, the gulf encompasses a temperate-tropical transition (Walker 1960). The species of phytoplankton—mainly warm-water cosmopolites—seem now to be reasonably well known (e.g., Round, 1967). Of the zooplankton, lists appear to be most complete for Foraminifera (Bradshaw 1959; Parker 1973), Chaetognatha, Siphonophora, and Scyphomedusae (Alvariño 1969), pontellid Copepoda (Fleminger 1964a, 1967a,b, 1975), and Euphausiacea (Brinton 1979; Brinton and Townsend 1980). Hyperiidean Amphipoda have been studied by Siegel-Causey (1982), whose results presage description of a diverse amphipod fauna.

Interest in examining the biology of gulf plankton in relation to oceanographic processes is increasing. This is due partly to the importance to Mexico of understanding regenerative cycles in these seemingly productive coastal waters, and partly to a developing awareness among oceanographers of the gulf's distinctive topography, including the presence of varved sediments at depths within the oxygen minimum, hydrothermal vents in deep waters, and the substantial containment of biota.

Oceanographic processes expected to be of significance to nutrient renewal and the distribution of organisms in the gulf were outlined by Brinton and Townsend (1980), following Roden and Groves (1959), Griffiths (1968), Alvariño (1969), Roden (1971), and Moser et al. (1974). The climate and circulation of gulf waters are influenced by seasonally reversing winds and changes in solar radiation. The seasonal range in surface temperature is extreme: in the northern part it varies between 14°C in February and 30°C in August, and in the southern part between about 20° and 30°C.

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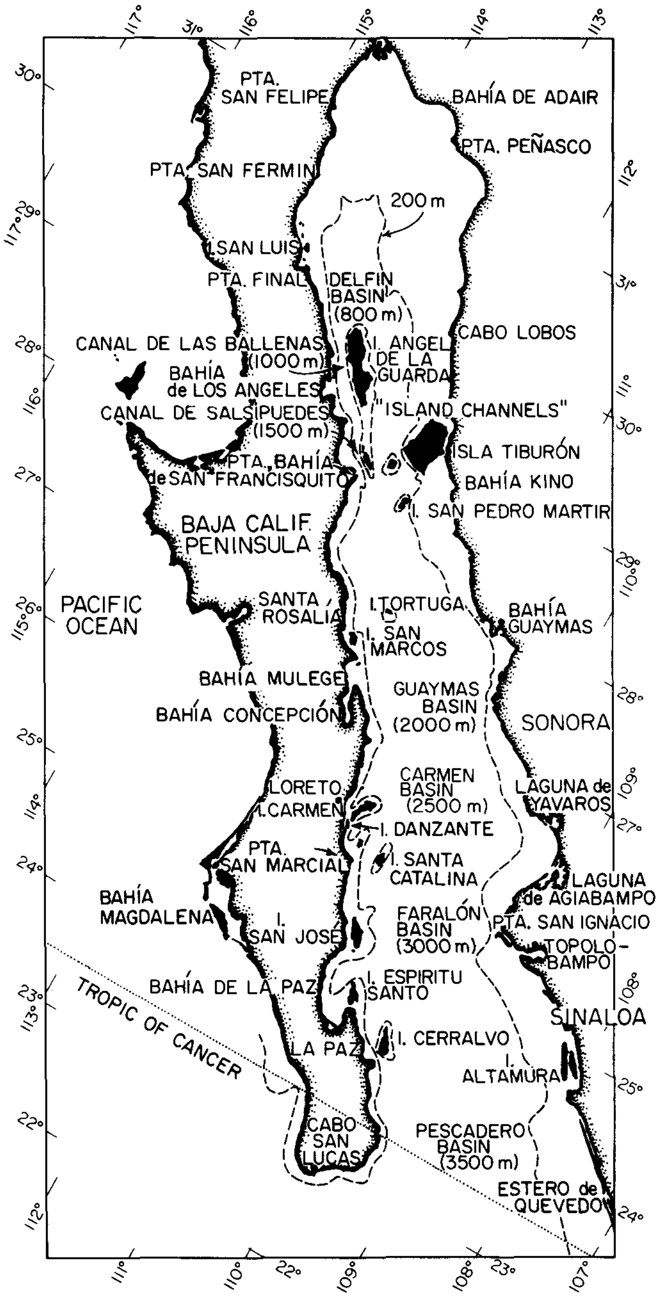


Figure 1. The Gulf of California.

Upwelling, determined by the divergence of the Ekman transport, is strongest along the eastern side of the gulf during the northeasterly winds of winter and spring, as verified by 1980 satellite images of cool plumes extending westward from the eastern coast; upwelling shifts to the western side with the southwesterly winds of summer and early fall, appearing less intense than in the opposite period (Badan-Dangon et al. 1985). During June 1957, the western side was 2° to 3°C cooler than the eastern.

Islands, particularly those along the western gulf, provide coastline that augments the mainland sites for mixing and upwelling. In channels, notably between Isla Angel de la Guarda and the Baja California peninsula, tidal mixing combines with along-channel current oscillations superimposed on turbulent eddies (Alvarez et al. 1984) to form a persistent cooling system. Island topography may be optimal for persistent upwelling because there is always some coastline parallel to the shifting wind. In the northernmost gulf, the amplitude of the semidiurnal tide and its energy release is 15 times that at the mouth (Filloux 1973). In turn, internal waves are forced by the tides, particularly spring tides (Fu and Holt 1984). Such features reduce the applicability of generalized explanations of nutrient renewal, plankton production, and species distributions in the gulf.

Evaporation exceeds runoff into the gulf, but surface salinity beyond embayments ranges only between 34.4‰ and 35.9‰. (Roden and Groves 1959). This compares with a maximum of about 34.6‰ in the open sea to the west (Love 1973). Therefore, salinity per se probably does not influence the distribution and abundance of plankton in the gulf. Estuaries and lagoons along the southeastern coast nevertheless contribute nutrients, as indicated by primary productivity maxima off that coast during August 1972, associated with lowered surface salinities of 34.4‰ to 34.5‰ (Gilmartin and Revelante 1978).

Diagrams of geostrophic flow during four 1957 cruises (Wyllie 1966) show mean surface flow to have been out of the gulf during February and April. Flow at 200 m—the daytime depths of certain vertically migrating zooplanktons—was much the same. Most winter outflow is along the Baja California coast (Rosas-Cota 1977). By June, surface flow had reversed, entering the gulf across much of the mouth, particularly the central axis and the eastern side (Rosas-Cota 1977), and persisting toward the north as a stream that shifted toward the eastern side by August. Flow at 200 m was opposite to surface flow during the summer (Wyllie 1966). While eastern tropical Pacific water reaches only to the gulf's mouth in winter, it begins to penetrate northward in spring (Alvarez-Borrego and Schwartzlose 1979).

Direct observations supplemented by computations of geostrophic flow have been made of apparent cyclonic cells of circulation extending across the width of the gulf during August 1978 (Emilsson and Alatorre 1980). Such a cell in the 0-50-m layer in the southern gulf provided inflow along the eastern shelf and outflow near the tip of Baja California, not unlike that shown by Wyllie (1966) for August 1957. Another broad eddiform structure seemed to be present farther north in the gulf. Features of this kind are pertinent in examining means of exchange among plankton populations within the gulf, and between the gulf and the adjacent Pacific. Such cells may relate to the basin topography of the gulf (Figure 1) or may be persistent segments in a long standing-wave in the gulf postulated by Sverdrup (1941), to be discussed in relation to the phytogeographical zonation. Alternatively, the cells may be formed from energy and shear provided by long internal or coastally trapped Kelvin waves that travel northward along the Mexican coast, mainly in summer, and become trapped in the gulf (Christensen et al. 1983). These waves have amplitudes up to 30 cm, periods of up to 10 days, and wavelengths of up to 1,000 km, but provide no appreciable volume transport. Recent evidence (Winant, pers. comm.) indicates that the cells may be not necessarily eddies, but merely zones separating intermittent tongues or jets of offshore flow.

Across the eastern tropical Pacific there is a layer in which oxygen is deficient owing to a combination of vertical stability in the water column and high productivity, with consequent near-deficit oxidative regeneration of nutrients. Between the thermocline and about 700 m, the concentration of oxygen is as low as 0.05 ml/l. According to data in Roden and Groves (1959) and Alvarez-Borrego (1983), the layer becomes diluted inside the gulf. For example, at 23°N, oxygen concentration of 0.1 ml/l was unusual at any season (during 1957) and never occurred in water above 300 m except near the western side in April. Moreover, the lowest oxygen concentration found half-way up the gulf (27°N) was 0.2 ml/l, at 500-m depth.

Oxygen deficiency in the eastern tropical Pacific appears to have much to do with (1) creating an environment for endemism and (2) sharply restricting a number of subtropical species and warm-water cosmopolites from establishing there. Plankton from depths within the oxygen minimum in the gulf was first reported in Sverdrup, Johnson, and Fleming (1946). Although low oxygen concentrations in the gulf appear not to be sufficiently shoal, extreme, or widespread to have played a dominating role in the selection of which species are present, influence upon the pelagic biota remains largely to be determined.

PHYTOPLANKTON

Taxonomy and Distribution

For this paper, phytoplankton include only the algae in the water column and surface sediments. Fossil phytoplankton, microalgae of the sedimentary rock, and primary production are not considered. The first four sets of collections (Allen 1923, 1937, 1938; Cupp and Allen 1938), from surface net samples, were analyzed for total cell numbers at each station, without details of the distribution of species. Osorio-Tafall (1943) described phytoplankton collected from the central and southern littoral during January 1942; in this excellent review article on the Gulf of California, he considered several aspects of natural histories (e.g., geology, hydrography) that might have been pertinent for interpreting species distributions. However, the limited scope of the sampling made it difficult to draw general conclusions.

Gilbert and Allen (1943) attempted a phytogeographical synthesis using phytoplankton collected during cruises of the *E.W. Scripps* (February-March 1939, October-December 1940) extending from the oceanic entrance of the gulf to the northern deltaic region. This first subsurface sampling to be carried out is significant, for as Round (1967) pointed out, surface productivity in the gulf is at times low because of photoinhibition, but during times of nutrient injection, surface waters may be abnormally rich. Thus, surface samples may be poor indicators of phytoplankton dynamics in the Gulf of California.

The systematic sampling led Gilbert and Allen (1943) to describe four water zones based on species distributions, but with boundaries tending to agree with the antinodes of Sverdrup's (1941) theorized internal wave along the axis of the gulf (Figure 2):

1. Zone A, "southern oceanic"
2. Zone B, "central," characterized by *Coscinodiscus wailesii*, now recognized as a temperate, coastal diatom (Cupp 1943)
3. Zone C, "northern," characterized by *Asterionella japonica*, now considered to be a neritic, widespread, warm-temperate diatom
4. Zone D, "inner," characterized by *Gonyaulax catanella*, now known to occur seasonally in many parts of the gulf as the principal dinoflagellate in toxic red tides.

The distribution of mean diameters of bottom-sediment particles followed a pattern that might have been generated by the wave postulated by Sverdrup (Revelle 1950), and provided support for the idea that such a wave might be a permanent feature of the gulf. Munk (1941) further showed that the theoretical characteristics of this wave were compatible with the gulf's physical topography.

Gilbert and Allen (1943) developed this hypothesis further. The internal wave, having three nodes, would be associated with three circulation cells, or zones, with boundaries at the antinodes. A fourth zone would exist in the northernmost gulf. Horizontal currents, strongest at the nodes, would diminish to zero at the antinodes. Because of the large period of this wave (seven days, or half the lunar fortnightly tide), the Coriolis force would produce circular currents in each zone, the direction in the central zone being opposite to

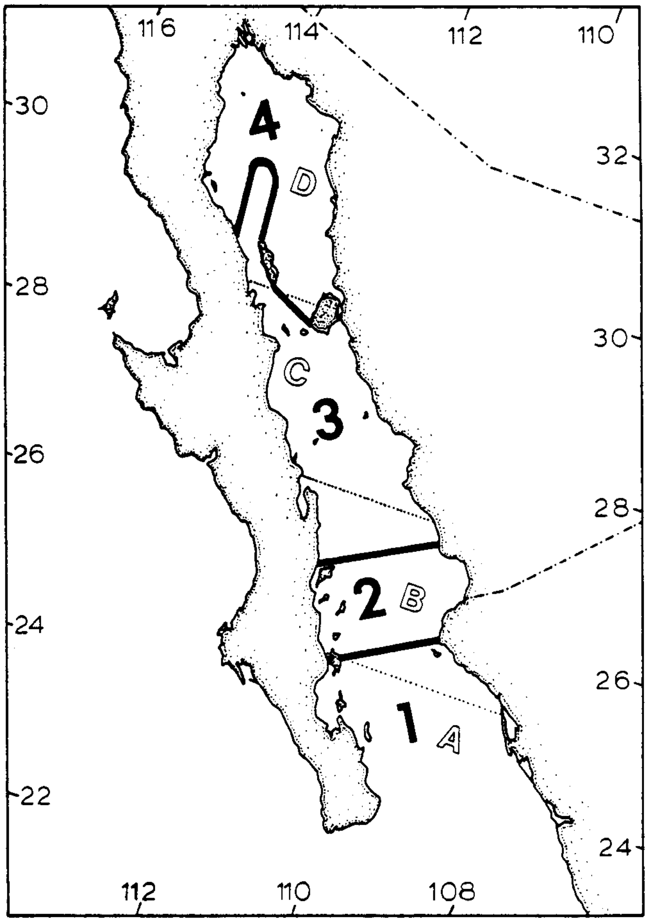


Figure 2. Phytoplankton distribution zones in the Gulf of California. *Dotted lines* indicate zones A-D proposed by Gilbert and Allen (1943); *solid lines* indicate zones 1-4 proposed by Round (1967).

directions in the northern and southern zones. Since the horizontal currents reverse every half period, the zones would tend to become isolated from each other, but frequent breakdowns of intercellular boundaries should be expected.

Gilbert and Allen (1943) found the northernmost zone to have the greater phytoplankton populations, but lower diversity than zones in the south. Indirect evidence was presented that the seasonal phytoplankton cycle is dependent, in the outer gulf (zones A, B, C), upon upwelling, and in the inner, shallow regions, upon convection processes (see Lepley et al. 1975). The two processes are thought to be initiated in late fall when northwestern winds bring about east-coast upwelling, and when surface cooling lowers the stability of water masses in the basins and shallow regions of the inner gulf. At the onset of summer, when winds reverse and weaken and the surface waters become heated and stratified, the spring phytoplankton growth terminates. Gilbert and Allen (1943) believed this model to be supported by the occurrence of greatest phytoplankton productivity in March.

Knowledge of gulf phytoplankton did not improve until Round's (1967) thorough treatment of net samples from March 1959 and 1960, and October-November 1959. He distinguished four zones, which had somewhat different, less artificially constrained boundaries from those of Gilbert and Allen (1943) (Figure 2). He derived a zonation scheme from the deposition of diatoms in surface sediments; however, differences between the two patterns are small and, because of the likelihood that current directions differ with depth, and affect the distribution of phytoplankton onto the bottom, the system of pelagic zonation is expected to be more appropriate in considering the living biota.

Zones 1, 2, and 3 correspond well with the hydrographic regions of Roden and Groves (1959) and support Round's contention that the zones reflect physical processes. Water in southernmost zone 1 is largely eastern tropical Pacific water, relatively depleted of nutrients because of a long residence time in zone 1 (Roden 1958); phytoplankton productivity is usually low, interrupted by seasonal injection of nutrients by upwelling. Griffiths (1968) gave some support for this, while noting that spring upwelling along western Baja California, 23°-24°N, is more intense than along the western coast of mainland Mexico near Cabo Corrientes. However, because a strong front off Cabo San Lucas prevents nutrient-rich water from the Pacific coast of Baja California from entering the gulf, production of phytoplankton in the southwestern gulf remains less than to the east. Reporting on armored dinoflagellates, Klement (1961) noted that numbers and abundances of *Peridinium* species decreased with distance into the gulf, whereas the *Ceratium* population showed a relative increase; the flora was generally tropical to subtropical, without endemics. In general, the diversity of phytoplankton species decreases in the central region (zone 2) compared to zone 1.

Zone 3 was distinguished by Gilbert and Allen (1943) (their zone C) on the basis of large numbers of *Asterionella japonica*; however, Round (1967) did not record this species at all. *Coscinodiscus lineatus*, *C. asteromphalus*, and *Stephanopyxis palmeriani* occurred in immense blooms during Round's sampling but were absent in Gilbert and Allen's study. Zones 2 and 3 are characterized by wind-driven upwelling of nutrient-rich water, and tide-driven turbulence near islands (Roden 1958). Conditions responsible for blooms recur year after year, but species dominating the blooms evidently differ (Round 1967).

Zone 3 also includes a tongue of water curving northward between Baja California and Isla Angel de la Guarda, thereby including island channels distinguished by Brinton and Townsend (1980) as a faunistic zone. Blooms of *Chaetoceros radicans* in 1937 and

Gonyaulax polygramma in 1959 are recorded from this locality. Such blooms to the west and north of Isla Angel de la Guarda may occur in the mixing of midgulf and northern gulf waters as the tidal wave ascending the gulf is deflected by Isla Tiburón into the deep, narrow Canal de Ballenas (Roden and Groves 1959).

The northern gulf (Zone 4) is characterized by a low phytoplankton diversity, with local intense blooms of *Gonyaulax polyedra* and *G. catenella*. Further information about the northern gulf biota is given by Brenner (1962) and Phleger (1964).

Round (1967) concludes that the components of gulf phytoplankton are of tropical origin and that there is little likelihood of endemic species occurring there; it is necessary to look south of 60°S in the South Pacific before the flora changes significantly.

All gulf phytoplankton species reported in the literature have been collated with respect to distributional records (table available from authors). Some patterns may be discerned: many species penetrate the gulf no farther than zone 1 (e.g., *Asterolampra marylandica, Biddulphia mobiliensis, Chaetoceros laevis,* and *Rhizosolenia castracanei*); others are found throughout the gulf (e.g., *Chaetoceros debilis* and *Cyclotella striata*); some species have been found as far north as zone 3, yet not in zone 2 (e.g., *Actinocyclus ehrenbergi, Coscinosira polychorda, Epithemia gibba*); the groups Biddulphioidea and Solenioideae are generally absent from zone 3, but the Discoideae and Actinodiscae are locally dominant there; zone 4 is characterized by low diversity of species, with occasional immense blooms. It may be noted that most collections were obtained during March of different years.

Licea-Duran (1974) examined systematics and distribution of diatoms in Laguna de Agiabampo in Sonora, and Gilmartin and Revelante (1978) sampled the phytoplankton of the lagoons and open waters of the gulf, southward from Isla Tiburón, in fall 1972. Gilmartin and Revelante's results from the open waters agree generally with Gilbert and Allen (1943) and Round (1967), but their southernmost floristic break was drawn at 26°N, north of that reported by Gilbert and Allen or Round (possibly because station positions differed between the studies). This apparent difference was attributed to decreased upwelling and high temperatures, which allowed a northward extension of tropical southern species such as *Trichodesmium hildebrantii, Climacodium biconcavum, Hemiaulus hauckii,* and *Chaetoceros laevis* (see also Gilmartin and Revelante 1978).

In the lagoons the composition and abundance of estaurine phytoplankton differed most from the adjacent open waters when flushing rates of the lagoon were low, and least when flushing rates were high. Some species were more abundant in the lagoons; for example, *Thalassionema nitzschiodes* in the north was replaced by *Skeletonema costatum* in southern hyposaline lagoons with low flushing rates. The lagoon flora was generally dominated by diatoms, except in two locations: Bahía Guaymas (zone 3) was dominated by the dinoflagellates *Gonyaulax digitale* and *Protoceratium reticulatum*, and Estero de Quevedo (zone 1) was dominated by *Gonyaulax minuta*.

Where dinoflagellates are numerous, phytoplankton maxima may change depth as the motile cells migrate during the 24-hour period. Kiefer and Lasker (1975) described a bloom in Coyote Bay of Bahía Concepción dominated by the dinoflagellate *Gymnodinium splendens* (1.0×10^5 cells per liter). The profiles of the concentration of chlorophyll *a* based on fluorescence profiles showed an upper layer at 6-m depth near noon, at 8 m at dusk, and at 15 m near midnight. Upward movement began at 0200, reaching 10 m by daylight. Diatoms contributing to these chlorophyll profiles included *Leptocylindricus danicus, Skeletonema costatum, Cerataulina bergonii,* and *Thalassiothrix frauenfeldii*.

Silicoflagellates were found by Murray and Schrader (1983) to be generally less than 2% of the silicious phytoplankton of the gulf, but up to 5% in blooms. Combining material from surface waters and surface sediments, Murray and Schrader found that the distributions of eight species were related to Round's three biogeographic zones. *Octatis pulchra* was associated with high primary productivity in the central gulf, north of 26°N, especially in the Guaymas and Carmen basins, but was also abundant at the mouth. *Dictyocha messanensis*—cosmopolitan in the North Pacific—tended to dominate where silicoflagellates were rare, as at the gulf's mouth. *D. calida* and two other unnamed tropical *Dictyocha* species were most abundant at the mouth, decreasing northward. *Dictyocha epiodon* and *Distephanus epiodon* are California Current species that sometimes enter the gulf.

Phytoplankton and Seston Biomass and Chlorophyll

Zeitzschel (1970) examined the roles of the four major phytoplankton taxa in the carbon budget of gulf waters. Dominance by diatoms was evident: they contained 50% of the carbon of living cells, but were only 10% of the number of cells (Figure 3). Naked flagellates, on the other hand, contained only 10% of all carbon, but constituted 70% of numbers. Dinoflagellates contributed 30% of the carbon and 15% of numbers, whereas the much smaller coccolithophores contributed about 10% of carbon and 5% of numbers.

Given as average proportions of total weight of seston (living, dead, and inorganic material combined)

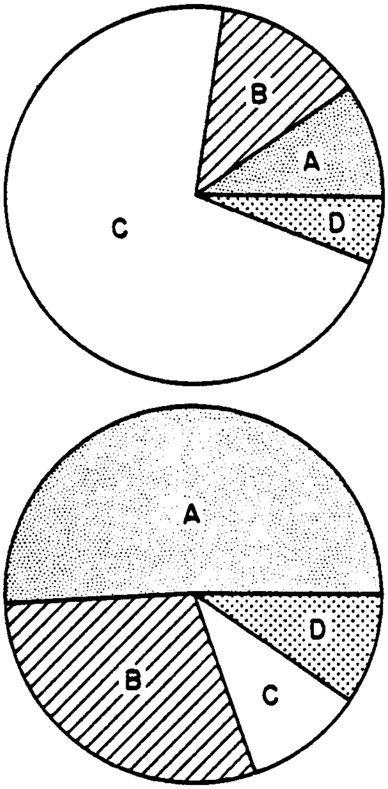


Figure 3. Average phytoplankton composition for samples collected at various localities in the Gulf of California, from Zeitzschel (1970). *Top*, percentage composition by number; *bottom*, percentage composition by carbon. *A*, diatoms; *B*, dinoflagellates; *c*, naked flagellates; *d*, coccolithophores.

in the euphotic zone, particulate carbon averaged 34%, chlorophyll *a* 0.09%, particulate nitrogen 5%, and phytoplankton carbon 3.3%. Kiefer and Austin (1974) subsequently examined the effect of phytoplankton concentrations on submarine light transmission in the gulf, and Kiefer and SooHoo (1982) showed that, of the suspended particles in gulf waters, chlorophyll pigments were the dominant light absorbers, with phaeopigments constituting 15%-20% of total chlorophyll pigments in the mixed layer.

Zeitzschel (Figure 4) showed, further, that the number of particles in the seston decreased with increasing particle size, from about 10^3 per ml for 3μ particles to 1 per ml for 30μ particles up to a size of about 100μ, above which numbers (and volumes) dropped sharply, especially in offshore water. The observations held for surface samples as well as for samples at 1% light depth (23-29 m). Detritus was found to average 88.6% of seston in the gulf (see discussion of marine snow under Zooplankton Biomass).

Estimations of phytoplankton concentration have been made over broad sections of the gulf by measuring chlorophyll *a* in water samples. Across the northern gulf during spring, Gendrop-Funes et al. (1978) found values in excess of 20 mg/m^3 only at the surface (Figure 5) and only in the northernmost region (Punta San Fermin across to near Punta Peñasco). Values greater than 10 mg/m^3 were observed both at the surface and at 30-m depth in the northernmost gulf and along the eastern side. Lowest values, 2 to 3 mg/m^3, were along the axis of the gulf.

The southern end of the gulf is poorer in chlorophyll *a*. Stevenson (1970) found values of 0.5 to 3 mg/m^3 during June at the mouth, with one measurement of 9 mg/m^3 near the eastern shore (Figure 6); June and August values were in the range of < 0.5 to 2 mg/m^3. Griffiths (1965) illustrated the distribution of chlorophyll *a* across an oceanic front at the mouth, noting the highest value, 0.6 mg/m^3, at the front.

Studies including the distribution of chlorophyll, zooplankton biomass, and other biological parameters in the eastern tropical Pacific outside of the gulf are in Holmes et al. (1957) and Longhurst (1976).

ZOOPLANKTON

Taxonomy and Distribution

Although zooplankton represents one or more trophic levels above the phytoplankton, studies of feeding and gut contents have not been done on zooplankton of the Gulf of California. Most studies have been of distribution and abundance in relation to environmental parameters such as currents, food supply, and water temperature, which undergo extreme seasonal and geographical changes.

The eastern and western sides of the gulf are scarcely 150 km apart, permitting more mixing of neritic and basin waters than is usual along an open coastline. Low concentrations of oxygen within the depth ranges of diurnal or seasonal vertical migrators (to 0.05 ml/l; Brinton 1979) have also been considered in interpreting biogeographical information in the gulf.

The Copepoda, Euphausiacea, and Amphipoda are usually the dominant Crustacea. Cladocera and Mysidacea become relatively conspicuous in the shallower part of the neritic zone. Alldredge and King (1980) emphasized the numerical importance of nearshore organisms, including certain harpacticoid copepods, mysids, and cumaceans, which are benthic in the gulf by day and pelagic at night.

The gulf provides extensive habitats for benthic, neritic decapod crustaceans—conspicuously Brachyura and Penaeidea—because of (1) a long coastline in relation to area, and (2) extensive shoal areas to the north and east. Larvae of these crustaceans are prominent in the zooplankton here, and a few have been described in detail (see Meroplanktonic Decapoda, below). Coastal-neritic and slope-water species of Copepoda also tend to be prominent in the gulf's mixed layer (see Copepoda, below). In this qualitative way,

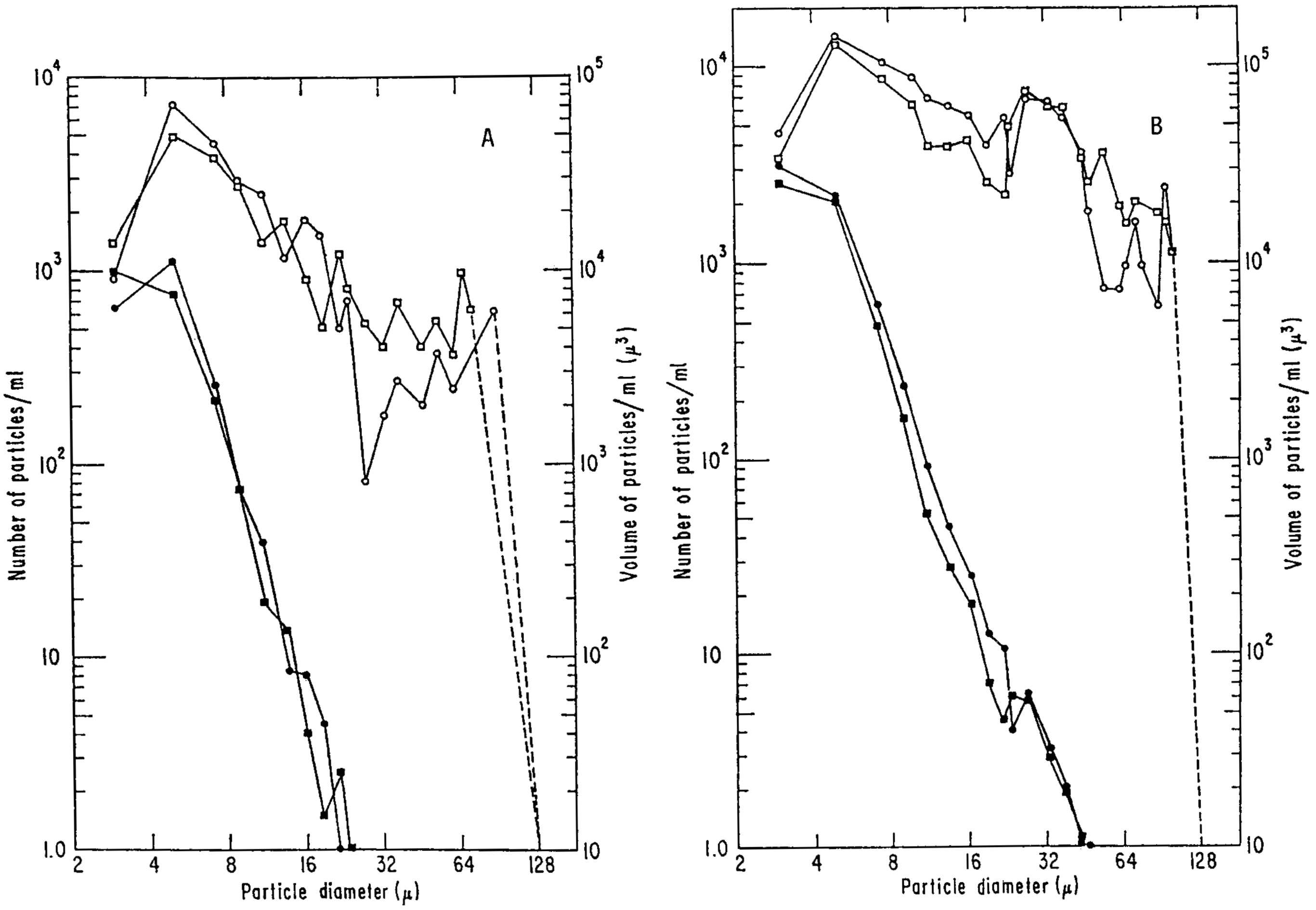


Figure 4. Total number of particles in seston (*solid symbols*) and total particle volume (*open symbols*) plotted against particle diameter. *Circles* indicate surface samples; *squares* represent 1% light depth. *Left*, at an offshore locality mid-Gulf of California (39 m); *right*, at a coastal locality, mid-gulf (23 m) (from Zeitzschel 1970).

the gulf plankton differs from that along the oceanic coast to the west, and from that in the deep sea.

Manrique (1977, 1978) quantified seven major zooplanktonic categories during a year-long study at two localities near Guaymas (Figure 7). He noted the following changes apparently related to the cold- and warm-water regimes of winter-spring and summer-fall:

1. Winter (December-January) plankton, even at this near-tropical latitude (28°N), was dominated by the temperate copepod *Calanus*, now recognized as *Calanus pacificus californicus*, discussed below. *Calanus* then constituted 35%-54% of the organisms caught, and the more coastal *Acartia tonsa* constituted 14%-50%. Sardine eggs appeared in January.
2. In February-March, and May-July, cladocerans (*Penilia, Evadne*) were important. (This was the first record of *Penilia avirostris* Dana in the eastern Pacific [Manrique 1971]).
3. Through May, *Acartia tonsa* dominated the copepods, declining in June with rapid warming from 17°C to 25°C. During October, *Acartia lilljeborgi* replaced *A. tonsa*. *A. lilljeborgi* is listed, below, as tropical.
4. In October, siphonophores increased significantly off Punta Guaymas (sta. 1).
5. At the more open coastal locality (sta. 1), brachyuran larvae peaked in June with summer warming, though they were more evenly present throughout the year at the more sheltered sta. 2.
6. During June-September, the chaetognaths *Sagitta enflata* (warm-water cosmopolite) and *S. euneritica* (coastal) were most evident.

These pioneering observations generate intriguing questions. For example, Cladocera, whose small size indicates a role in using diminutive food particles, appears to have been succeeded by the relatively large and voracious larvae of Brachyura, which were then followed by a bloom or intrusion of Siphonophorae —often versatile carnivores. Extending and broadening such studies are clearly important to our understanding the composition of zooplankton communities and the food webs functioning within them.

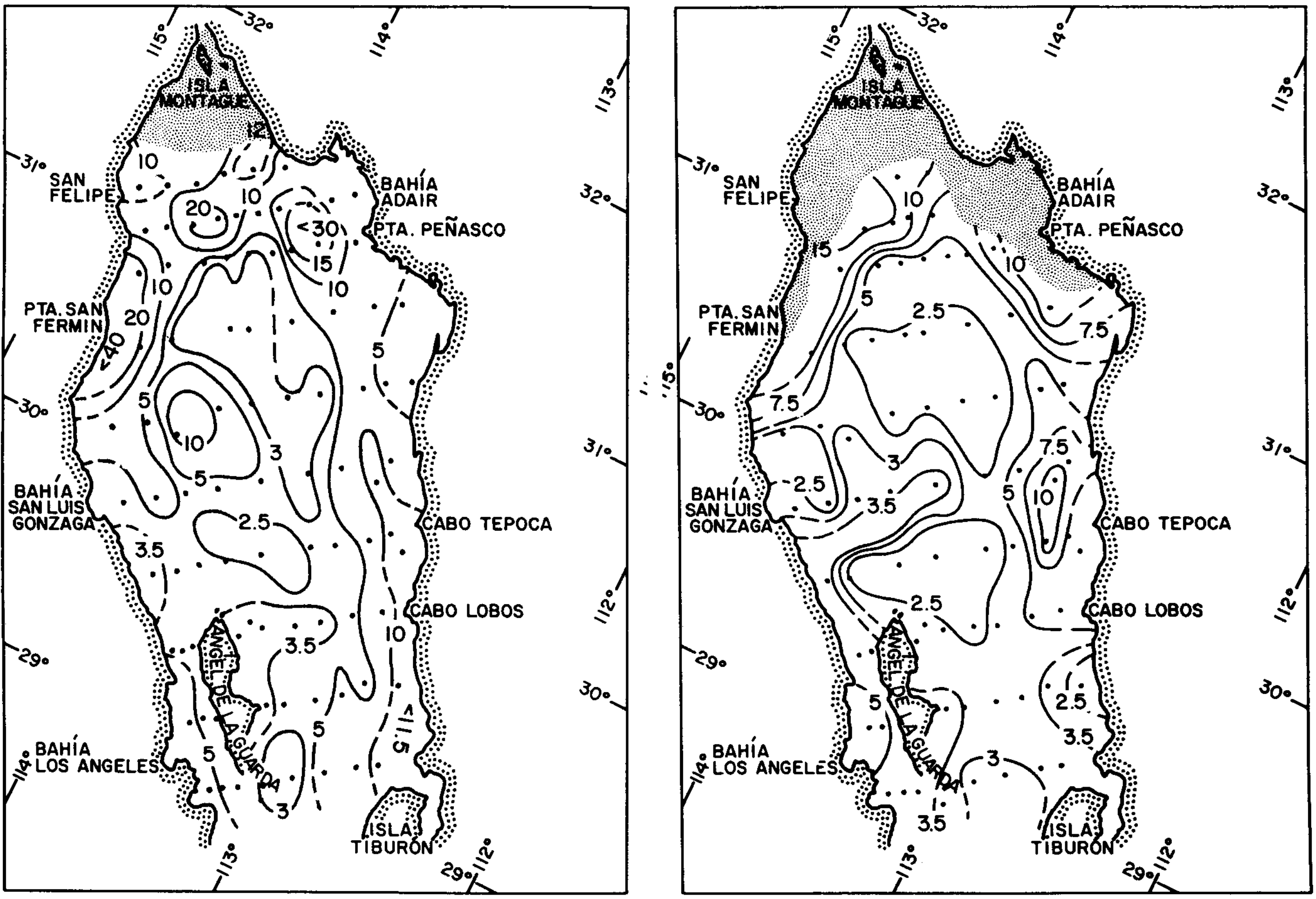


Figure 5. Distribution of chlorophyll *a*, mg/m^3, in the northern Gulf of California in spring. *Left*, at the surface; *right*, at 30-m depth (from Gendrop-Funes, et al. 1978).

Rhizopoda (Protozoa)

Of the living planktonic Foraminifera and Radiolaria, only the former have been studied in the gulf. Information on Foraminifera in the sediments is given in Natland (1950), Bandy (1961, 1963), Ingle (1973), Lankford and Phleger (1973), and Phleger (1964). Radiolaria in recent sediments are considered by Bandy (1961) and Benson (1964).

Studies of water-column Foraminifera by Bradshaw (1959) and Parker (1973) complement each other. Bradshaw provides pictures of Pacific-wide distributions, including occurrences in the southern part of the Gulf of California during September-October (1952). Parker provides an annotated species list with illustrations of some species, while updating the nomenclature, and gives gulf-wide distributional data for March-April (1959). Whereas Parker's samples were mainly from 50-0-m vertical tows with a 17-cm net of 0.6-mm mesh, Bradshaw's were from a 1-m net of the same mesh, hauled obliquely from 140 m. The species are described in Parker (1962).

Three species associated with the temperate North Pacific are prominent in the Gulf of California:

1. *Globigerina bulloides* was the most abundant foraminiferan in the northern half of the gulf in March-April samples, while at low density at most localities in the southern gulf. During September-October, it became still rarer in the south. Stratified sampling showed maximum numbers of living *G. bulloides* at 10-m depth, and dominance by this species to be below 50 m. (*G. bulloides* occurs throughout the California and Peru currents and occupies the subarctic Pacific and the zone of transition, 35°-45°N; there are scattered records across the subtropical and tropical Pacific.)

2. *Globigerina quinqueloba*, during March-April, was present throughout the gulf excepting the northern shelf region. During September-October, it was not observed in the southern gulf. This species has stronger high-latitude affinities than *G. bulloides*, being predominant in the subarctic Pacific.

3. *Globoquadrina dutertrei* (=*Globigerina eggeri* in Bradshaw [1959]), during March-April, showed highest densities in the northernmost gulf where *Globigerina qinqueloba* was lacking. Records farther south were few from both the spring and late-summer sets of samples. *G. dutertrei's* vertical distribution was

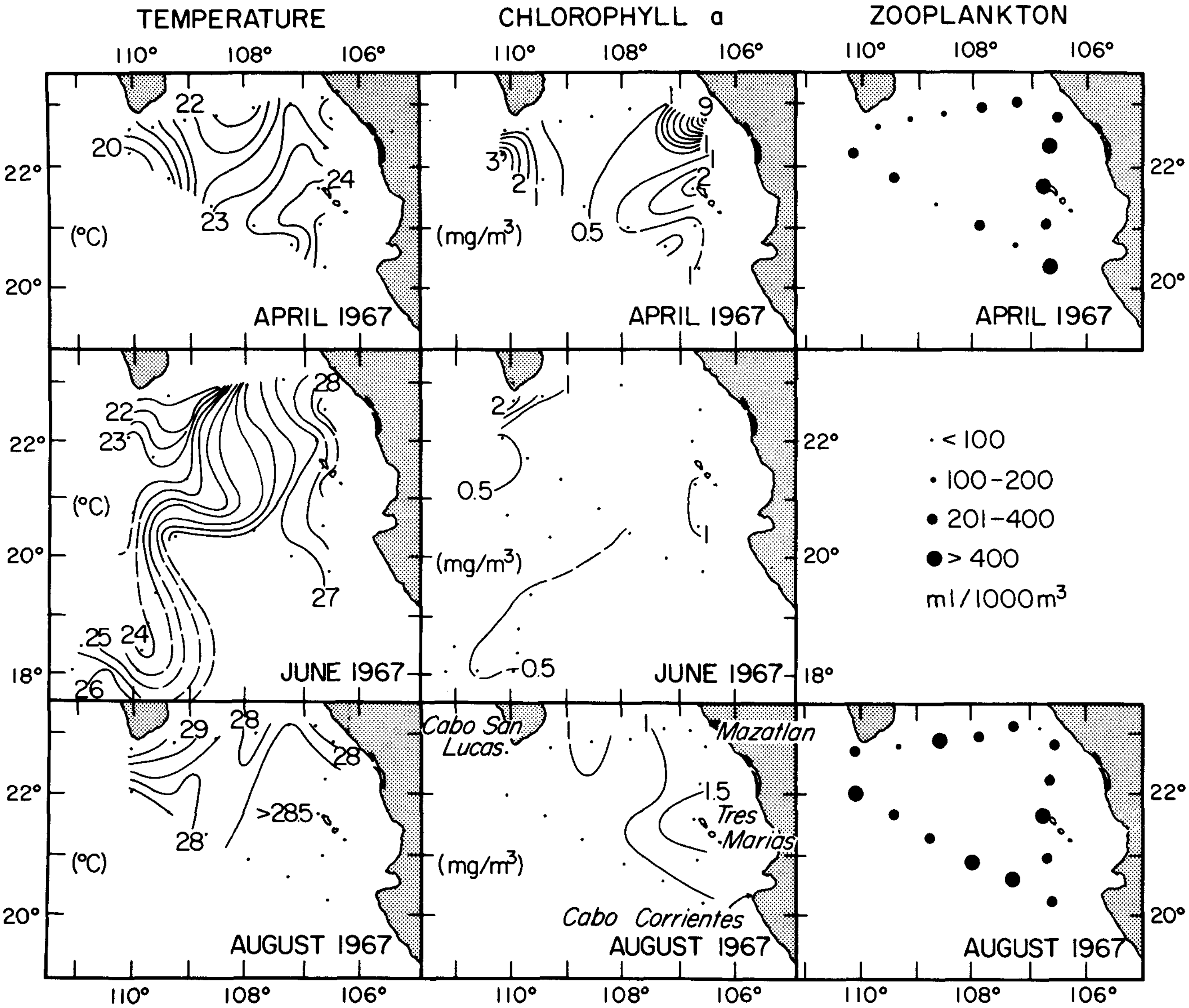


Figure 6. Distributions of surface temperature, chlorophyll *a*, and zooplankton, 0-300 m, across the mouth of the Gulf of California during April, June, and August 1967 (after Stevenson 1970).

centered at 50 m. This species occupies the subarctic-subtropical zone of transition, 35°-45°N, in the North Pacific, and extends the length of the California Current as far as the mouth of the gulf.

Four species with warm-water affinities, representing four genera, were frequent in the southern half of the gulf:

1. Most abundant during both March-April and September-October was *Globigerinita glutinata*, a true cosmopolitan species, occurring at all latitudes, though at high density only in the eastern tropical Pacific.

2. *Globigerinella siphonophera*, a warm-water cosmopolite, was also frequent in the southern gulf during both seasons.

3. *Globorotalia enfracta* was common in the southern gulf in March-April, but was not reported in September-October.

4. *Globigerinoides sacculifer* was more frequently recorded in spring than in late summer. Its vertical range was centered at 50 m, or deeper than most species.

Nine additional tropical or tropical-subtropical species occurred sparsely and only in the southern part of the gulf. *Globigerina falconensis* (=*G. bulloides*, part, in Bradshaw); *Globigerina rubescens*; and *Globigerinella adamsi* (=*Globigerinella* sp. in Bradshaw) were observed only in March-April. On the other hand, *Globigerinoides conglobatus*, *Globigerinoides ruber* (=*G. rubra* in Bradshaw), and *Globorotalia cultrata* (=*Globigerina eggeri* in Bradshaw) appeared most frequently during September-October, whereas *Orbulina universa* was observed only in late summer

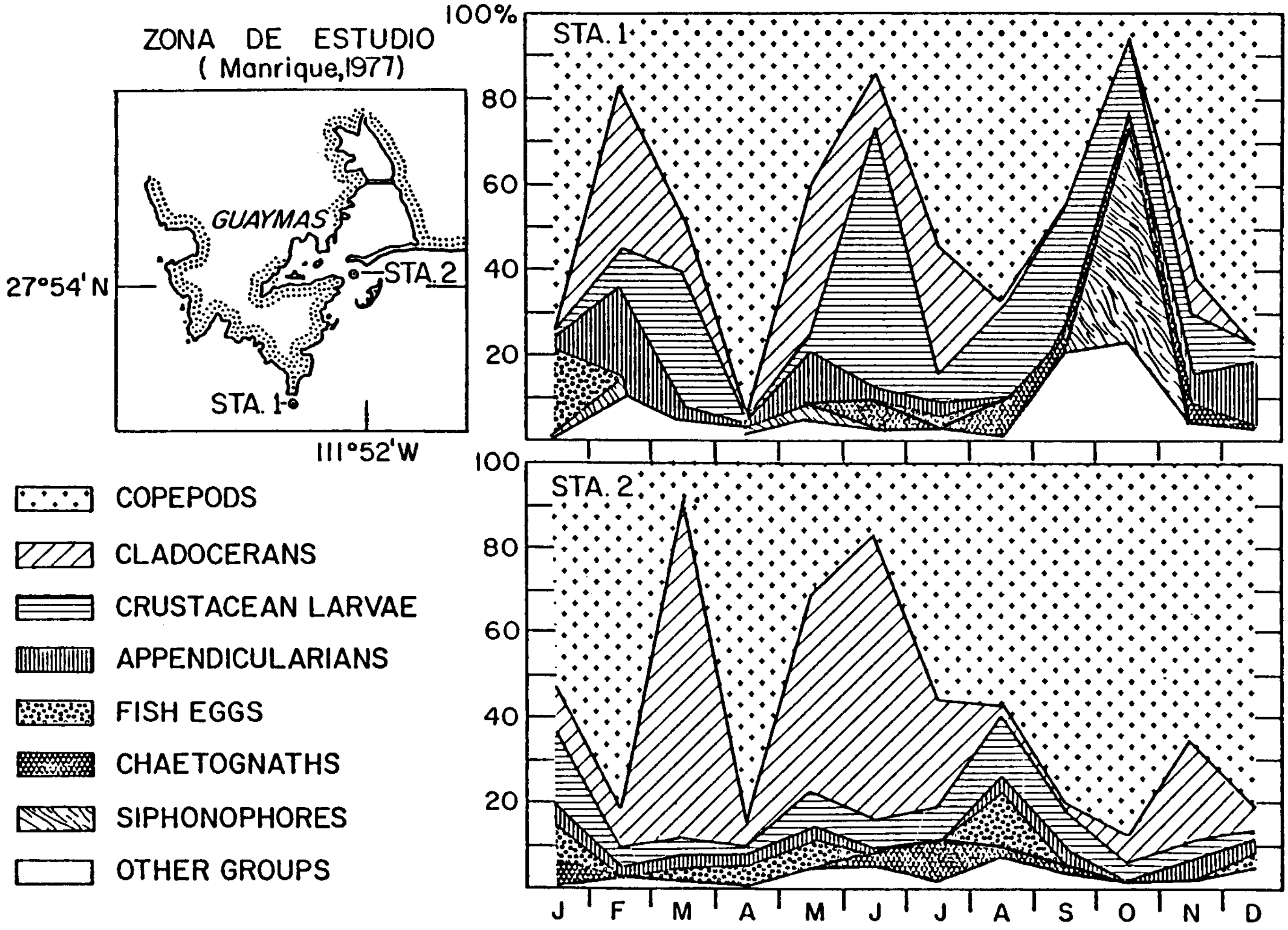


Figure 7. Proportions of principal groups of zooplankton sampled at two localities through the 12 months of 1971 near Guaymas (from Manrique 1977).

samples. *Hastigerina pelagica* and *Pulleniatina obliquiloculata* were infrequent in the southern gulf during both seasons.

Parker remarked surprise at predominance of the cool-water *Globigerina bulloides* in the northern gulf and at absence of the warm-water cosmopolite *Globigerina calida* during March-April. Bradshaw had found *G. calida* ("*G.*sp.") in the southernmost gulf during September-October. Parker found overall densities of foraminiferans to be greatest in the southern part of the gulf, in association with highest diversity of species. Median abundance values for the two regions were 130/m^3 and 14/m^3, respectively, with a maximum of 882/m^3 at a station near the mouth of the gulf.

Medusae (Coelenterata)

Maas (1897) described a new medusa from collections in the gulf in 1891 by the U.S. Fish Commission steamer *Albatross*. This was the anthomedusan *Chiarella centripelalis*, which occurred from the mid to southern gulf. Alvariño (1969) considered this species to be of the gulf's tropico-equatorial fauna. The trachomedusan *Homoeonema typicum* was also described by Maas "from the Gulf of California," but the station (no. 2637) proves to have been in the Gulf of Mexico. Maas also listed the two deep-sea genera of Narcomedusae, *Periphylla* (*P. dodecabostrycha* Brandt + P. *mirabilis* Haeckel?) from mid- and southern gulf, and *Atolla alexandri*, now considered *A. wyvillei*, from mid-gulf.

Bigelow (1909) added eight species, from *Albatross* collections off the mouth of the gulf, 20°-22°N, in 1904-05:

Scyphomedusae: *Nausithoë punctata* Kölliker, *Pelagia panypyra* Perón

Narcomedusae: *Cunina peregrina* Bigelow, *Solmundella bitentaculata* Quoy and Gaimard

Trachomedusae: *Liriope tetraphylla* Chamisso, *Aglaura hemistoma* Perón and Lesueur, *Agalantha digitale* var. intermedia Bigelow, *Rhopalonema velatum* Gegegenbaur.

Bigelow's paper contains descriptions and illustrations of many more medusae from the eastern tropical Pacific, including a particularly diverse group from Acapulco harbor.

Bigelow (1940) recorded four species obtained by the *Zaca*. In addition to *Chiarella centripelalis* Maas (1897), he listed *Polyorchis penicillate* (Eschscholtz), *Periphylla hyacinthina* Streenstrup, and *Chromatoenema erythrogonum* Bigelow.

Of the species that Bigelow recorded in the gulf, four were among nine species + *Obelia* spp. listed in Alvariño's (1969) analysis of plankton from the February and April 1956 CalCOFI cruises and from deep trawl collections of the Vermilion Sea Expedition.

Alvariño considered *Liriope tetraphylla*—a warm-water cosmopolite, though not characteristic of the eastern tropical Pacific—to be an indicator of California Current water in the gulf. The species was present in the southernmost gulf in both February and April and at a mid-gulf locality in February.

Five medusae were believed by Alvariño to maintain indigenous populations in the gulf: *Rhopalonema velatum* was throughout noncoastal waters from the island channels, 29°N, southward; *Obelia* spp. were at a coastal station in the northern gulf near Punta Peñasco, 31°N; *Philiopsis diegensis* has a tropical range in the Pacific and occurred in mid-gulf; *Leuckartiara octona*, known also from the California Current, occurred in mid-gulf; *Atolla wyvillei*, a bathypelagic, widespread species in Pacific basins, occurred from the Ballenas Channel southward.

Species considered tropical migrants into the southern gulf, and appearing only in the February samples, were *Chiarella centripetalis, Aglaura hemistoma,* and *Solmundella bitentaculata. Colobonema sericeum* occurred at the mouth of the gulf only in April, but was also in deeper Vermilion Sea Expedition samples from the southern gulf.

Siphonophorae (Coelenterata)

Siphonophores are conspicuous among gelatinous zooplankton of the gulf, particularly in the southern zone. There, diversity of plankton species is greatest, while quantity of "meaty" crustaceans is low.

Distributions of siphonophores in the Pacific are given in Alvariño (1971). Bigelow (1911) described and illustrated numerous species from the eastern Pacific, only one of which, *Porpita pacifica* Lesson, was from the gulf—in oceanic waters at the mouth. Other papers important in identifying siphonophores are those of Sears (1953) and Totten (1954) reporting on material from the Indian Ocean, and Totten and Bargmann (1965).

Occurrences of 18 species during two 1956 cruises in the gulf were reported by Alvariño (1969); 3 were regarded as having permanent populations there:

1. *Muggiaea atlantica* occurred in mid-gulf in February and throughout the gulf in April. This warm-temperate species occupies the subarctic-central transition zone of the North Pacific (40°-45°N) and the California Current southward to the mouth of the gulf (cf. the euphausiid *Nematoscelis difficilis*).
2. *Stephanomia bijuga* has the same range as *Muggiaea atlantica* in the California Current (47°-23°N), but was concentrated in northern and mid-gulf sectors; two records were obtained at the gulf's mouth (23°N).
3. *Stephanomia rubra* was scattered and sparse in the northern and southern gulf. This species occurs in the California Current, 39°-26°N, and widely in the tropics except for the eastern tropical Pacific.

Alvariño regarded three species as indicative of California Current influence: (1) *Lensia challengeri* penetrated to mid-gulf during both February and April, but appeared mainly along the deep-water axis of the gulf; (2) *Eudoxoides spiralis* and (3) *Agalma spiralis* were present in the southern gulf, only during February. These three species are warm-water cosmopolites, 40°N to 40°S in the Pacific. *Eudoxoides spiralis*, however, is conspicuously lacking in the oxygen-deficient part of the eastern tropical Pacific off Mexico and Central America.

Five species were considered tropical-equatorial, though all occur in the southern part of the California Current, and also show scattered records in central Pacific waters. Four of these were recorded at the mouth of the gulf, with a few individuals in mid-gulf: *Lensia campanella, Chelophyes contorta, Diphyopsis mitra*, and *Bassia bassensis. Ennogonum hyalinum* occurred in February, and only in mid-gulf.

Five additional siphonophores were recorded from water over deep basins of the gulf sampled during the Vermilion Sea Expedition: (1) *Bargmannia elongata* and (2) *Chuniphyes moserae* are deep (below ca. 250 m [Alvariño 1967]) inhabitants of mid- and low-latitudes, 45°N to 47°S. (3) *Sulculeoria angusta* is a warm-water cosmopolite, 40°N to 40°S. (4) *Rosacea plicata* is a true cosmopolite, arctic-to-antarctic, which evidently submerges to > 250 m in low latitudes. (5) *Erenna bedoti* is not known from elsewhere in the Pacific.

Observations from a diving saucer off Cabo San Lucas (Barham 1966) showed that siphonophores of the order Physophorae participate in vertical migrations with organisms of the sonic scattering layer. This layer rose near to the surface at the approach of night from a daytime depth of 300-400 m. The Physophorae are characterized by gas-filled flotation zoids (pneumatophores) at the terminal end of the anterior region (nectosome). Sonic impulses generated by the ship produce an echo reflecting from the pneumatophore. Siphonophores of the genus *Stephanomia* (= *Nanomia*), or related Physophorae, were believed by Barham to play this role in sound reflection. Genera of Physophorae recorded from the gulf include *Agalma*, *Bargmannia*, and *Erenna*, as well as *Stephanomia*.

Studies of feeding by various species of siphonophores, particularly in the Gulf of California (Purcell 1981a), showed a high order of prey selection among different suborders. Cystonectae, having large gastrozoids, fed primarily on fish larvae. Physonectae, having few large gastrozoids, fed on both large and small copepods and a variety of larger zooplankton. Calycophorae, having many small gastrozoids, fed on small zooplankton, notably copepods. Maximum prey size was correlated with gastrozoid length in all 14 species studied, and number of ingested prey was correlated with their abundance in surrounding waters. A study of feeding energetics in *Rosacea cymbiformis* by Purcell (1981b) showed caloric consumption in a 4-6-hr feeding period after sunrise to be 0.109-0.365 cal/gastrozoid, with daily intake projected to be 2.4-8.2 times that needed to balance metabolism. Large active copepods, crab zoea, pelagic molluscs, mysids, and juvenile shrimp were selected at frequencies above *in situ* abundances.

The Gelatinous Plankton —Direct Observations

The fragile gelatinous zooplankton have been studied extensively by means of direct observation through use of scuba diving equipment. Hamner and colleagues (1975), particularly Madin (1974) and Alldredge (1976a, b), have attempted to identify adaptive strategies of these forms in several tropical water masses, including the Gulf of California. The gelatinous group includes Hydromedusae, Siphonophora, Scyphomedusae, Ctenophora, Heteropoda, Pteropoda, Thaliacea (salps), and Appendicularia. Many of these groups are poorly sampled by conventional plankton nets, not only because of their delicacy, but also because of swimming or, in the case of pteropods, avoidance-sinking reactions. Hamner et al. (1975) presented a general review of ecological problems being studied by the direct approach. The workers mentioned above emphasize examining the efficacy of filter-feeding mechanisms, including mucous structures, in collecting, concentrating, and transporting particulate organic matter by pteropods, salps, and appendicularians. These animals were found to use mucous sheets, nets, strands, and filters in conjunction with ciliated surfaces to collect a broad size range of organic material.

Complex spherical mucous "houses"—never retained by plankton nets—produced by species of appendicularians in the gulf were studied by Alldredge (1976b). Species varied with respect to frequency and orientation of feeding and pattern of swimming within the house. However, the largest species, *Megalocercus huxleyi*, was generally observed (95% of time) feeding with the tail and body in a horizontal position and the filtering screen anterior to the body. The other species most often fed with the tail downward and the trunk and feeding filter parallel to the surface. These species were *Stegosoma magnum*, *Oikopleura intermedia*, *O. cornutogastra*, *O. rufescens*, *O. longicauda*, and *O. fusiformis*.

Alldredge found that appendicularians could build new houses in 1½ to 5 minutes, but rarely abandoned houses in response to predation by sergeant major fish (*Abudefduf* sp.), medusae, chaetognaths, and ctenophores. Larvae of the euphausiid *Nyctiphanes simplex* and adults of the calanoid copepod *Scolecithrix danae* were observed to rest on the surface of houses or to dart over the plankton-filled filters.

Macroscopic organic aggregates consisting largely of discarded appendicularian houses reached densities of 44 to 1130/m^3 in the gulf (Alldredge 1976a). Such aggregates were believed to affect the distribution of plankton by introducing spatial heterogeneity and physical structure into an environment often thought to be unstructured.

Alldredge (1981) measured grazing rates of the small appendicularian *Oikopleura dioica* and the larger *Stegasoma magnum* in the gulf by estimating their effect on the concentration of carbon particles in the 2-12 μm size range. The two species filtered seawater equivalent in carbon content to 5.2%-10.7% of natural rate of increase of indigestible-size carbon particles, with the total grazing community capable of depleting the carbon at a rate considerably greater than its replacement. Direct field evidence showed that gulf appendicularians exert significant grazing pressure on natural food assemblages.

Madin (1974) observed feeding behavior of salps (Tunicata:Thaliacea) in the gulf. Data were obtained near Isla Carmen (also from a locality in the Atlantic, near the Bahamas). Ninety-one percent of observed salps were feeding with a continuously renewed mucous net. Food particles ranged from < 1 μm to ca. 1 mm. Digestion was noted as incomplete; because fecal pellets contained much undigested material, they were believed to be a means for transporting significant amounts of carbon out of surface waters.

Madin observed six species (indication was not given as to which were in the Gulf of California and which in the Atlantic study area): *Cyclosalpa affinis*,

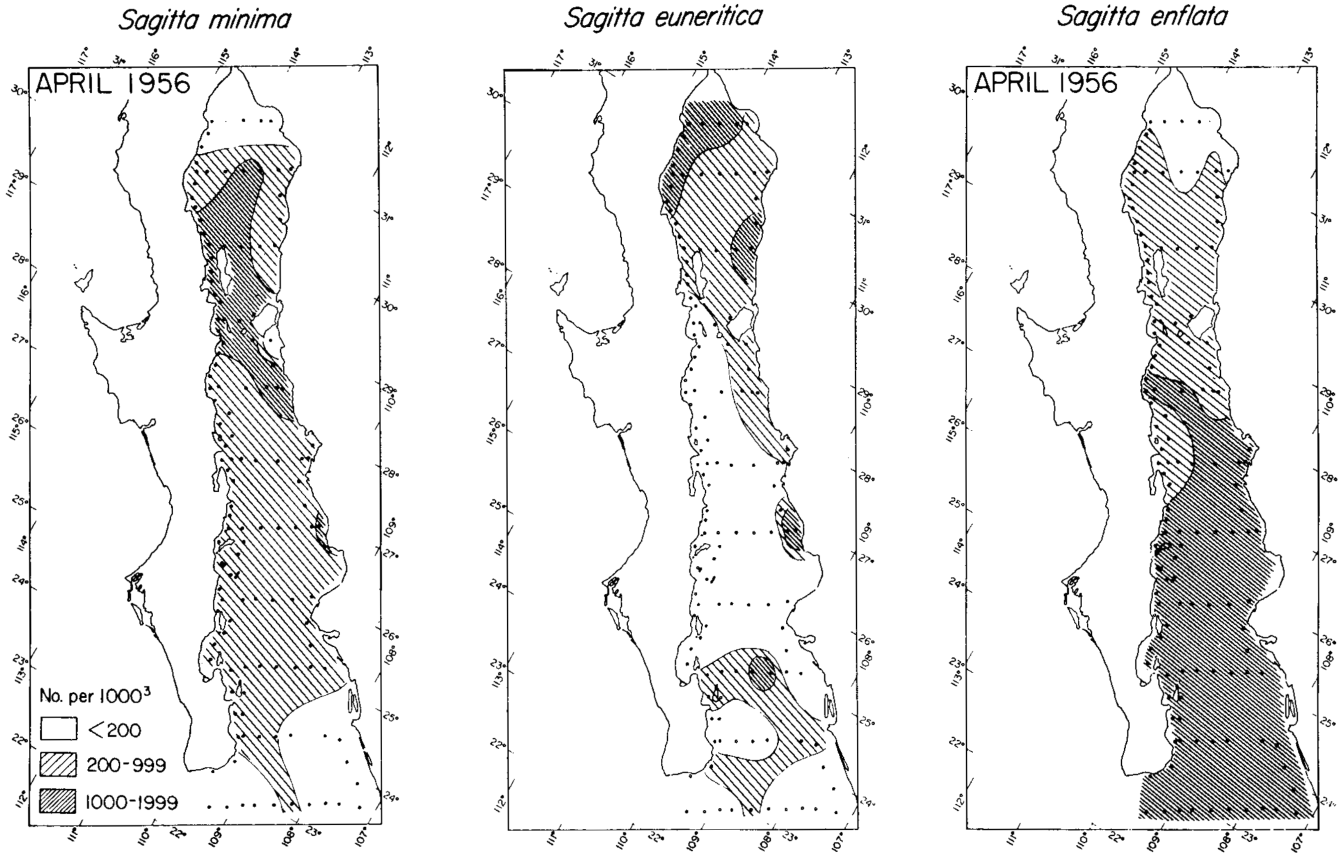

Sagitta minima *Sagitta euneritica* *Sagitta enflata*

Figure 8. The three most abundant species of Chaetognatha sampled in the Gulf of California by the April 1956 CalCOFI cruise (after Alvariño 1969).

C. pinnata, *Pegea confoederata*, *Salpa maxima*, *Thalia democratica*, and *Weelia cylindrica*. All have been found in the southern part of the California Current (Berner 1967). Salps from plankton samples from the gulf have not been studied; only *Thalia democratica* has been reported (see Plankton Biomass). Associations of Amphipoda Hyperiidea with Salpidae (Harbison and Madin 1977) are now understood to be a regular aspect of the ecology of both groups of animals (see Amphipoda).

Heteropod and pteropod molluscs have not been examined in gulf plankton. Their distributions in the California Current are described in McGowan (1967).

Chaetognatha

Alvariño (1969) reported 17 species of Chaetognatha in the gulf, compared to 25 in adjacent waters to the west. The species' Pacific biogeography is shown in Bieri (1959) and Alvariño (1964a), and distributions in the California region are in Alvariño (1964a, 1965, 1967). Aspects of bathymetric distribution are in Alvariño (1964b, 1967), and the species are described in Alvariño (1963).

Four species were widely distributed in superficial (0-140-m) layers sampled during February and April 1956, according to Alvariño.

1. The large species *Sagitta enflata* was abundant (> 2/m^3) during February, except along the western margin of the gulf, and, during April, in nearly all of the gulf except in island channels (ca. 29°N) and northward (Figure 8). *S. enflata* is a warm-water cosmopolite, which Bieri found to have highest densities in the productive equatorial belt and near coasts of Baja California and Central America.
2. *Sagitta minima*, in February, was abundant in mid-gulf and sparse in the southern gulf. In April, high numbers were on the western side, with maxima in the island channels (Figure 8). This species is strongly associated with northern and eastern boundary regions of the North Pacific Central Water Mass, and Bieri found it lacking in eastern tropical Pacific waters near Central America.
3. *Sagitta euneritica* occurs in marginal waters of the gulf, but its distribution can extend over the basins. Alvariño found highest densities over the northern shelf in April (Figure 8) and the shelf in February. This species in endemic to waters of California, Baja California, and the gulf.
4. *Sagitta decipiens* is a small species considered mesopelagic in most oceanic regions, with a depth dis-

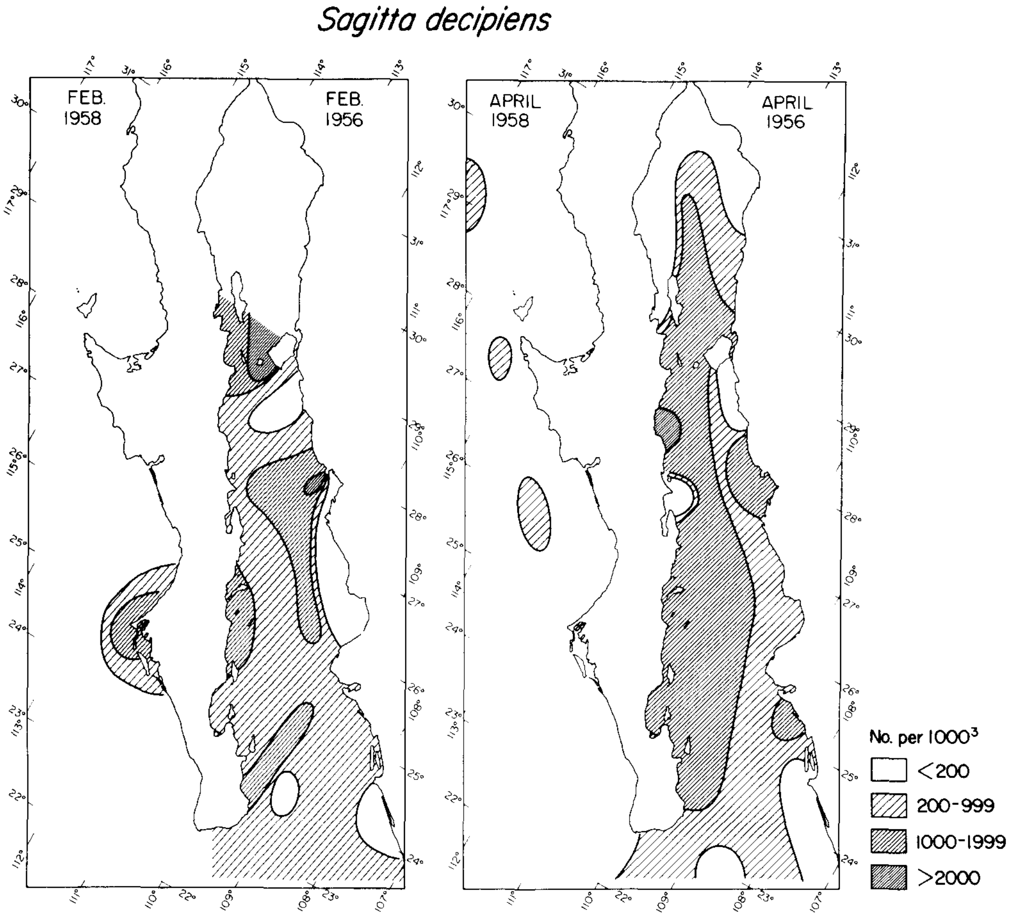


Figure 9. Distribution of the chaetognath *Sagitta decipiens* in the gulf during February and April 1956 (after Alvariño, 1969) and to the west of Baja California during February and April 1958 (after Alvariño 1965).

tribution centered near 200 m. During February and April it occurred throughout the gulf in the 0-140-m layer sampled, though at uneven density (Figure 9). It was all but absent over the northern and southwestern shelves. *S. decipiens* occurs widely in the warm-water belt of the Pacific (40°N to 40°S). The species has proven to be patchy and sparse in the upper layer sampled by CalCOFI in the eastern North Pacific—hence the high frequency noted in the upper layers of the gulf was of particular interest to Alvariño, who considered that this distribution could result from the low concentration of oxygen < 2 ml/l) below 200 m, compressing this species to lesser depths.

While *S. decipiens* appears, in the gulf, to "emerge" from its more typical mid-depth habitat, other mesopelagic species—*S. macrocephala* and *S. maxima*—do not, judging by their appearance only in relatively deep samples obtained during the 1969 Vermilion Sea Expedition. The three bathypelagic *Eukrohnia* species—*E. bathypelagica*, *E. fowleri* and *E. hamata*—also were present in collections from deep basins, from mid-gulf southward.

Of several chaetognath species appearing only in the southern half of the gulf, *S. bierii* ranged farthest north—to mid-gulf, 28°N (Figure 10). This species occurs widely in the eastern tropical Pacific but is commonest at cool northern and southern margins of the region, including much of the California Current (cf. *Euphausia eximia*, Figure 16). Alvariño believed this species' stronger presence in the gulf during February 1956, as compared with April, to indicate relatively strong influence of California Current waters.

Sagitta hexaptera was sparse in the 0-140-m layer sampled in the gulf. *S. pacifica* was present only in the southernmost part. These species are warm-water cosmopolites with ranges of 40°N to 40°S in the Pacific, much like *S. enflata*. However, Alvariño notes that *S. hexaptera* lives beneath 100 m, whereas *S. enflata* is above that depth. *S. hexaptera* and *S. pacifica* occur at low density throughout the southern part of the California Current and off the western coast of Mexico, with *S. pacifica* the more offshore (Central Pacific fauna) of the two. On the other hand, *S. enflata* was at high density both in the gulf and in oceanic waters off Mexico.

Other *Sagitta* scarcely penetrating the gulf but present at its mouth during both February and April

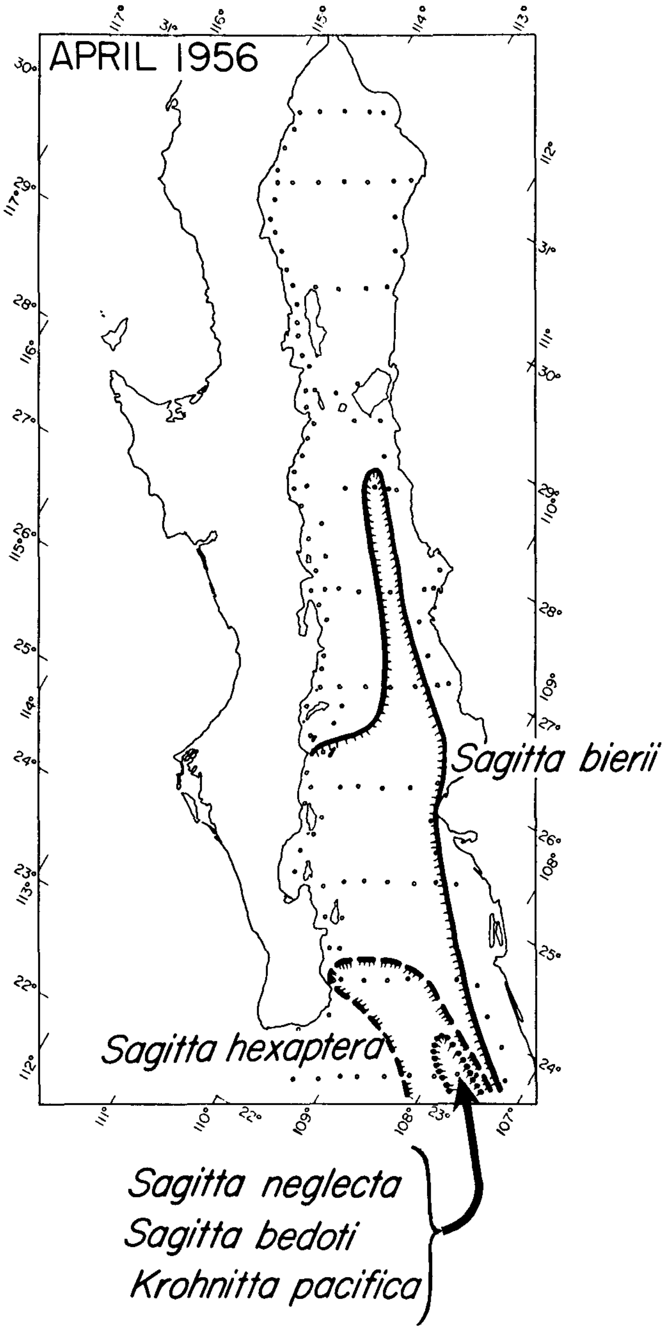


Figure 10. Distribution of the eastern Pacific chaetognath *Sagitta bierii* in the Gulf of California during April 1956, and of two eastern tropical Pacific species, *S. neglecta* and *S. bedoti*, and of tropical *Krohnitta pacifica* (after Alvariño 1969).

were (1) species with particular affinity for the eastern tropical Pacific, e.g., *Sagitta bedoti* and *S. neglecta* (Figure 10), and (2) the broadly equatorial *S. regularia*.

Two species of *Krohnitta*—*K. pacifica* (Figure 10) and *K. subtilis*—are, respectively, tropical and 40°N-40°S in range. Both are absent from the eastern tropical Pacific off southern Mexico and Central America. In the gulf they occurred only at the mouth (23°-24°N). These, and the *Sagitta* species present only near the mouth, tended to penetrate farther into the gulf during the cooler regime of February as compared with April.

Notably absent from the gulf were (1) *Sagitta scrippsae*, typical of the cooler part of the California Current; (2) *Sagitta bipunctata* and *S. zetesios*, particularly adapted to oligotrophic Pacific central waters, as opposed to the equatorial zone and the California Current, and (3) species of Bieri's "equatorial west-central" group, e.g., *Pterosagitta draco*, found in the southern and offshore waters of the California Current, and *Sagitta ferox* and *S. robusta*, appearing not to range north of the Tropic of Cancer (23°27′N).

Medina's (1979) data were from two cruises in the southern half of the gulf (28°N, southward) in 1977. Chaetognaths represented up to 18% of the total number of organisms. *Sagitta enflata* was again the dominant species in the gulf, both in relative abundance and in frequency of collection. On occasion, it formed 100% of chaetognaths. *S. minima* followed *S. enflata* in abundance. The presence of *S. euneritica* and *Krohnitta pacifica* along the east coast of the gulf was interpreted, following Alvariño, as indicating penetration of waters from outside the gulf. Medina emphasized problems related to the existing confusion in the taxonomy regarding identification of *S. neglecta*, *S. regularis*, and *S. bedoti*. *S. bedoti* was found well within the gulf in 1977, whereas Alvariño had found it only at the mouth in 1956.

CRUSTACEA

Copepoda

Published literature on planktonic calanoid copepods does not offer a general taxonomic guide to the species inhabiting the gulf; neither does it provide a species list representative for the region, or information about geographical, seasonal, and vertical distribution of numerically dominant species. Unpublished studies on the gulf's Calanoida, discussed below, indicate that most of the species are also found in the equatorial sector of the Pacific Ocean. Special regional qualities are provided by the small number of species endemic to the eastern tropical Pacific, the few species that are endemic to coastal waters within the gulf, and a number of species typically found in the eastern Pacific off California and Baja California.

Taxonomically useful general introductions to the gulf's offshore species may be found in reports of Grice (1961), Mori (1964), and Park (1968), and generic keys published by Giesbrecht (1892), Rose (1933), Brodskii (1967), Bradford (1972), and Dawson and Knatz (1980). However, in view of many more recent advances in copepod systematics, these references should not be used for critical identifications without referring to the most current literature on the taxon under consideration.

Manrique (1977) has already noted the scarcity of published knowledge dealing with the gulf's planktonic copepod fauna. Taxonomic and distributional studies are sparse, and scattered among a handful of papers dealing largely with other regions. Giesbrecht (1895) reported on nine copepod species found at two stations within the gulf sampled by the U.S. Fisheries steamer *Albatross*. Wilson (1950) confirmed three of Giesbrecht's identifications and recorded 32 additional species from four *Albatross* stations. The credibility of Wilson's *Albatross* records is diminished by a frequent lack of agreement between the species listed in his 1950 report and the identity of the voucher specimens deposited by Wilson in the U.S. National Museum (e.g., Fleminger 1965).

Biogeographic appreciation of the copepod fauna in the gulf was brought into perspective only recently. In atlases depicting the distribution of planktonic species in the eastern North Pacific adjacent to California and Baja California, Fleminger (1964a, 1967a) recorded many species collected at stations near the mouth of the gulf. Taxonomic reports characterize a handful of coastal water species that have been collected within the gulf (Johnson 1964; Fleminger 1964b, 1967b; Fleminger and Hulsemann 1973; Manrique 1977). Turcott-Dolores (1972) reported on copepods in the Laguna de Yavaros (ca. 27°N) on the Sonoran coast, while also describing monthly variations in temperature, salinity, and phytoplankton biomass. At the Boca de Yavaros, where waters were most gulflike, the tropical *Acartia lilljeborgi* predominated, followed by *Acartia* sp. (possibly *A. tonsa* or a species close to *A. californiensis*) and *Pseudodiaptomus* sp. (probably *P. wrighti*). Generic studies that report on gulf occurrences of offshore species include one on *Clausocalanus* by Frost and Fleminger (1968), one on *Pontellina* by Fleminger and Hulsemann (1974), and one on *Eucalanus* by Fleminger (1973). Two recent studies provide qualitative and quantitative data on horizontal and vertical distribution of a number of planktonic copepods in the eastern equatorial Pacific south of the gulf's mouth (Arcos and Fleminger 1986; Chen 1986).

Fleminger (1975) considered geographical and morphological relationships among coastal and offshore species of *Labidocera*. Species of this genus provide evidence for a multitude of temperate to tropical planktonic habitats within the gulf (Figure 11). The three species of the "*Labidocera jollae* group" tend to be associated with oligotrophic, "blue-water" environments, and generally occur at low densities. *L. jollae* is a California Current species inhabiting coastal waters roughly between Cape Mendocino (40°N) and Bahía Magdalena (25°N). Inside the gulf, *L. jollae* is replaced by *L. kolpos*, which extends from the northernmost gulf to 25°N along the eastern coast during winter. The tropical species *L. diandra* appears to be sporadic in the gulf, apparently with considerable seasonal variation. It may reach to mid-gulf on the western side and to about 25°N on the eastern side, at the southern limit of *L. kolpos*. The highest frequency of captures of *L. diandra* occurs between Cabo Corrientes southward to the Gulf of Tehuantepec.

Species of the "*Labidocera trispinosa* group" occur at higher densities. Although their ranges overlap broadly with those of the "*L. jollae* group," species of the two groups do not co-occur; that is, they are not often found in the same net samples. The "*L. trispinosa* group" has relatively "green-water" or eutrophic affinities. *L. trispinosa* is the California Current species. *L. johnsoni* is present in the northern gulf and extends southward along the eastern coast to Mazatlán (22°N) in winter. Tropical *L. lubbocki* has been recorded only along the eastern coast of the gulf—to 26°N; its apparent absence from the southwestern gulf indicates the general lack of green-water habitats there.

Three other more offshore *Labidocera* species, not forming a sibling group, often mix with the coastal water species of the *jollae* and the *trispinosa* groups. Related only at the generic level, the three have been combined in Figure 11 because of their offshore habitat preferences. *L. acuta* is common in the southern California Current and throughout the Gulf of California. Its broadly neritic tendencies are seen in its frequent occurrences in mid-gulf. The broadly tropical *L. acutifrons* is found in the southernmost extension of the California Current and in the gulf along its western side, as far north as Isla San Marcos, 27.5°N. The equatorial species *L. detruncata* also appears in the southernmost California Current and in the southern gulf, from 26°N southward.

A new spinocalanid copepod, *Isaacsicalanus paucicetus*, was discovered just west of the mouth of the gulf on the East Pacific Rise (Fleminger 1983). The new genus and species was collected by the submersible *Alvin* near the seafloor at about 2600-m depth, adjacent to a hydrothermal vent that raises bottom-water temperature from 5° to 15°C. This copepod appears to be of the unique invertebrate fauna associated with such vents.

We anticipate that many of the species inhabiting the California Current (Fleminger 1964a, 1967a) will also be found in the Gulf of California. In fact, unpublished notes on gulf calanoid copepods accumulated by Fleminger while studying the distribution of several copepod genera inhabiting the gulf confirm this. These rec-

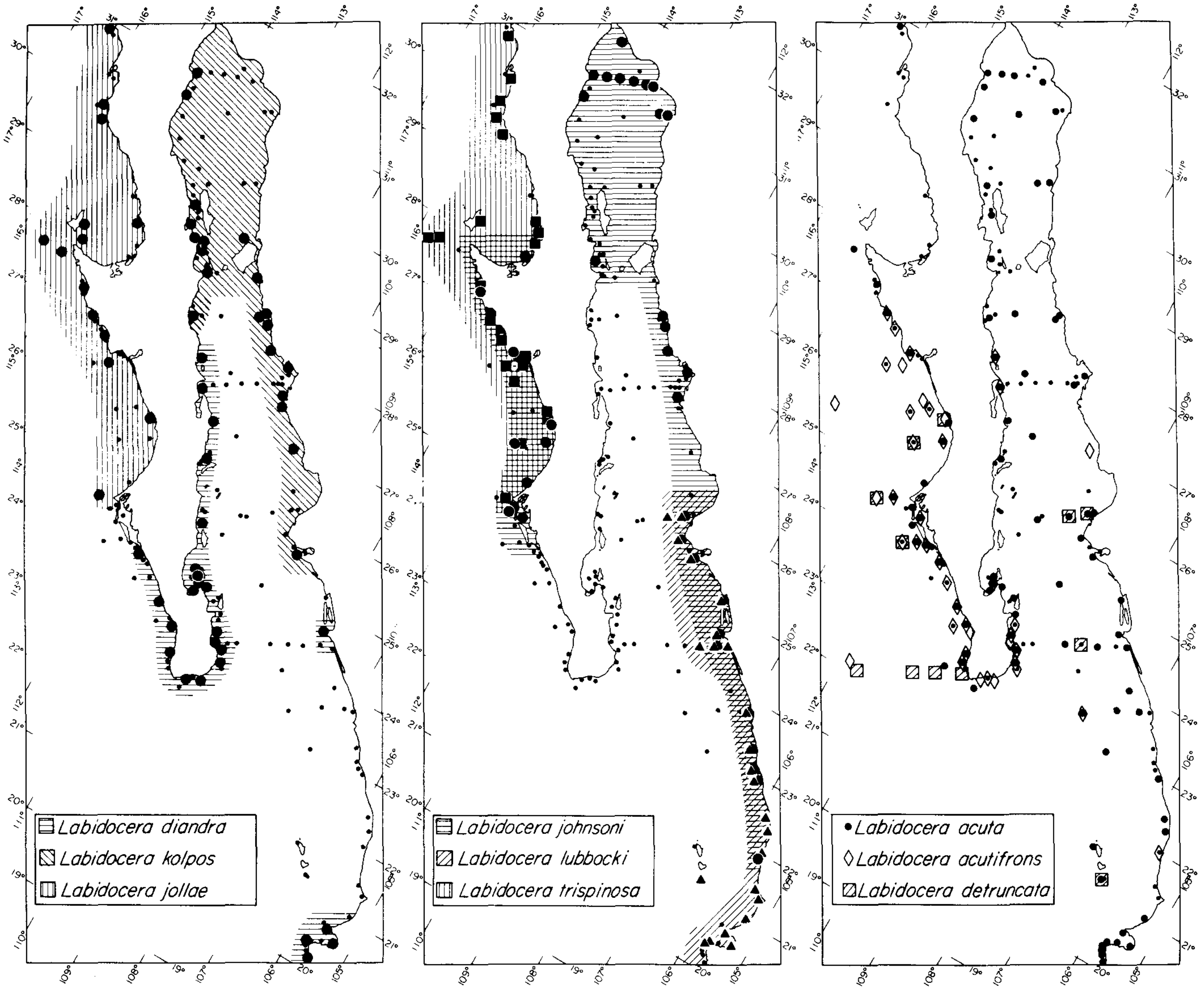


Figure 11. *Labidocera* copepods of the Gulf of California. *Left*, the "*Labidocera jollae* group," illustrating faunistic breaks on both sides of Baja California, and a break on the eastern side of the gulf. *Middle*, overlapping ranges of three species of the "*Labidocera trispinosa* group," an inshore "green-water" group whose members do not usually co-occur in samples with species of the "*L. jollae* group." *Right*, three *Labidocera* species, not closely related, which mix with both of the above groups. All have more offshore habitat preferences: two are oceanic, *L. acutifrons* being broadly tropical, whereas *L. detruncata* is equatorial; *L. acuta* is broadly neritic and equatorial.

ords, added to the published records reviewed above, appear to provide a largely complete list of the calanoid copepod species to be found in the gulf's uppermost 100 m (Table 1). A tentative biogeographical-ecological census of these species is presented in Table 2.

Ostracoda

Although ostracods are a conspicuous group in the gulf's plankton, there are no reports dealing with them in these waters. Müller (1895) reported only three species in material collected by the *Albatross* inside the gulf. Most notable of these were the type specimens of the large deep-sea species *Gigantocypris pellucida* from the Guaymas and Carmen basins in mid-gulf. Müller also reported two species of Halocypridae from the gulf: *Chonchoecia armata* Claus and *C. agassizii* Müller.

A few species have been recorded from the California Current to the west of Baja California: *Chonchoecia giesbrechti*, *C. daphanoides*, *C. strilola*, and *Halocypris brevirostris* (Haury 1976).

Amphipoda

The gulf's amphipod fauna is diverse. Siegel-Causey (1982) recorded 119 species of Hyperiidea (55 considered rare), belonging to 16 families. Distributions were related to water types, based largely upon 1956 and 1957 cruises. In the world oceans, most amphipod species are broadly distributed; although many are warm-water cosmopolites or have extensive

TABLE 1
Planktonic Copepods That Have Been Found in the Gulf of California

The following abbreviations signify favored habitat, biogeographic affinities, and relative abundance where available data clearly indicate a trend.

Habitat: e = estuarine waters; c = coastal waters; m = mesopelagic depths of oceanic waters; n = broadly neritic waters; o = oceanic mixed layer.

Biogeographic affinities: temp. = temperate; trop. = broadly subtropical to tropical; equat. = equatorial; end. = endemic to the Gulf of California and contiguous waters to the north or south.

Relative abundance: a = abundant, usually occurring at or near the highest rank in order of numerical dominance; w = abundance or widespread occurrence appears in the cooler months; s = abundance or widespread occurrence appears in the warmer months.

Calanoida

Acartia danae	o, trop.
A. lilljeborgii	c, equat., a-s
A. negligens	o, trop.
A. tonsa, s.l.	c, temp.-trop., a
A. sp.*	c

*One or more undescribed forms that appear to be related to *A. californiensis*.

Acrocalanus andersoni	n, equat.
A. gracilis	n, equat.
A. inermis, s.l.	o, equat.
A. longicornis	n, trop.
A. monachus	n, equat.
Aetideus armatus, s.l.	n, trop.
Augaptilus longicaudatus	m
*Calanus pacificus, s.l.**	n, temp., a-w

*Appears in Manrique's (1977) list as *C. helgolandicus*, a species *sensu stricto* found only in the N. Atlantic, Mediterranean, and Black Sea.

C. tenuicornis	o, temp.
Calocalanus pavo	o, trop.
C. pavoninus, s.l.	o, trop.
C. plumulosus, s.l.	
C. styliremis, s.l.	o, trop.
Candacia bipinnata	n, temp.
C. catula	n, equat.
C. curta	n, trop.
C. pachydactyla	o, equat.
C. pofi	n, equat.
C. truncata	n, equat.
Canthocalanus pauper	c, equat., a
Centropages furcatus	n, trop., a
C. gracilis	o, trop.
*C. kroyeri**	

*This species is well known from neritic waters of the eastern temperate N. Atlantic and Mediterranean. In view of the absence of *kroyeri* from the other studies on gulf copepods and in fact from elsewhere in the Pacific, this record reported by Wilson (1950) is considered unreliable.

Clausocalanus farrani	o, trop.
C. furcatus	o, trop., a
C. jobei	o, temp.
C. mastigophorus	o, trop.
C. parapergens	o, trop.
Ctenocalanus vanus, s.l.	n, temp.
Euaetideus acutus	n, trop.
E. bradyi	n, trop.
Eucalanus attenuatus, s.s.	o, equat.
E. crassus	n, trop.
*E. inermis**	m-o, equat., end.

*Includes Wilson's (1950) *E. muticus*, regarded by A.F. to be a junior synonym of *E. inermis*.

E. pileatus	c, trop., a
E. sewelli	o, trop.
E. subcrassus	n, equat.
E. subtenuis	o, equat., a
Euaugaptilus hecticus	m
Euchaeta acuta, s.l.	o, trop.
E. longicornis	m, equat.
E. media	o, trop.
E. rimana	o, trop.
E. spinosa	m
E. wolfendini	c, equat.
Euchirella sp.*	m

*An undescribed form inhabiting the eastern tropical Pacific.

E. venusta	m
Haloptilus acutifrons	m
H. chierchiae	m
H. longicornis, s.l.	o, trop.
H. ornatus	m
Heterorhabdus papilliger	o, trop.
Heterostylites longicornis	m
Labidocera acuta	n, equat., a
L. acutifrons	o, trop.
L. detruncata	o, equat.
L. diandra	c, equat., end.
L. johnsoni	c, temp., end.
L. kolpos	c, temp., end., w
L. lubbocki	c, equat., end.
Lucicutia clausi	m
L. flavicornis	o, trop.
L. gaussae	o
L. gemina	o
L. grandis	m
L. ovalis	o
Mecynocera clausi	o, trop.
Metridia brevicauda	m
M. curticauda	m
Microcalanus sp.	m
Nannocalanus minor	o, trop.
Neocalanus gracilis	o, trop.
Paracalanus crassirostris, s.l.	e & c
P. denudatus	o, trop.
P. nanus	n

Continued on next page

TABLE 1 *(continued)*

P. parvus, s.l.	c, trop. & temp., a
Pareuchaeta californica	m
P. grandiremis	m
Phaenna spinifera	m
*Pleuromamma abdominalis**	
*Wilson's (1950) Gulf of California records of *P. robusta* are probably based on misidentification of *abdominalis*.	
P. gracilis	o, trop.
P. indica?	
*Pontella agassizi**	o, equat., end
*Wilson's (1950) Gulf of California record of *P. atlantica* is probably based on misidentification of *agassizi*.	
Pontellina plumata, s.l.	o
P. sobrina	o, equat., end.
Pontellopsis occidentalis	n, temp., end.
P. lubbocki	n, equat., end.
P. regalis	o, trop.
Pseudodiaptomus euryhalinus	e & c, end.
P. wrighti	e & c, end.
Rhincalanus nasutus	n, temp., a-w
Scaphocalanus curtus	o, trop.
S. echinatus	o, trop.
Scolecithricella abyssalis	o
S. ctenopus	o
S. nicobarica	o
S. tenuiserrata	o, trop.
Scolecithrix bradyi	o, trop.
S. danae	o, trop., a
*Temora discaudata**	n, trop., a
*Wilson's (1950) records of *T. stylifera* from the Gulf of California are in error (Fleminger and Hulsemann 1973) and probably represent the misidentification of *T. discaudata*.	
Temoropia mayumbaensis, s.l.	m
Undinula darwinii	o, equat.
U. vulgaris	n, trop., a
Cyclopoida	
Copilia mirabilis	
C. quadrata	
Corycaeus anglicus	
C. brehmi	
C. clausi	
C. dubius	
C. flaccus	
C. latus	
C. lautus	
C. obtusus	
C. ovalis	
C. speciosus	
Farranula rostrata	
Oithona plumifera	
O. nana	
Oncaea media	
O. minuta	
Sapphirina gemma	
S. nigromaculata	
S. opalina	
Harpacticoida	
Euterpina acutifrons	
Macrosetella gracilis	
Microsetella rosea	

The above information has been collated from papers reviewed in the text and from unpublished notes of A.F. Unpublished data on the gulf's copepod fauna were obtained primarily from examination of 1-m CalCOFI net and ½-m net macroplankton samples collected by oblique and horizontal tows at depths shallower than 150 m and from stations shown in Figure 11.

vertical ranges, highest densities of given species tend to be in either a tropical, subtropical, or warm-temperate zone. Seasonal variation in the gulf was such that in February (1957), 75% of hyperiid species occurring at the mouth, and 25% at 26°N were considered to be tropically derived; in August, 75% at 26°N and 50% at the island channels (29°N) were tropical. North of the islands diversity was low, but abundances were high. Of the gulf's eight "abundant" species, six occurred the full length of the gulf.

Species of the cooler part of the California Current (Bowman 1953)—e.g., *Dairella californica*, *Paraphronima crassipes*, *Vibilia woltereck*i, and *Hyperoche medusarum*—were rare in the gulf. However, certain abundant and widely distributed species of the California Current—e.g., *Vibilia armata*, and *Primno brevidens*—were also abundant throughout the gulf. The most abundant, *Lestrigonus bengalensis*, was observed in the California Current (Bowman 1953) to show a bias toward neritic waters, like the gulf's most abundant euphausiid, *Nyctiphanes simplex* (below).

There were three patterns of distribution, as follows:

1. Present at mouth of gulf in winter-spring, advancing northward in summer: classified as uncommon (unc), common (com), abundant (abd); temperate (temp), subtropical (s-t), tropical (t); epipelagic (epil), mesopelagic-epipelagic (meso-epi)

Hyperiidae	
Hyperietta stebbingi	unc, temp, epi
Lestrigonus schizogeneios	com, temp, epi
Phronimopis spinifera	abd, temp, epi
Themistella fusca	com, temp, meso-epi
Phronimidae	
Phronima stebbingi	unc, temp, epi
Phronima bucephala	com, s-t, epi
Phronima atlantica	com, s-t, meso-epi
Phronimella elongata	unc, cos, epi

Lycaeopsidae	
Lycaeopsis neglecta	com, temp, epi
Lycaeopsis thimistoides	unc, temp, epi
Lycaeopsis zamboangae	com, temp, epi
Phrosinidae	
Phrosina semilunata	unc, cosmo, meso-epi
Pronoidae	
Eupronoe maculata	com, cosmo, epi
Paralycaea hoylei	unc, s-t, epi
Lycaeidae	
Brachyscelus globiceps	com, s-t, epi
Brachyscelus crusculum	unc, s-t, surf
Oxycephalidae	
Oxycephalus clausi	com, temp, meso-epi
Oxycephalus piscator	unc, s-t, epi
Rhabdosoma whitei	com, s-t, epi
Platyscelidae	
Platyscelus serratulus	com, s-t, epi
Amphithyrus bispinosus	com, temp, meso-epi
Amphithyrus sculpturatus	unc, temp, epi

2. Found near mouth of gulf only, all seasons

Hyperiidae	
Hyperioides longipes	com, s-t, epi
Hyperioides sibagnis	unc, t, epi
Phronimidae	
Phronima curviceps	unc, t, epi
Lycaeopsidae	
Lycaeopsis pauli	unc, s-t, epi

3. Scattered along length of gulf, all seasons

Scinidae	
Scina borealis	com, cosmo, meso-epi
Vibilidae	
Vibilia armata	abd, temp, epi
Hyperiidae	
Hyperiietta vosseleri	com, s-t, epi
Lestrigonus shoemakeri	abd, s-t, epi
Phrosinidae	
Primno brevidens	abd,
Phronoidae	
Eupronoe armata	com, s-t, epi
Lycaeidae	
Lycaea bovallioides	com, s-t, epi
Lycaea serrata	unc, s-t, epi
Thamneus platyrrhynchus	com, s-t, epi
Oxycephalidae	
Simorhynchotus antennaris	abd, cosmo, meso-epi
Platyscelidae	
Tetrathyrus pulchellus	abd, temp, meso-epi
Parascelidae	
Thyropus edwardsi	abd, s-t, epi

Siegel-Causey (1982) discussed the well-known association of hyperiids with gelatinous zooplankton—salps, medusae, siphonophores. The importance of a gelatinous substrate was recognized, pointing to the probability of facultative associations rather than obligate, host-specific parasitism. Consistent co-occurrences (e.g., *Vibilia* spp. and salps), were nevertheless evident.

Mysidacea

In our examinations of plankton samples from the gulf, it has been evident that the Mysidacean fauna is rich. However, no significant work has yet been done on it. Tattersall's (1951) extensive review of the worldwide distribution of mysids, in which there are many useful keys, descriptions, and illustrations, cites species from both Mexican coasts, but not from the gulf.

TABLE 2
Biogeographical and Habitat Qualities of Gulf Region Calanoid Copepod Fauna

Biogeographical types	No. of species	% of total
Temperate		
Estuarine-coastal	4	5
Neritic	5	6
Oceanic	2	2
Subtotal	11	13
Tropical-subtropical		
Estuarine-coastal	2	2
Neritic	8	10
Oceanic	30	36
Subtotal	40	48
Equatorial		
Estuarine-coastal	7	8
Neritic	10	12
Oceanic	9	11
Subtotal	26	31
Not placed	7	8
Total	84	100
Habitat Groups (biogeographical types combined)		
Estuarine-coastal	13	15.5
Neritic	23	27.5
Oceanic	48	57
Total	84	100
Endemics	11	13
Nonendemics	73	77
Total	84	100

Hansen (1912) recorded *Euchaetomera plebeja* from material collected in 1904-05 by the *Albatross* off Cabo San Lucas. Steinbeck and Ricketts (1941) listed *Archeomysis* sp. (near to *A. maculata*) and *Mysidopsis* sp. at Punta Marcial. Unidentified mysids were among the nearshore "demersal" zooplankton that migrated from a benthic daytime habitat into the water column at night, observed near Isla Danzante, 26°N (Alldredge and King 1980).

The mesopelagic (below ca. 300 m) species are better known. Of the Eucopiidae, *Eucopia australis* was found by Faxon (1893, 1895) in the southern gulf in material from the 1891 cruise of the *Albatross*. Faxon also listed *Gnathophausia willemoesii* from deep water near Islas Tres Marias. Clarke (1962) referred *G. willemoesii* to *G. zoea* in his extensive study of the genus *Gnathophausia*. He recorded two species from the gulf, from trawl collections made during the Vermilion Sea Expedition: *G. zoea*, again near the mouth of the gulf (20°-23°N) and *G. gigas* from the Faralón Basin (25.5°N). Neither the wide-ranging *G. ingens*, which has not been found in the eastern tropical Pacific where oxygen is deficient within the mid-depth habitat of this species, nor the warm-water cosmopolite *G. gracilis* were found in the gulf.

Pequegnat (1965) compiled the world distributions of four species of *Gnathophausia* and gave a key to eight species of the genus. However, there were no records in the gulf.

Euphausiacea

Euphausiids are prominent in oceanic and offshore-neritic waters of the gulf, but most species avoid the closest coastal zone. First records from the gulf were in Ortmann (1894) from collections obtained by the *Albatross* off Guaymas and about 50 miles farther south. The four species listed were incorrectly identified; they were among the eastern tropical Pacific species later described by Hansen (1911). Hansen (1915) reexamined Ortmann's material and recorded *Nyctiphanes simplex*, *Euphausia distinguenda*, *E. eximia*, and *Nematoscelis difficilis* from the gulf. (Ortmann had referred these, respectively, to *Nyctiphanes australis*, *Euphausia mucronata*, *E. pellucida*, and *Nematoscelis microps*.) Hansen also recorded *Nematoscelis difficilis* off Isla Santa Catalina (26°N) and "enormous numbers" of *Nyctiphanes simplex* from Bahía San Luis Gonzaga (30°N) in March 1889. Steinbeck and Ricketts (1941) observed water "soupy" with *N. simplex* off Punta San Marcial (25.5°N).

Hansen's 1912 report on euphausiids from the 1904-05 cruises of the *Albatross* included records of four species at the mouth of the gulf during October 1904: *Euphausia lamelligera*, *E. tenera*, *E. diomedeae*, and *E. distinguenda* off Cabo Corrientes (20°-21°N) and *E. distinguenda* again, near Cabo San Lucas (22° 45′N). Most of the species inhabiting the eastern tropical Pacific were described and illustrated in this report, including 10 of the 13 now known from the gulf. Further descriptions of euphausiids of this region are in Hansen (1910), Boden et al. (1955), and Brinton (1975). Larval stages of species reported from the gulf have been described: *Nyctiphanes simplex* (Hansen 1910; Boden 1951); *Euphausia eximia* (Knight 1980); *E. gibboides* (Knight 1975); *E. distinguenda* (Hansen 1910); *E. tenera*, *E. diomedeae*, *Stylocheiron* spp. (Brinton 1975); *Nematoscelis difficilis*, and *N. gracilis* (Gopalakrishnan 1973).

Brinton (1962) described subspecific forms of *Stylocheiron affine* and *S. longicorne* and showed distributions of euphausiids in the southern part of the gulf during October 1952 (shown in greater detail in Brinton and Townsend 1980). These distributions are of two kinds: (1) species with a population inhabiting the gulf but absent from the southernmost end and thereby appearing to be disjunct from the conspecific population that is widespread in the warm-temperate segment of the California Current (*Nyctiphanes simplex*, *Nematoscelis difficilis*, and *Euphausia eximia*); and (2) tropical species that were present in the southern gulf (*Nematoscelis gracilis*, *Euphausia distinguenda*, *E. lamelligera*, and *E. tenera*).

The RV *Te Vega* subsequently obtained a series of 55 Tucker trawl collections along the deep-water axis of the gulf, from the mouth to north of Isla Angel de la Guarda (30°N) during September-November 1967 as part of an ecological reconnaissance of deep scattering layers (Dunlap 1968). For this material, Vega-R. (1968) worked out the quantitative relationships of the major taxa. The euphausiids, analyzed by Mundhenke (1969), included most of the species previously recorded from the gulf. Of significance were (1) documentation of occurrences of *Nematoscelis difficilis* throughout the gulf, (2) an apparent lack of *Nyctiphanes simplex* south of mid-gulf (27°N), and (3) northward penetration to the Canal de las Ballenas, (29°N) by *Euphausia distinguenda*, *E. eximia*, and nearly that far by *Nematobrachion flexipes*. Ranges of these species were thus extended well to the north of *Albatross* records. Notably absent from this report were *Euphausia lamelligera* and the genus *Stylocheiron*. However, *Euphausia gibboides*, well known as an offshore species in the California Current, was recorded in substantial numbers northward to the Guaymas Basin; these records need confirmation. Subsequently, *E. gibboides* has not been found in the gulf, though Brinton (1979) reported an isolated instance at the middle of the mouth at 21°N in June 1974, together with another disjunct southerly occurrence—of *Stylocheiron longicorne* in a patch of low-salinity water from the California Current, evidently from the northwest.

Brinton and Townsend (1980) presented a picture of seasonal development in populations of euphausiids throughout the gulf, based on bimonthly 1957 cruises. Sampling was to a depth of 140m—sufficient for the subadult stages of most gulf species, and for nighttime catches of vertically migrating adults.

Of the nine regular inhabitants of the gulf, those common both to the gulf and the warm-temperate California Current—*Nematoscelis difficilis* and *Nyctiphanes simplex*—consistently had the broadest ranges in the gulf (Figure 12). They were most abundant and reproductive during February-April and February-June, respectively, before August heating (Figure 13). Tropical *Nematoscelis gracilis* showed a range generally complementary to that of *N. difficilis*. *Euphausia eximia*, considered adapted to margins of the oxygen-deficient waters of the eastern tropical Pacific, consistently occupied only the southern half of the gulf. The three tropical *Euphausia* species—*E. distinguenda*, *E. lamelligera*, and *E. tenera*—like *E. eximia*, occupied the southern gulf in February-April, expanding northward during June-August (Figure 14), consistent with Mundhenke's finds. Like the temperate-subtropical species above, the tropical species scarcely reproduced in the gulf during the warm season.

Although most euphausiids have oceanic ranges, there is a species with neritic affinity (Brinton 1962) corresponding to each of ten Pacific littoral provinces. Two of these species occur in the gulf. *Nyctiphanes simplex*'s range corresponds with Ekman's (1953) American Temperate-Tropical Zone, and *Euphausia lamelligera*'s with the Pacific Tropical American. *N. simplex* is abundant in any of the marginal waters of the gulf, and *E. lamelligera* is generally abundant along the broad southeastern shelf (Brinton and Townsend 1980).

In *N. simplex* (Figure 12), maximum production of larvae was in February, when waters were coolest— to 14°C in mid-gulf. In April, high abundances were along both sides of the gulf as far south as the mouth (24°N). There, cool surface temperatures (17°-20°C) persisted, evidently at that time due to upwelling. By August, when temperatures increased to 28°-31°C (Figure 13), numbers of young were reduced (Figure 12), recruitment was at a minimum, and the distributions retracted from both the northernmost shelf region and from the mouth.

Nematoscelis difficilis (Figure 12) is the other euphausiid to occupy most of the gulf in 1957, particularly in February, when high densities extended to the mouth, assuring at least seasonal exchange with the California Current population. In April, instances of high density were scattered, and from June to August a reduced population was concentrated toward the west in cooler water (Figure 13). Brinton and Townsend (1980) pointed out that during June and August high temperatures would be expected to limit *N. difficilis* to below 100 m, and shoaling of the 1.5 ml^{-1} oxygen surface to less than 100 m could further narrow the vertical range, thereby restricting this species from much of the southern gulf by August.

There was near-constancy throughout the year in numbers of adults of both *N. simplex* and *N. difficilis*. Numerous *N. difficilis* larvae of February apparently led to an April-June peak in juveniles, and then a stock of young adults in August, expected to reproduce during the ensuing winter.

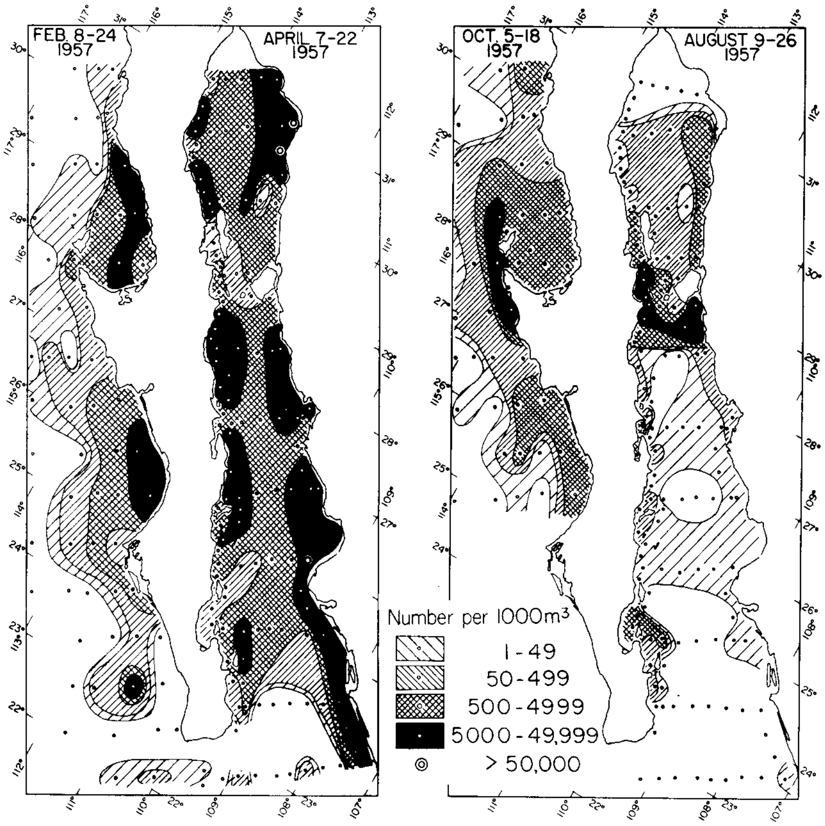
Euphausiid biomass in the gulf was found to be intermediate between that in the richest and poorest parts of either the California Current or the eastern tropical Pacific, with largest standing stocks corresponding to places and times where *Nyctiphanes simplex* and *Nematoscelis difficilis* were most abundant. Values of 50 to 200 cc/1000 m^3 for euphausiids and > 1000 cc for zooplankton were as high as any reported from mid- to low latitudes in the Pacific.

Nine euphausiid species were reported from zooplankton samples obtained in the gulf off the coast of southern Sinaloa in April and August 1981 and January 1982 during the SIPCO cruises of the RV *El Puma* (Sánchez Osuna and Hendrickx 1984). The dominant species was *Euphausia lamelligera*, while *E. distinguenda*, *E. eximia*, and *E. lamelligera* were the most frequently collected. Biovolume measurements indicated that euphausiid shrimps contributed up to 31% of the total biovolume of the catch.

Profiles of vertical distribution of euphausiids west of southern Baja California and across the mouth of the gulf during April-May 1974 illustrate intermingling of California Current and eastern tropical Pacific faunas (Brinton 1979). *Nematoscelis difficilis* (juveniles and adults, Figure 15) remained, day and night, at depths above low oxygen concentrations (ca. 1.0 ml^{-1}); *Nematoscelis gracilis* (Figure 15) and other tropical species, on the other hand, migrated down to daytime depths within the oxygen minimum. *Euphausia eximia*, neither strictly tropical nor temperate, tended to avoid low oxygen concentrations tolerated by the tropical species (Figure 16). More coastal *Nyctiphanes simplex* (Figure 17) remained above about 100 m day and night at nearshore localities, but there was a suggestion of vertical migration in mid-gulf.

Stylocheiron affine and *S. longicorne* are similar

Nyctiphanes simplex



Nematoscelis difficilis

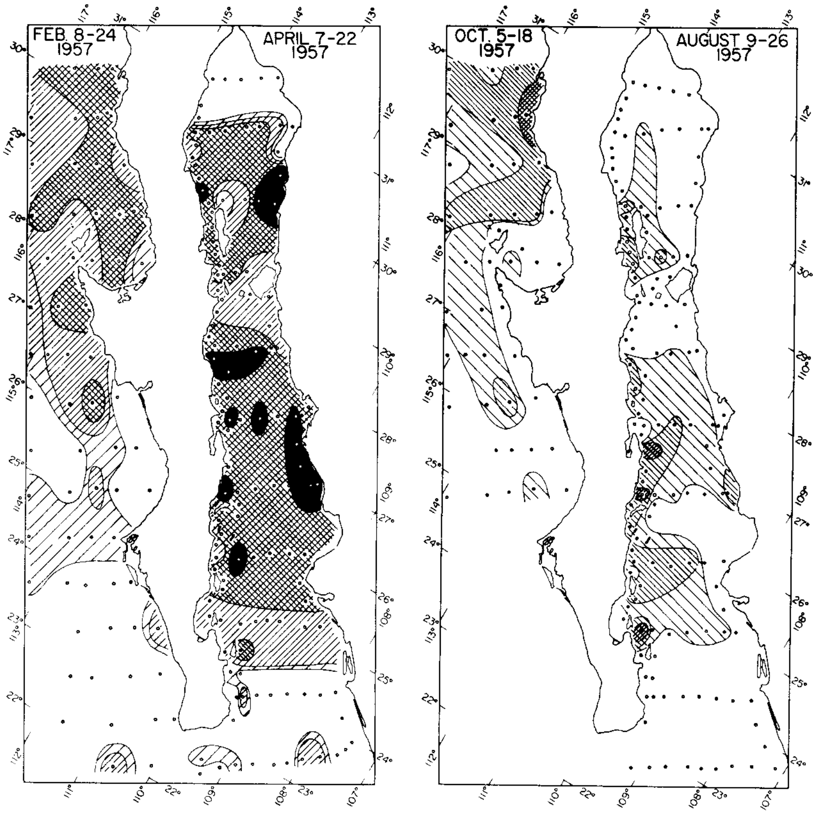


Figure 12. April and August 1957 distributions of the euphausiids *Nyctiphanes simplex* and *Nematoscelis difficilis* in the Gulf of California (after Brinton and Townsend 1980), and February and October distributions to the west of Baja California (after Brinton 1967).

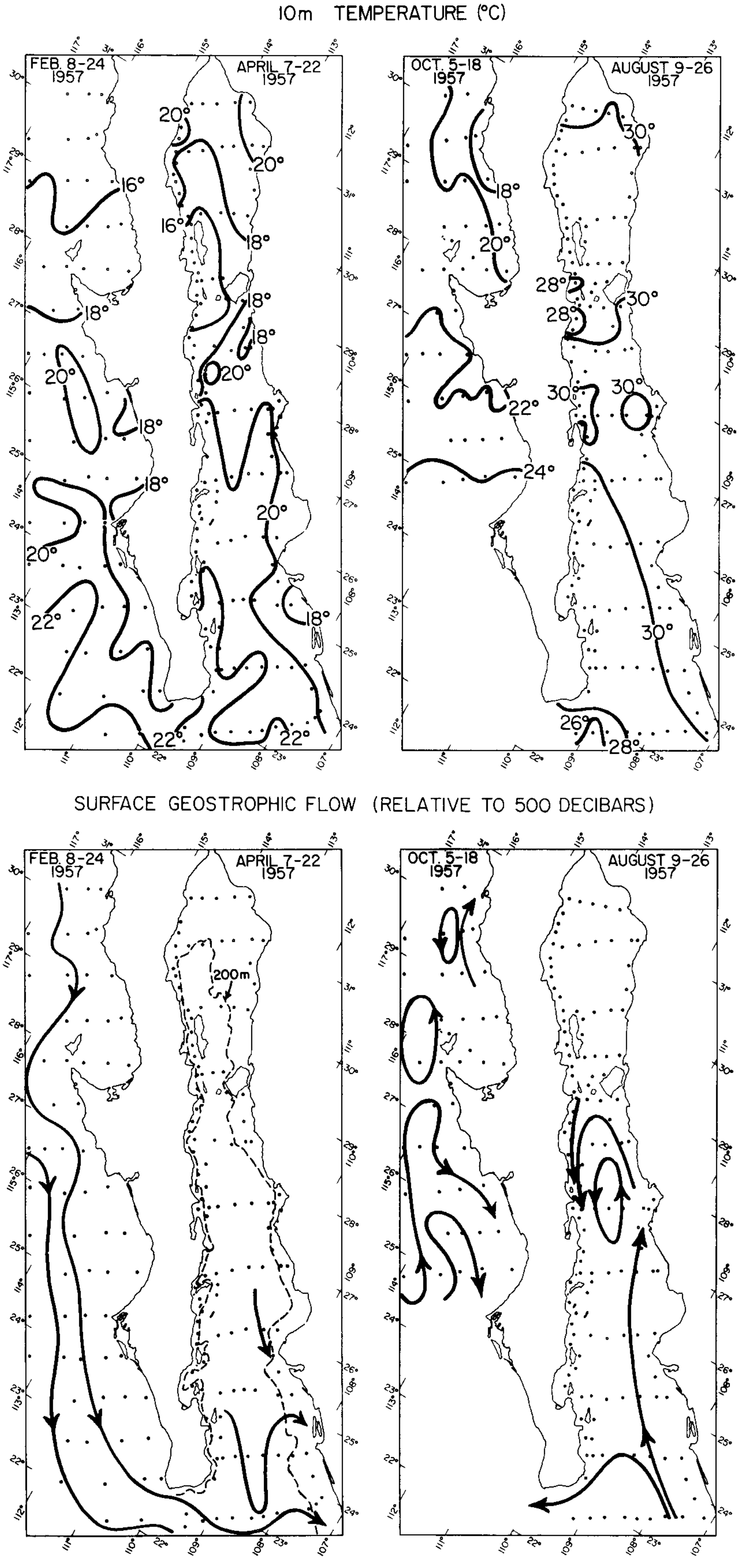


Figure 13. April and August 1957 distribution of 10-m temperature and upper-level geostrophic flow in the Gulf of California, and February and October 1957 distributions to the west of Baja California (after anonymous 1963, and Wyllie 1966).

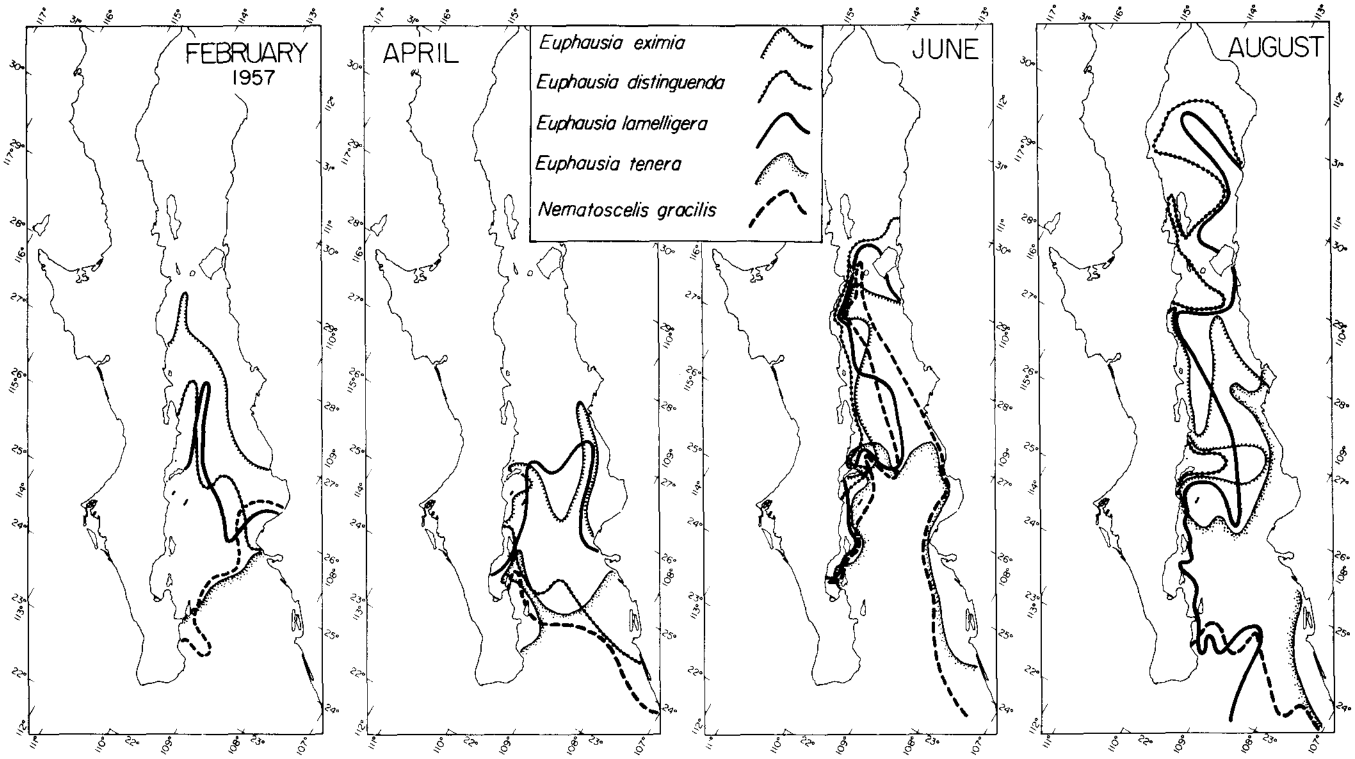


Figure 14. Variation in limits of range in the Gulf of California, during February to August 1957, of the indigenous population of *Euphausia eximia* and of the four tropical euphausiid species (after Brinton and Townsend 1980).

euphausiids that, here, appear not to engage in vertical migration. Both live above the layer having oxygen concentration < 0.5 ml^{-1} (Figure 18), but *S. affine*, which inhabits the upper part of the thermocline, ranges north to south across the eastern tropical Pacific, above the oxygen-deficient water, whereas the somewhat deeper-living *S. longicorne* cannot. Why no species of this genus significantly penetrates the gulf is not understood.

Pelagic Penaeidea (Decapoda)

Of the family Sergestidae, Burkenroad (1937) reported *Sergestes halia* Faxon near Mazatlán and in the mouth of the gulf; *Sergia phorca* (Faxon) in mid-gulf (27° to 28°N); and *Sergestes similis* Hansen, characteristic of cool waters of the California Current, off Isla Tiburón.

Judkins (1972) confirmed that *Sergestes similis* occurs in a seemingly isolated population in the gulf, north of about 25°N. Thus it is a member of the warm-temperate fauna of the North Pacific (cf. *Calanus pacificus californicus*, *Nematoscelis difficilis*) that occupies part of the gulf. Judkins found no other sergestids in Vermilion Sea Expedition trawls from the gulf.

Like many euphausiids, sergestids are strong vertical migrators. Unlike most euphausiids, they tend not to move upward beyond the thermocline. Larval development in *Sergestes similis* has been described in detail by Knight and Omori (1982).

Judkins (1978) provided keys and descriptions for species of the diverse "*Sergestes edwardsii* group" of *Sergestes*. Although none of this group has been reported from the gulf, four of its species occur in the eastern tropical Pacific and one in the California Current.

Species of the genus *Lucifer* seem to occur in the surface layers of all tropical and subtropical seas. *Lucifer typus* was reported at the mouth of the gulf by Burkenroad (1937).

Of the mesopelagic Penaeidae, only *Benthesicymus tanneri* Faxon is known to occur in the gulf (Faxon 1893, 1895). The widespread genus *Gennadas* seems to be absent.

Pelagic Caridea (Decapoda)

These large, apparently nonmigrating, mesopelagic carideans are represented in the gulf, according to Faxon (1893, 1895), by *Acanthephyra curtirostris* Wood-Mason, caught by the *Albatross* north of Islas Tres Marias as well as at mid-gulf, and by *Hymenodora glacialis* (Buchholz) from the mid- and southern gulf.

The genus *Notostomus* and the family Pasiphaeidae, which commonly occur at depths inhabited by

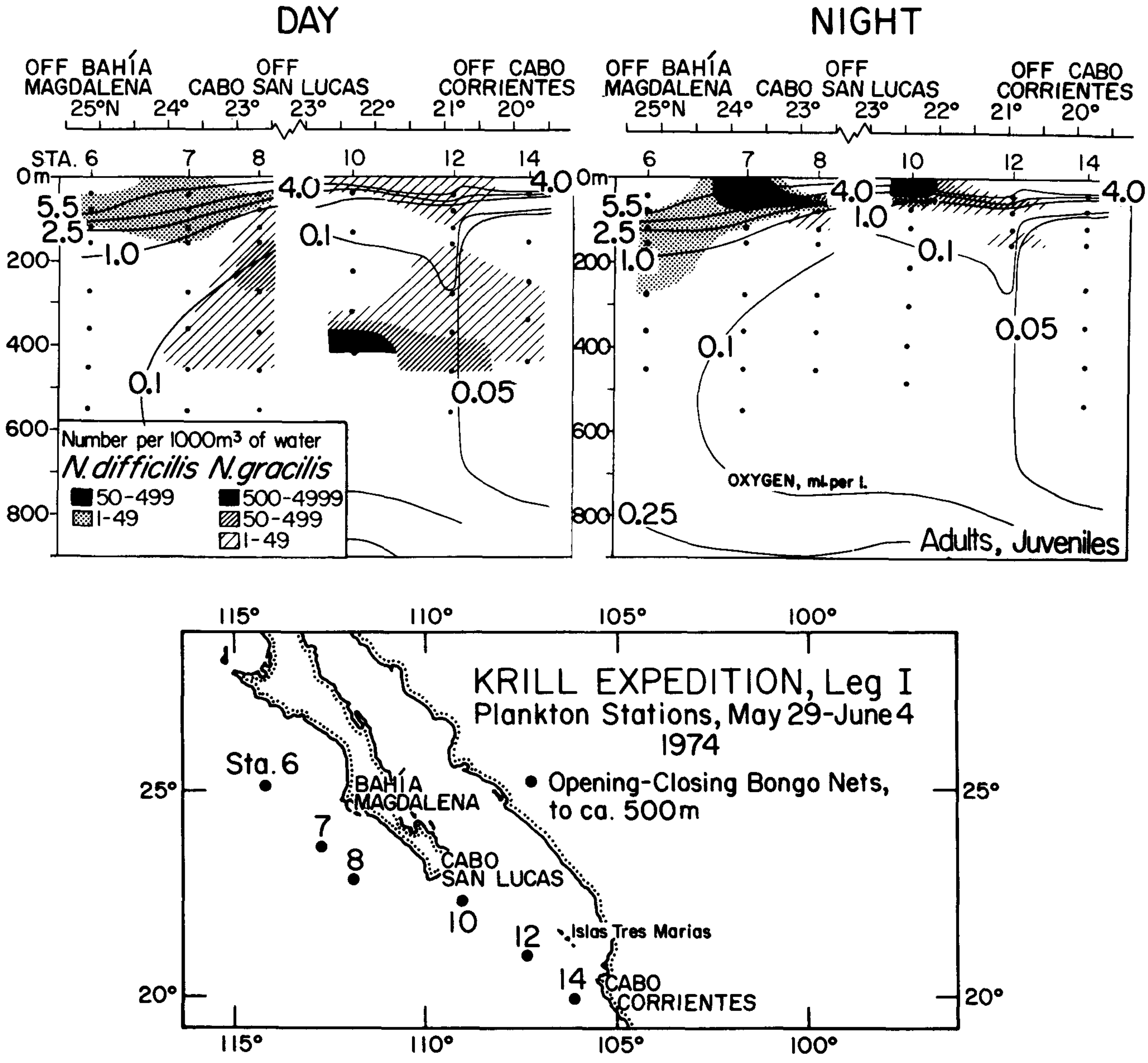


Figure 15. Vertical distributions of three life phases of the warm-temperate euphausiid *Nematoscelis difficilis* and tropical *N. gracilis*, from Bahía Magdalena to Cabo Corrientes. The line of stations is indicated on map, *below*.

Acanthephyra and *Hymenadora*, have not been reported from the gulf.

Pelagic Larvae of Benthic Decapod Crustaceans

An extensive literature exists dealing with behavior and distribution of *Penaeus* postlarvae in the Caimaanero-Huizache lagoons of the southeastern gulf (22°N). Many of these papers arose from the program on lagoon ecology and shrimp fisheries conducted by the Universidad Nacional Autónoma de México in cooperation with the University of Liverpool. However, little work on the pelagic larvae of these species, appropriate for this review, has been carried out. In fact, only a few gulf species of decapod meroplanktonic larvae have been examined in any detail.

Planktonic larvae of four species of *Penaeus*, with emphasis upon *P. brevirostris*, were examined from coastal waters off Sinaloa and Sonora (Cabrera-Jiménez 1983). Taxonomic characters for separation of postlarvae were considered.

Johnson (1968, 1971, 1975), studying the phyllosoma larvae of Palinuridae (spiny lobsters) and Scyllaridae (slipper or shovelnose lobsters) in the eastern tropical Pacific, indicated occurrences in the gulf and provided a key for identification (1971). The commonest palinurid in the gulf was the tropical

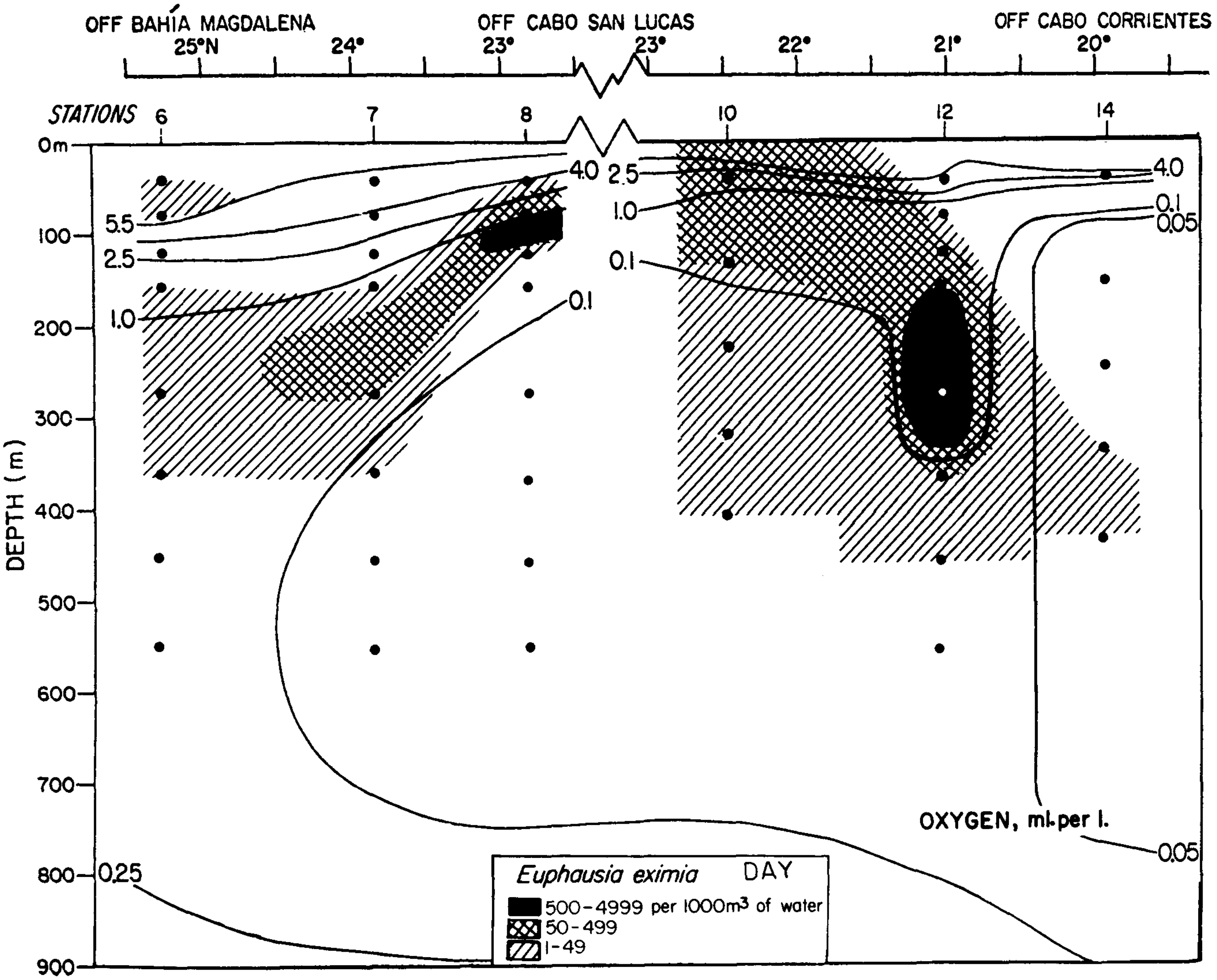


Figure 16. Vertical distributions of four life phases of the eastern Pacific euphausiid *Euphausia eximia*, from Bahía Magdalena to Cabo Corrientes (see Figure 15 for map).

Panulirus inflatus, which, outside the gulf, ranges from Bahía Magdalena (25°N) to the Gulf of Tehuantepec (16°N). The closely related *P. gracilis* also occurs the length of the gulf, from Kino Bay (31°N) southward (Chapa-Saldaña 1964), but Johnson (1971) found its larvae to be rare in the gulf.

Warm-temperate *Panulirus interruptus* occurs along southern California, southward to Bahía Magdalena. Johnson found larvae only in the northern gulf. Thus California Current and gulf populations appear to be separated.

Only two species of scyllarid lobsters are known from the eastern tropical Pacific, and both occur in the gulf (Johnson 1971). Phyllosoma larvae of *Evibacus princeps* occurred along the entire gulf during the August 1957 CalCOFI cruise but were not present in June samples. Larvae of *Scyllarides astori* appeared in August samples from the southern gulf. A few larvae of a third gulf species, not yet known, were designated "Phyllosoma x."

Planktonic larvae of primitive burrowing crabs of the family Raninidae are known from the gulf (Knight 1968). Although two species, *Raninoides benedicti* and *R. ecuadoriensis*, have been found as adults in the gulf (Garth 1948, 1960), only the larvae of *R. benedicti* have been recognized. Identification was confirmed by rearing larvae obtained in plankton tows from near Cabo Corrientes. Larval development of this species is described by Knight. Larvae of *R. benedicti* in plankton samples show that it extends into the gulf to about 27°N, near Bahía Concepción. This species and *R. eucadoriensis* are tropical, ranging southward to Ecuador.

Two species of the sand crab *Emerita* (family Hippidae) are known from the gulf. *E. analoga* occurs from at least as far north as British Columbia south-

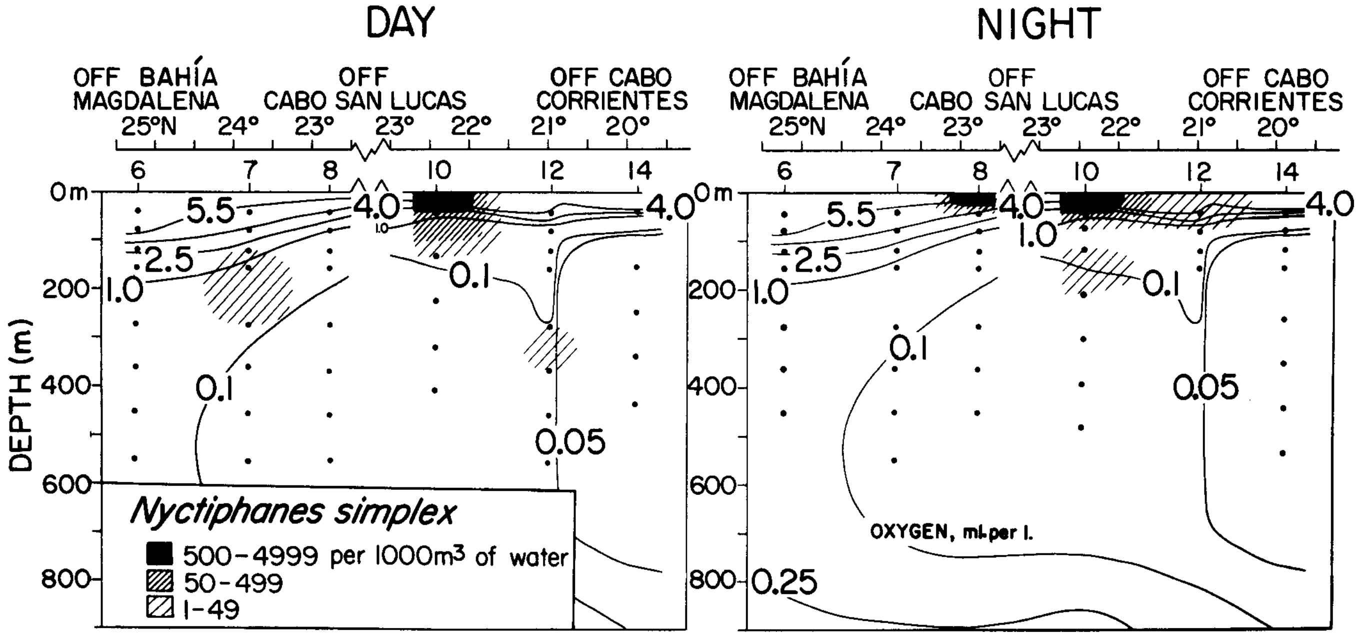


Figure 17. Vertical distribution of the euphausiid *Nyctiphanes simplex*, from Bahía Magdalena to Cabo Corrientes (after Brinton 1979). (see Figure 15 for map).

ward to Bahía Magdalena (records reviewed in Knight 1967). An isolated population has been found in the gulf at Bahía de San Francisquito (28.5°N) in the western gulf (Efford 1969), and *analoga*-like larvae have been recorded in gulf plankton (Knight 1967). *E. analoga* larvae from California waters are described in Johnson and Lewis (1942).

Tropical *Emerita rathbunae* has been also collected from Bahía de San Francisquito (Steinbeck and Ricketts 1941) and southward; Knight (1967) described its larval development, based on larvae hatched from an ovigerous female collected at Mazatlán.

Demersal Zooplankton

Mobile organisms that periodically emerge from the benthos and swim in the water column were termed "demersal plankton" by Alldredge and King (1980). Distances of such vertical migrations were measured by Alldredge and King (1985) on a subtidal and sand flat in the gulf: (1) small forms—copepods, ostracods, and amphipods—remained within 30 cm of the bottom except at full moon, when many swam upward 1 m or more; (2) syllid polychaetes swam upward at least 2 m; and (3) many large forms, > 2 mm, swam throughout the water column, an activity interpreted as a means of dispersal. In a northern cove of Isla Danzante in the central gulf, demersal copepods were dominated by *Cyclopina schneideri*, with *Pseudocyclops* sp. the predominant calanoid.

Zooplankton Biomass

Zooplankton biomass is often expressed as wet displacement volume. Such volumes are particularly biased when large amounts of "jelly plankton" are included. In the California Current, and probably also in the gulf, displacement volume of zooplankton of average composition may be converted to either dry weight or carbon using the following factors from Lasker (1966): dry weight = 17.2% of wet weight (or volume); carbon = 42% of dry weight; carbon = 7.2% of wet weight.

The plankton retained by a given type of net depends, in part, upon the mesh size, as well as upon towing procedures. Nevertheless, different methods provide useful information as to rich and poor areas and ranges of variability in the standing stock.

A first description of the distribution of zooplankton biomass in the gulf was that of Farfan (1973), working in the northernmost area. Values were expressed as dry weight for the full water column, < 50 m in the region studied (Figure 19). Amounts of plankton ranged from < 5 mg/m^3 to < 150 mg/m over broad areas. Values in excess of 100 mg/m^3 were toward the western side in January. March values were generally low, followed by an April-October period when conspicuous maxima fanned out from the northernmost deltaic region.

Cummings (1977) interpreted the distribution of zooplankton biomass in the northern gulf in terms of seasonal upwelling postulated by Roden (1958, 1964), and found correlations between plankton peaks and presumed upwelling maxima.

Griffiths (1968) plotted zooplankton displacement volumes, 0-300 m, across the mouth of the gulf and off southwestern Baja California during spring 1960

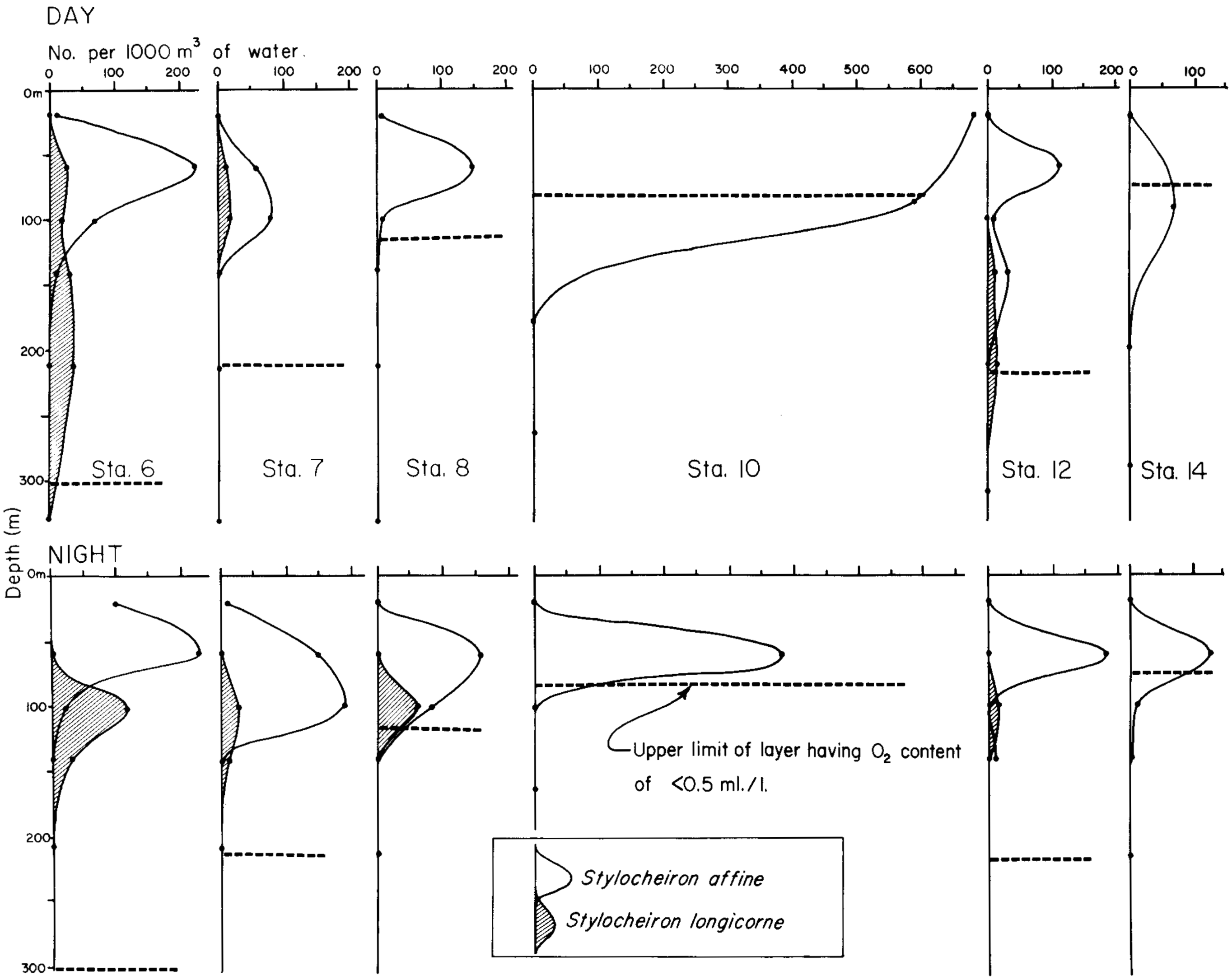


Figure 18. Vertical distributions of the related *Stylocheiron* euphausiids, *S. affine* and the somewhat deeper-living *S. longicorne*, in relation to the upper limit of the layer having oxygen concentration of <0.5 ml/l. Stations extend from off Bahía Magdalena to near Cabo Corrientes (see Figure 15 for map). (after Brinton 1979)

(Figure 20). Values of < 50 to > 200 cc per 1000 m^3 were erratically distributed across this region of oceanic fronts. Highest values were to the south of Bahía Magdalena, near Islas Tres Marias, and across the gulf from Cabo San Lucas to near Mazatlán (23°30′ N).

The 1956 and 1957 CalCOFI cruises, which covered much of the gulf, yielded collections for mapping plankton biomass in the 0-140-m layer. These collections were particularly oriented toward sampling the larger zooplankton, especially larval fishes (Moser et al. 1974). The mesh width of 0.6 mm used in these surveys fails to retain any of the material discussed by Zeitzschel, above, and, of the phytoplankton, hardly more than the largest *Coscinodiscus* cells.

The displacement volumes (Figure 21) show dense April peaks in biomass throughout the gulf, consisting largely of the copepod *Calanus pacificus californicus*, the chaetognath *Sagitta enflata*, and the two euphausiids *Nyctiphanes simplex* and *Nematoscelis difficilis*. High values in April of both years tended to be along the eastern side. However, highest values (> 1000 cc per 1000 m^3) were at five localities on the western side of the northern gulf in April 1957, where small salps (*Thalia democratica*) were in bloom. August and February volumes were generally low, with February 1956 being significantly poorer than February 1957 (Table 3). These volumes are of the same order as those found in rich parts of the California Current: coastal and oceanic regions north of Point Conception, and coastal waters of southern California and western Baja California (cf. Isaacs et al. 1969, 1971; Smith 1971, 1974; Fleminger et al. 1974).

Profiles of vertical distribution of zooplankton biomass were obtained by opening-closing bongo nets along the western coast of southern Baja California and

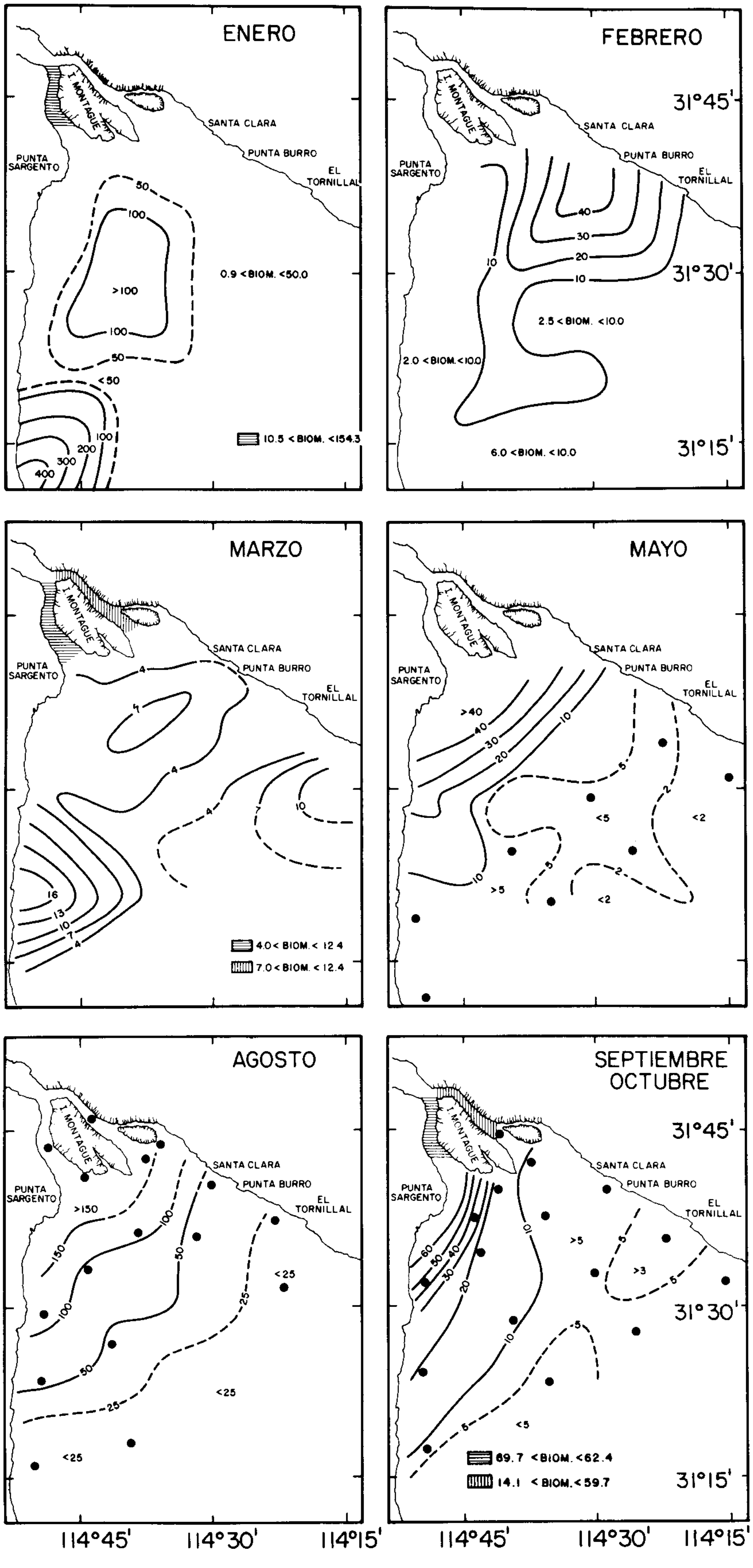


Figure 19. Distribution of zooplankton biomass in the northern Gulf of California during three seasons. Values are expressed as mg dry weight per m^3, for the water column (from Farfan 1973).

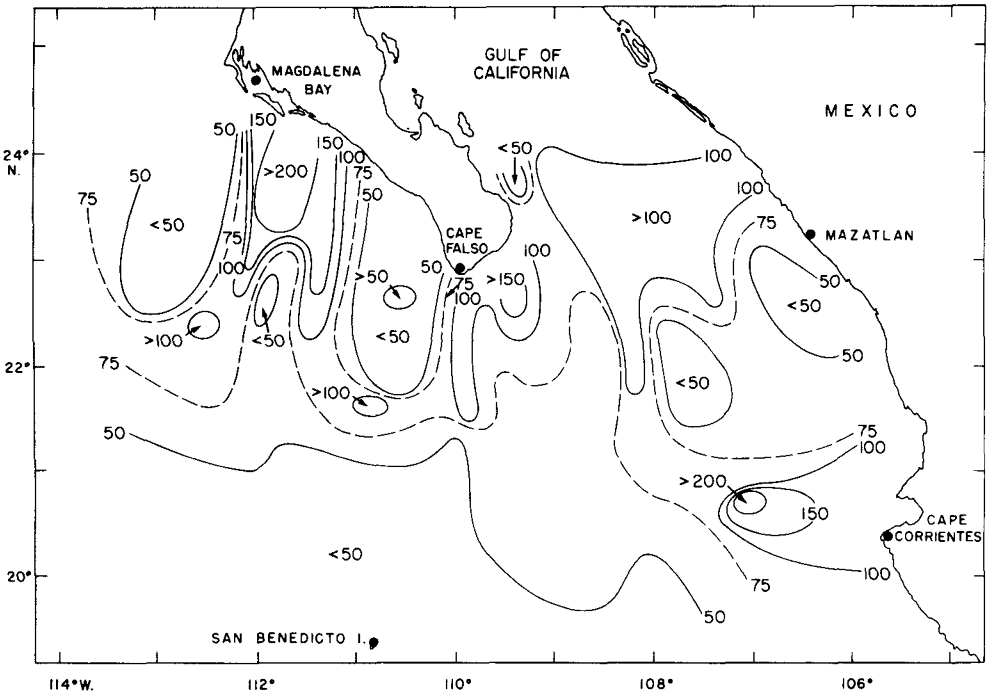


Figure 20. Distribution of standing crop of zooplankton, cc displacement volume per 1000 m^3 of water, in layer between the surface and 300 m in the region of the mouth of the Gulf of California, spring 1960 (from Griffiths 1968).

across the mouth of the gulf (Figure 22) during May-June 1974 (Brinton 1979). Highest values were just west and south of Cabo San Lucas, and on the opposite side of the gulf, off Cabo Corrientes. Maxima were at or near the surface. Nighttime maxima exceeded daytime maxima, but values in excess of 25 cc/1000 m^3 extended down only to about 100 m at night, compared with 400 m in daytime.

High values to the west of Cabo San Lucas included numerous young stages of the semipelagic red crab, or langostina, *Pleuroncodes planipes* (Reptantia, Galatheidae) (Figure 22). Only a few individuals were caught across the mouth of the gulf. The nighttime distribution of *Pleuroncodes* showed dispersal to greater depth than in the daytime, thereby differing from the upward nighttime migration of euphausiids, described above. The pelagic phase of *P. planipes* in the California Current was analyzed by Boyd (1963) and Longhurst (1967a). Adults occur widely in the gulf south of Isla Tiburón, though the RV *Alejandro de Humboldt* reported largest catches on the Sonoran coast between Isla San Pedro Martir and Guaymas (Mathews et al. 1974).

An abundance of material appearing to consist of plankton detritus is evident to anyone who has traversed the gulf during calms seas. This material belongs to the approximately 88% of the seston consisting of detritus reported by Zeitzschel (1970). Ephemeral, amorphous aggregates of matter are conspicuous to the naked eye in surface waters but are not retained by plankton nets. Alldredge (1979) developed techniques to measure and enumerate such aggregates. She found that "marine snow" composed of aggregates of 3 mm or more made up 4% to 8% of total particulate organic carbon, nitrogen, protein, carbohydrate, lipid, and particulate dry weight in surface samples from the gulf: 20% of these aggregates were of recognizable zooplankton origin. The most abundant zooplankton-produced aggregates were found to be the discarded appendicularian houses of *Oikopleura* sp., *Megalocercus huxleyi*, and *Stegosoma magnum*. Agglutination around nuclei of zooplankton-produced mucous appeared to be a common mechanism for compounding small particles into macroscopic marine snow.

TABLE 3
Seasonal Variation in Average Zooplankton Biomass (Displacement Volume per 1000m^3)

CalCOFI cruise	x	S.D.
5602	171	±121[a]
5604	408	±313
5702	355	±224
5704	490[b]	
5706	334	±334
5708	244	±180

[a] Isla Tiburón southward, only
[b] Becomes 782 ± 1618 when five samples having numerous small salps, *Thalia democratica*, are included.

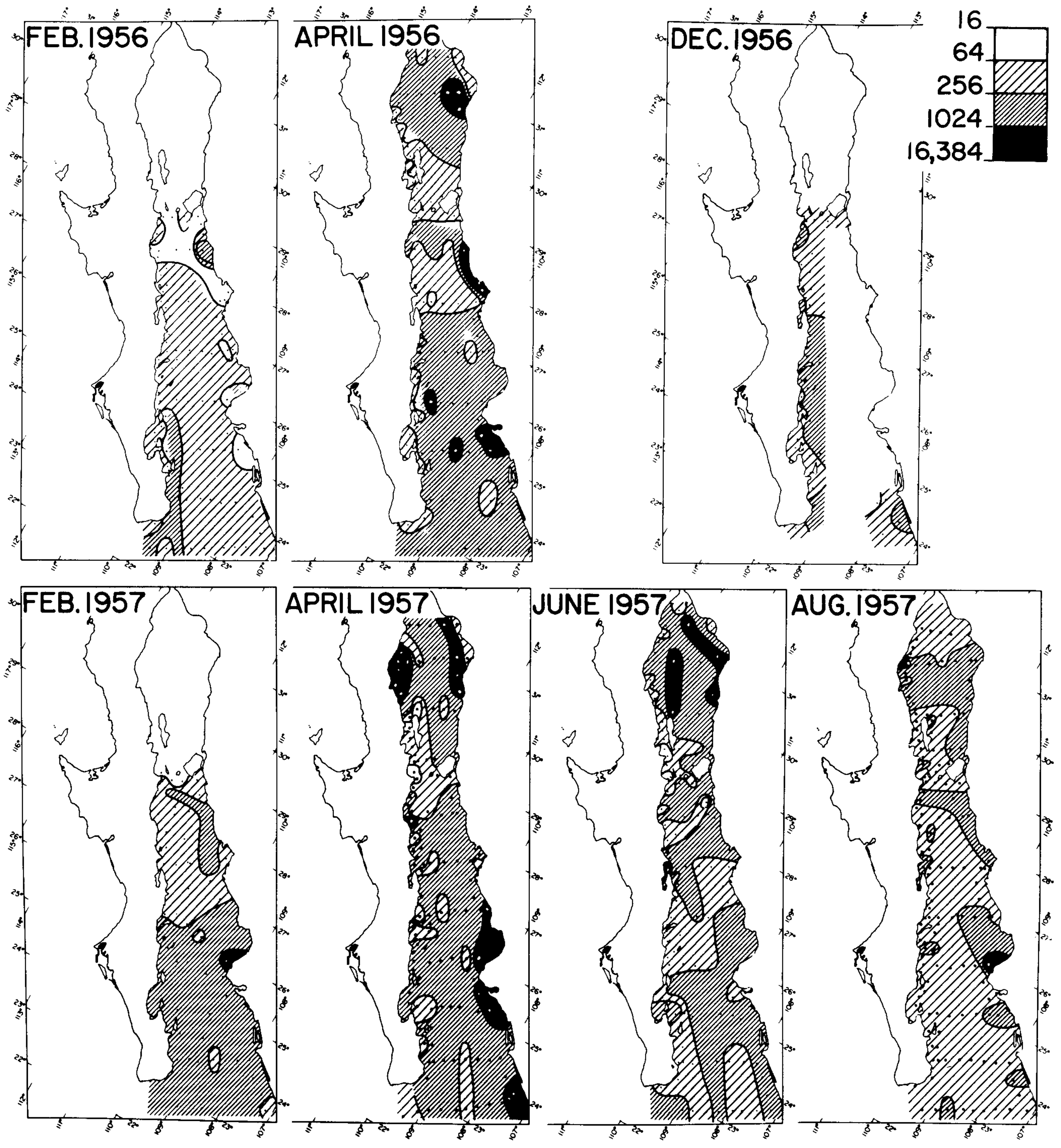


Figure 21. Zooplankton displacement volume, cc per 1000 m^3 in the 0-140-m layer sampled by CalCOFI during 1956-57 in the Gulf of California, by means of a 1-m ring net of 0.6-mm mesh width.

Bioluminescence

During a November-December 1981 cruise to the north end of the Canal de las Ballenas, Lapota and Losee (1984) observed bioluminescing plankton: larvae of the euphausiids *Nyctiphanes simplex* (calyptopis II and furcilia I-III stages and juveniles) and *Euphausia eximia* (calyptopis I); calanoid copepods *Centropages furcatus*, *Paracalanus indicus*, and *Acrocalanus longicornis*; cyclopoid copepods *Corycaeus speciosus* and *C. latus*; the dinoflagellates *Ceratium breve*, *C. horridum*, and *C. gibberum*. The observations indicated the importance of some of the

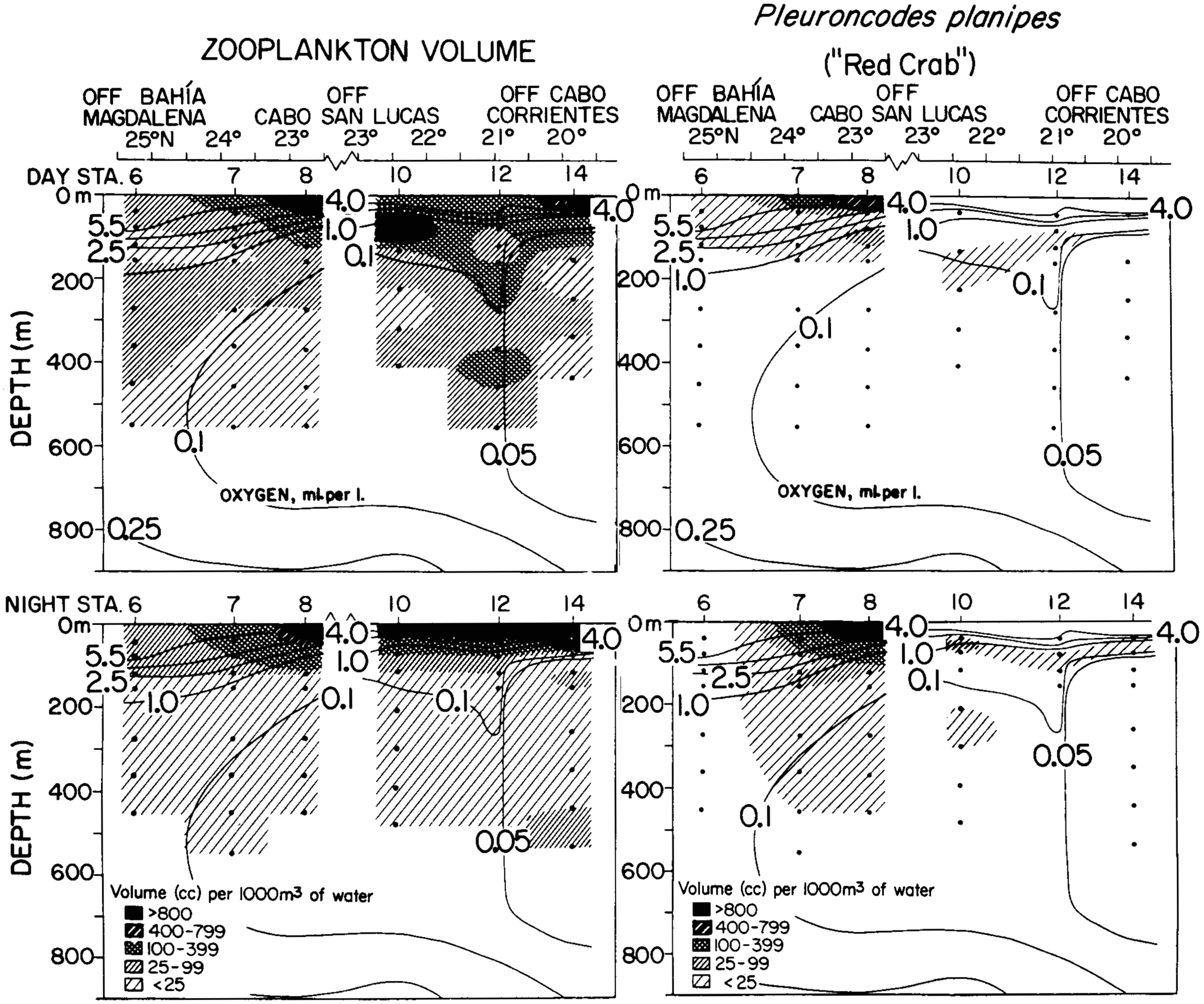


Figure 22. Day and night vertical profiles of biomass (wet displacement volume) of total zooplankton and the red crab, *Pleuroncodes planipes*, across the terminal part of California Current and the mouth of Gulf of California. Reference isolines are oxygen concentrations. (See Figure 15 for station positions, May-June 1974.)

smaller copepods and euphausiid larvae to surface bioluminescence.

GENERAL CONCLUSIONS

The plankton analyzed to date has been related to specialties of investigators. Much available material remains to be analyzed. That obtained by CalCOFI or independently by vessels of the Scripps Institution of Oceanography (e.g., the Vermilion Sea Expedition) is catalogued in Snyder and Fleminger (1965, 1972) and Snyder (1979). Examples of lists of material obtained by Mexican vessels are in Granados and Villaseñor (1974) and Departamento de Pesca (1978). What has been caught has been, in part, a function of the kind of net and mesh size used and of the depths sampled; there is no all-purpose sampler.

Differences between schemes of phytogeographical zonation proposed by Gilbert and Allen (1943), based on single dominant species, and by Round (1967), which took into consideration species diversity and amounts of phytoplankton, demonstrate that there may be substantial seasonal and year-to-year changes in species distributions and local productivity in the gulf. On the other hand, the above workers, together with Brinton and Townsend (1980) and Siegel-Causey (1982), working on euphausiid and amphipod crustaceans, respectively, agreed on the existence of (1) a zone north of Islas Tiburón and Angel de la Guarda that is largely neritic and has the greatest (ca. 15°C) seasonal range in temperature, and (2) a southern zone at the mouth, particularly toward the west, in which most groups of plankters are sparse, though not

Foraminifera, and in which tropical species occur regularly. Between these two zones—from the island channels, 29°N, to the Faralón Basin, 25°N—is a region of seasonal flux. Here, in summer, the temperate species either tend to submerge beneath the warming, decreasingly productive surface layer, or become diminished in numbers; i.e., the foraminiferans *Globigerina bulloides* and *G. quinqueloba*, the euphausiid *Nematoscelis difficilis*, and the copepod *Calanus pacificus californicus* are replaced in the upper layers by tropical species.

Moser et al. (1974) emphasized the widespread gulf occurrence of the larvae of two commercially important fishes having cold-water affinities. Larvae of the Pacific mackerel, *Scomber japonicus*, averaged high in abundance among the larvae of all fishes in the gulf, and larvae of the Pacific sardine, *Sardinops sagax caeruleus*, somewhat less, depending on which CalCOFI cruise, 1956 or 1957, is considered. Larvae of five species constituting most of the gulf's depauperate midwater fish fauna were generally the most abundant: the Pacific lightfish *Vinciguerria lucetia*; the small gadoid fish *Bregmaceros bathymaster*; three Myctophidae—*Diogenichtys laternatus*, *Triphoturus mexicanus*, and *Benthosema panamense*; and the deepsea smelt *Leuroglossus stilbius*. It may be noted here that pelagic crustacean groups having many midwater representatives elsewhere are, like midwater fishes, depauperate in the gulf. There are no midwater euphausiids here, and there appear to be few such mysids and decapods.

One of us (A.F., unpublished data) has found that the enormous gulf population of the copepod *Calanus pacificus californicus* submerges from its winter-spring feeding levels above about 100 m to depths of 200-300 m at which it rests during summer—within layers of relatively low oxygen content. This submergence matches the behavior of *Calanus* to the west of Baja California (Longhurst 1967b; Alldredge et al. 1984). Therefore, the appearance of sparse *Calanus* in the gulf during the summer of 1957 (Figure 23) may have been because only the strongly heated upper 140 m was sampled.

Evidence that such deep submergence may not take place in the euphausiid *Nematoscelis difficilis*, which has the same warm-temperate range as *Calanus pacificus californicus* in the California Current, is the fact that numbers of adult *N. difficilis* in the 0-140-m layer did not decrease significantly in August, as compared with April (Brinton and Townsend 1980). Younger stages were then much reduced, consistent with the pattern in all euphausiid species. *N. difficilis* appears to have a broad vertical range of about 50 m to 200 m, day and night, which may be its means of accommodating to the seasonal extremes in surface temperatures. The sergestid decapod *Sergestes similis* of the northern gulf and the California Current also avoids surface layers, whatever the temperature or season.

Coastal waters of the gulf may support dense stocks of the more neritic species at any season, but buildups of common forms—temperate or tropical—appear during late winter to spring, when vertical mixing and upwelling seem to be most intense. Certain warm-temperate, neritic and slope-water species of the California Current occur throughout the gulf, though highest densities are usually over the northern shelf or along the gulf's margins. These include the chaetognath *Sagitta euneritica* and the euphausiid *Nyctiphanes simplex*, which range the full length of the gulf but not south of it.

Species groups of coastal copepods in the gulf provided pictures both of mutually exclusive warm-temperate and tropical ranges (the "*Labidocera jollae* group," Figure 11) and of weakly overlapping ranges that could be considered either warm-temperate or tropical (the "*Labidocera trispinosa* group"). The only example of endemic gulf plankton we have found is in this genus, *Labidocera kolpos*; the only nearly endemic example is *L. johnsoni*. Manrique (1977) noted, near Guaymas, the strong winter-spring buildup of *Acartia tonsa* and the almost total replacement of this species in the summer by tropical *A. lilljeborgi*.

In the Copepoda and Euphausiacea, the relatively few temperate species tend to achieve higher densities within the gulf than do warm-water species—notably in winter and spring; but in the Amphipoda, tropically derived species make up the greater numbers. For the overall gulf, including the outer reaches to the south, 60% of foraminiferan species are considered tropical, subtropical, or both, as are 87% of chaetognaths, 86% of calanoid copepods (Table 2), 65% of hyperiid amphipods, and 82% of euphausiids. The North Pacific Central Water Mass euphausiid fauna was conspicuously absent from the gulf. Species that proliferate at the productive margins of the eastern tropical Pacific (called tropical-subtropical in the above percentages) were strongly represented by the chaetognath *Sagitta bierii* and the euphausiid *Euphausia eximia*.

Numbers of tropical-subtropical species of calanoid copepods exceed numbers of tropical and temperate species combined (Table 2). Of these, the majority (75%) were oceanic, the remainder neritic or estuarine-coastal. A similar ratio of oceanic to neritic species prevails in chaetognaths and euphausiids.

The complexities of advection occurring across open tropical and subtropical oceans, together with

Calanus pacificus californicus Brodskii

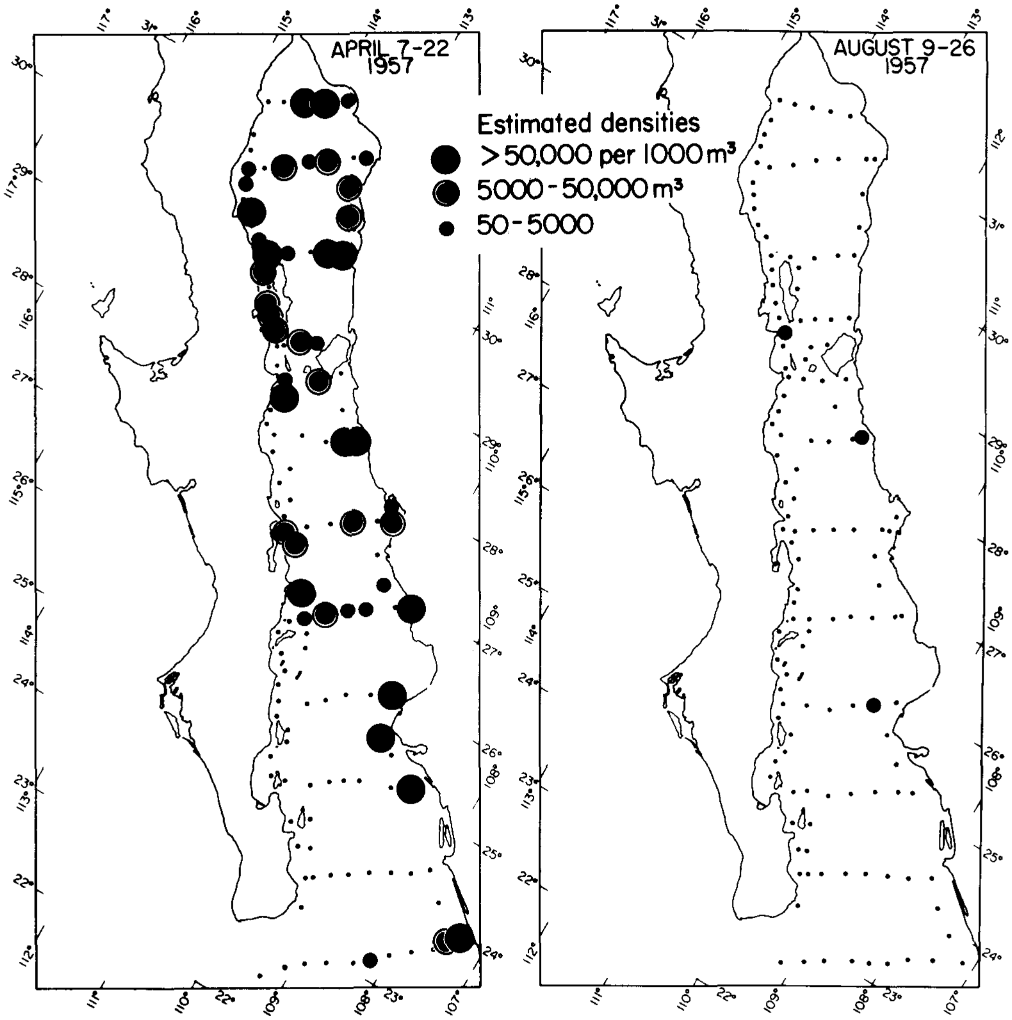


Figure 23. Roughly estimated abundance of the copepod *Calanus pacificus californicus* in the 0-140-m layer sampled by CalCOFI during April and August 1957.

weak seasonal change relative to high latitudes, seems to have inhibited study of population developments in most warm-water biotas. However, in the semienclosed gulf, strong seasonality in environmental properties, together with understanding now being obtained of water exchange among zones of the gulf and across the mouth, suggest that unique opportunities exist here for profitable examination of pelagic life processes.

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FRAME TRAWL FOR SAMPLING PELAGIC JUVENILE FISH

RICHARD D. METHOT
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The frame trawl is a micronekton net designed to sample pelagic larval and juvenile fish that avoid plankton nets and pass through the mesh of large midwater trawls. The mouth of the frame trawl is a rigid, square frame with an area of 5 m^2. The bridle attaches at two points and leaves the mouth relatively unobstructed and vertical at all tow speeds. A modified Isaacs-Kidd depressor can be attached behind the frame for midwater sampling, or floats can be attached for surface sampling. The frame trawl compares favorably with other similar-size samplers. In sea trials, juvenile anchovy and other species up to 200 mm long, and thousands of 15-20-mm anchovy larvae have been collected.

RESUMEN

La red de marco es una red para micronecton diseñada para muestrear larvas y juveniles de peces pelágicos que evitan redes de plancton y pasan a través de la malla en redes de media agua de gran tamaño. La boca de la red de marco es un marco rígido, cuadrado, con un área de 5 m^2. La brida se afirma en dos lugares, manteniendo la boca relativamente libre de obstrucción y en posición vertical a cualquier velocidad de arrastre. Un depresor Isaacs-Kidd modificado puede ser adicionado detrás del marco en caso de muestreo a media agua o, pueden ser agregados flotadores para muestreo superficial. La red de marco presenta ciertas ventajas con respecto a otros muestradores de tamaño similar. En muestreos experimentales, se colectaron juveniles de anchoveta y otras especies de hasta 200 mm de largo, y miles de larvas de anchoveta de 15-20 mm.

INTRODUCTION

Studies of recruitment variation in marine fishes have focused on the early larval stages. Certainly these animals have a high mortality rate, and variations in prey abundance, predators, and ocean currents probably cause substantial variation in this mortality. The capability to detect larvae in poor physiological condition is now well developed (Theilacker 1986), but this is only one step in the study of recruitment variation. Several important questions have not been addressed: How rapidly does the high larval mortality decline? Where are large, old larvae found if adverse drift is a significant factor? Most important, what is the earliest life stage at which an index of recruitment can reliably be made?

There are two aspects to this last question. The first concerns variation in mortality with respect to life stage; larval fish studies cannot provide the final answer to recruitment variation if juvenile mortality varies substantially. The second aspect concerns our ability to sample each life stage. Late larvae and juveniles effectively avoid standard plankton samplers (Murphy and Clutter 1972), leaving a gap in our knowledge until the larger juveniles become available to commercial fishing gear and large midwater trawls (Mais 1974).

The goal is development of a quantitative sampler for late larval and juvenile pelagic fish. This sampler will elucidate larval drift and migration, and extend the survivorship curve throughout the larval life stage. Surveys of late larvae will make it possible to partition recruitment variation into two components: one explainable by variation in larval mortality and the other probably caused by variation in juvenile mortality.

Ideally, a new sampler should: (1) filter a large volume in order to detect rare organisms; (2) be unobtrusive to reduce avoidance by larger organisms; (3) retain little plankton to reduce sorting costs; and (4) be easy to handle. Because the late larval and juvenile stages of some species are surface-associated, it should be possible to tow the sampler near the surface, yet away from disturbance caused by the towing vessel. Because other species inhabit deep waters, it is important to be able to open and close the net's mouth. All of these design characteristics are affected by mouth area, tow speed, mesh size, and bridle design.

The primary target for this sampler is 15-60-mm northern anchovy (*Engraulis mordax*). This size range overlaps the larvae captured by the 70-cm bongo plankton nets and the juveniles captured by 10-15-m midwater trawls. The plankton net has 0.505-mm mesh, and filters about 150 m^3 when sampling along an oblique trajectory from 70 m to the surface (Smith and Richardson 1977). The midwater trawl has variable mesh with a cod-end liner of about 6 mm and a mouth area of over 100 m^2; it filters over 100,000 m^3 in a horizontal tow (Mais 1974). The new sampler should have

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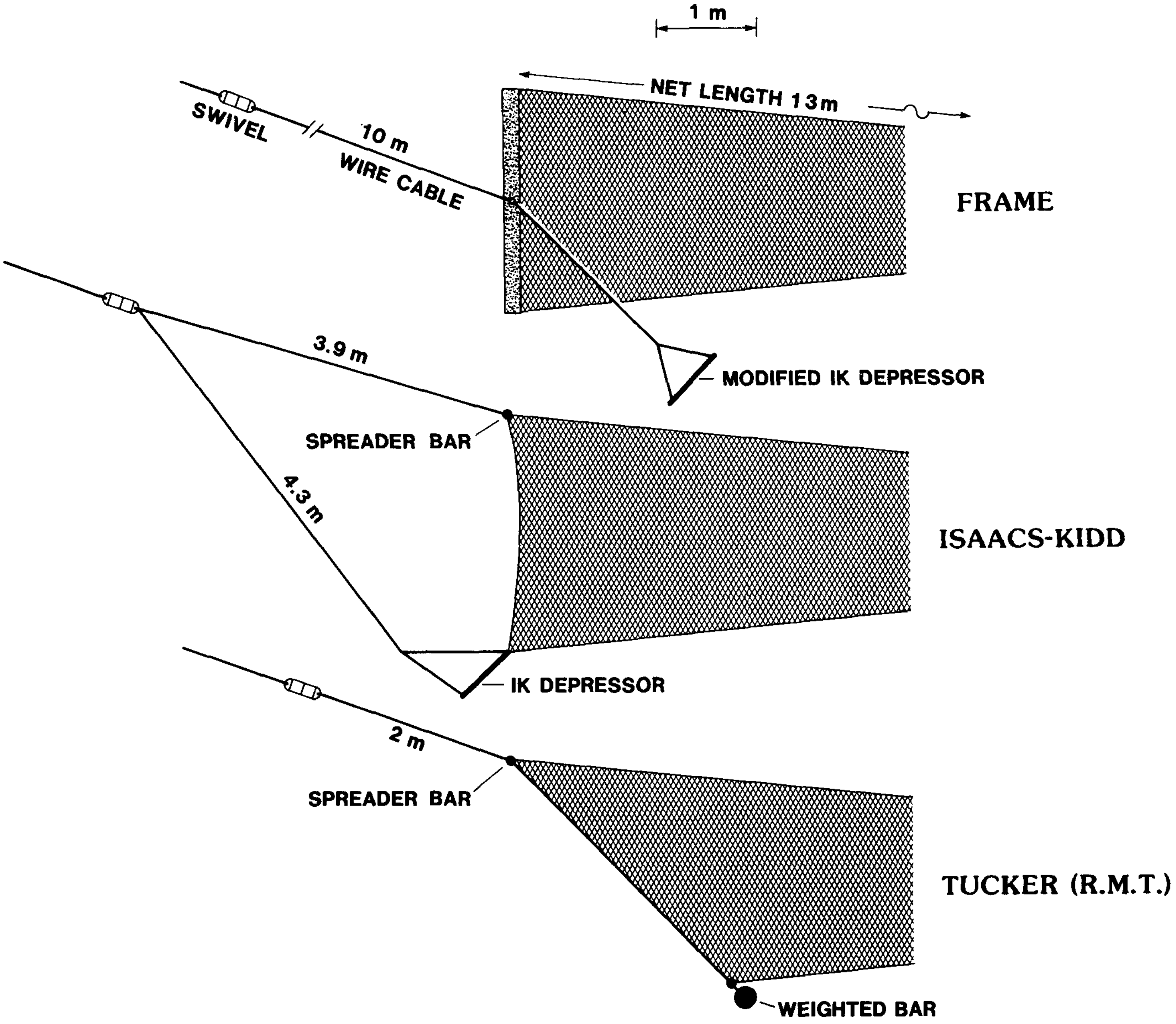

Figure 1. Profiles of Isaacs-Kidd midwater trawl, Tucker trawl (rectangular midwater trawl), and frame trawl. All are drawn with a mouth area of $5m^2$.

2-mm mesh to retain most 15-mm larvae and extrude most plankton, and it should be able to easily filter 10,000 m^3 to detect less-abundant late larvae and juveniles.

This target volume can be obtained by a large, slow net or a smaller, faster net. Whether juvenile fish can avoid a large, slow net more easily than they can avoid a small, fast net is uncertain. The disturbance created by the fast net may negate any advantage of its speed. The target volume is difficult to achieve with a small, fast net because the range of reasonable speeds (0.5-3.0 m/sec) is less than the range of reasonable mouth areas (1.0-100.0 m^2). A compromise of size and speed seems reasonable, with attention to making the net as quiet and unobtrusive as possible.

Two widely used candidates for this sampler (Figure 1) are the Tucker trawl (Tucker 1951), also called rectangular midwater trawl (Baker et al. 1973), and the Isaacs-Kidd midwater trawl (Isaacs and Kidd 1953). The rectangular midwater trawl (RMT) has been built in sizes ranging from 1 m^2 to more than 25 m^2 and is usually equipped with an opening-closing mechanism for the net's mouth. A common design has a 8-m^2 mouth area, 4.5-mm mesh, and a 291-kg weight in the lower bar (Baker et al. 1973). The disadvantage of this design is that the mouth angle (and area) vary with tow speed because the bridle attaches only to the top of the net frame. This restricts the RMT's tow speed to less than about 1.0 m/sec.

The Isaacs-Kidd midwater trawl (IKMT) was de-

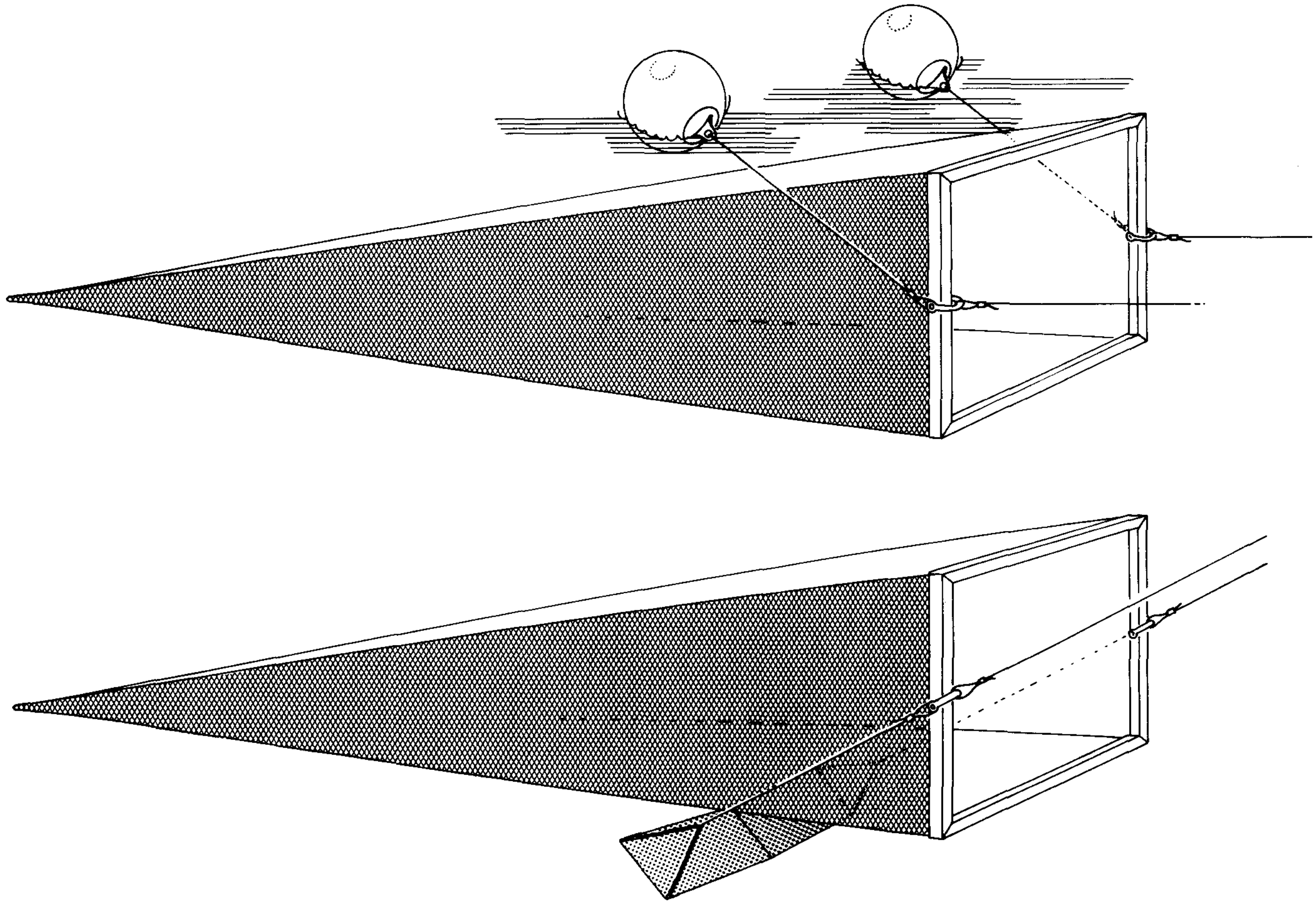

Figure 2. The frame trawl in its surface configuration with floats (*above*), and in its subsurface configuration with the Isaacs-Kidd depressor (*below*).

signed to be a fast (2.-3. m/sec), deep-diving net for sampling mesopelagic organisms. A common size has a depressor width of 3 m and a mouth area of about 7-8 m^2. The disadvantage of the IKMT is that the depressor is located at the leading edge of the lower portion of the net, where it and its bridle must create substantial disturbance and increase avoidance by larger fish. In addition, neither the RMT nor the IKMT are effective near-surface samplers: they must either be towed very near the vessel or use unreasonably large floats.

A fixed-frame trawl with integral depressor was developed by Matuda et al. (1978) for sampling Antarctic krill. Their goal was the same as mine: to improve on the tow speed and mouth angle limitations of the RMT, and on the lower-bridle disturbance of the IKMT. The 2.5 × 2.5-m sampler they designed has only an upper bridle and maintains a nearly vertical mouth opening and constant ratio of depth to wire over a wide range of tow speeds. This design succeeds in moving the bridle away from the net's opening, but the upper and lower depressor built into the frame must substantially disturb the flow of water near the net's mouth. Matuda et al. (1978) note inflated flowmeter readings that probably resulted from the lower bridle's deflecting water toward the net's mouth.

DESCRIPTION OF FRAME TRAWL

The frame trawl described here (Figures 1 and 2) is a medium-size net (Pearcy 1983) that shares some characteristics of the bongo, the RMT, and the IKMT. The mouth of the net is surrounded by a rigid square frame, and the long bridle attaches only to the midpoints of two opposite sides. These features give the frame trawl a vertical mouth at all tow speeds, and its mouth is nearly free of obstruction by the bridle (Figure 3). Bridle extensions can be attached to a modified Isaacs-Kidd depressor or to floats, so the frame trawl can quickly be converted from a midwater trawl to a surface trawl. The frame trawl described here has 2-mm mesh, a mouth area of 5 m^2, and a routine tow speed of 2.0 m/sec. It is designed primarily for quantitative oblique tows in the upper 100 m of the water column and cannot be opened or closed during a tow.

The frame is constructed of heavy (schedule 80) steel pipe with an inside diameter of 3.2 cm (1.25-inch) welded to a 10-cm (4-inch)-wide strip of 0.64-cm

Figure 3. Photograph of the frame trawl being deployed. The depressor hangs below the net frame at this time, then trails farther aft during the tow. The two sides of the bridle are held together by the block (pulley) and separate farther when more tow cable is let out. Rigid clip-on cable fairings are on the lower portion of the bridle to reduce cable vibration. A flowmeter is in the lower left corner of the frame.

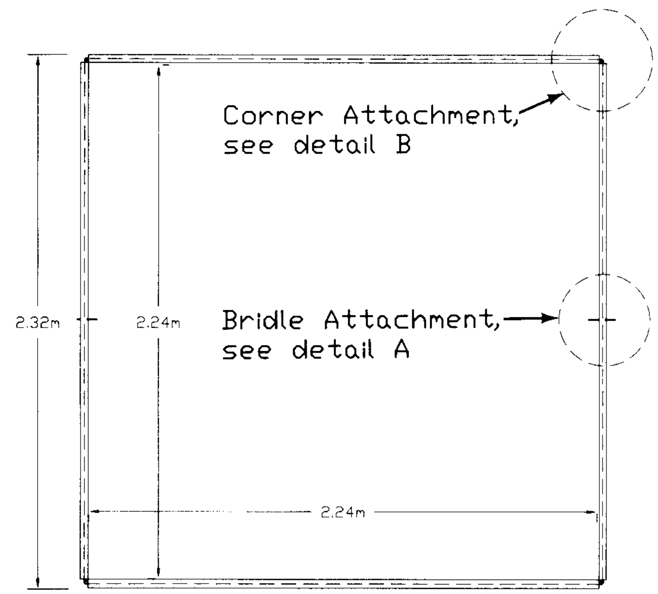

Figure 4. Dimensions of the frame trawl with 5 m^2 mouth area. See Figure 5 for construction details.

(0.25-inch) plate steel (Figure 4). U-shaped bridle attachments made of 1.3-cm (0.5-inch) steel rod are welded to a reinforced section of the midpoint of each side (Figure 5). A corner bracket of 0.95-cm (0.375-inch) steel is welded to each end of the top and bottom and bolted to the two sides. The total mass of the frame in air is 106 kg; this could probably be safely reduced by narrowing the plate steel to about 7.5 cm.

The depressor is a dihedral, as designed by Isaacs and Kidd (Figure 6). Its dimensions are 2.44 m × 0.61 m (8 ft × 2 ft). The depressor used in the frame trawl differs from the original Isaacs-Kidd depressor in the bridle attachment. The original design had an asymmetric triangle attached by hinges to each end of the depressor. The bridle was attached to the forward-directed apex of the triangles, and the net was attached to the trailing edge of the depressor. The triangular arms were shaped so that the depressor would maintain an angle of attack (45°) that maximized the downward force.

The frame trawl has nothing attached to the trailing edge of the IK depressor; therefore the shape of the triangular arms must be modified to maintain the 45° angle of attack. Trials with a small model in a laboratory flume indicated that an isoceles triangle is a suitable shape, but the angle of attack of this modified IK depressor varies with tow speed. At zero speed, or when the depressor is very heavy, it will hang straight down with no angle of attack and generate no downward force other than its weight. At very high speed or when it has negligible weight, the depressor swings farther back and up until it is vertical (90° angle of attack) and generates maximum drag but no downward component to this drag. The mass of the depressor (65 kg in air) gives it an intermediate angle of attack. At a speed of 2.0 m/sec the 5-m^2 frame trawl dives deeper if a 35-kg (75-lb) weight is added to the depressor; the scope (ratio of wire out to net depth) was about 3.0 with the weight attached and 4.0 without the weight. The added weight brings the depressor's angle closer to the 45° optimum. A steep wire angle (low scope) is desirable because it moves the bridle farther out of the mouth opening (Figure 2).

The two floats are heavy-duty vinyl fishing floats. Each has a volume of 200 liters.

The bridle is constructed of 11-mm (7/16-inch) cable. The main bridle consists of two 10-m sections (Figure 7). At one end they come together at a swivel, which is connected to the towing cable. The opposite ends of the main bridle sections terminate at swivels attached to the U-shaped brackets inside the frame. These swivels at the brackets may be unnecessary if torque-balanced cable is used for the bridle. Attached to the U-shaped brackets on the trailing edge of the frame are 1.5-m sections of cable that terminate with quick-release connectors. These connectors can be attached either to the modified IK depressor or to the floats. The total mass of the bridles is 32 kg.

The net is constructed of knotless black nylon 1/8-inch stretch mesh (2 mm × 3 mm oval pores) and black nylon webbing (5-cm width, seat belt strap material). There are eight longitudinal straps and nine circumferential straps (ribs). The mesh material is sandwiched between two layers of strap material, and the entire sandwich is sewn through with zigzag stitching. The net is attached to the frame by extending the eight longitudinal straps about 50 cm beyond the mouth of the net (Figure 8). Heavy, 10-mm (3/8-inch) grommets are set in these strap extensions and in the mouth rib. The straps are looped around the frame, and the grommets in the strap are bolted to the grommets in the mouth rib. The mesh has low porosity, about 23%, and the length of the net is 10 m, so the ratio of pore area to mouth area is low (1.6) when allowance is made for the substantial area occluded by straps. Increasing the net length to 13 m and reducing the number of ribs to two (plus the rib around net mouth) would increase the ratio of pore area to mouth area to about 2.6.

The terminal end of the net is attached to a section of 20-cm-diameter plastic pipe. A cod end constructed of 0.505-mm mesh is attached to the terminal end of the pipe with a band clamp.

The net of 2-mm mesh sandwiched between 5-cm-wide nylon straps has proved difficult to repair. Rips in the net often require replacing sections of the straps, and it is difficult to achieve sufficient strength in longitudinal strap junctions that are resewn.

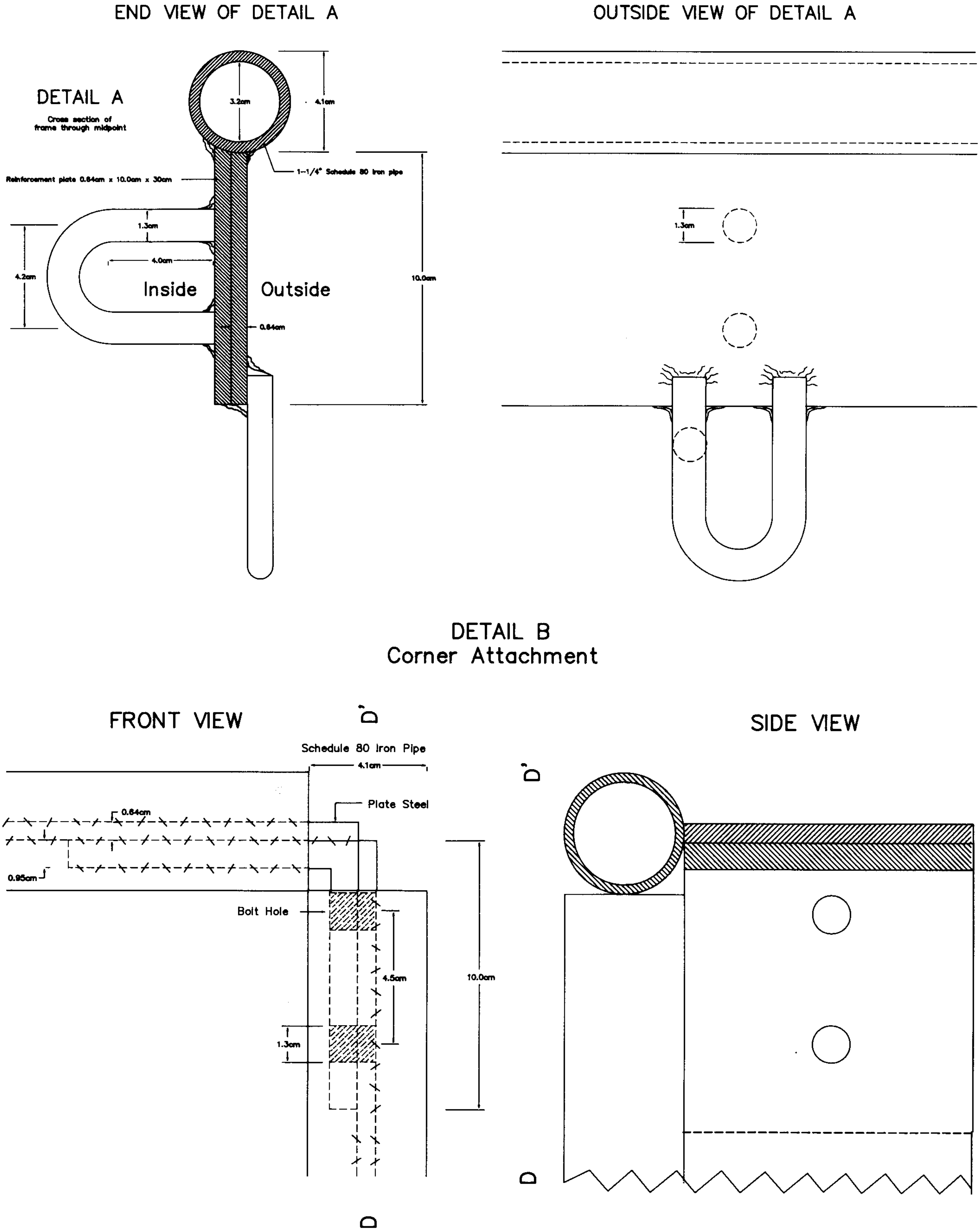

Figure 5. Construction details of the frame trawl: *detail A*, bridle attachment; *detail B*, corner attachment.

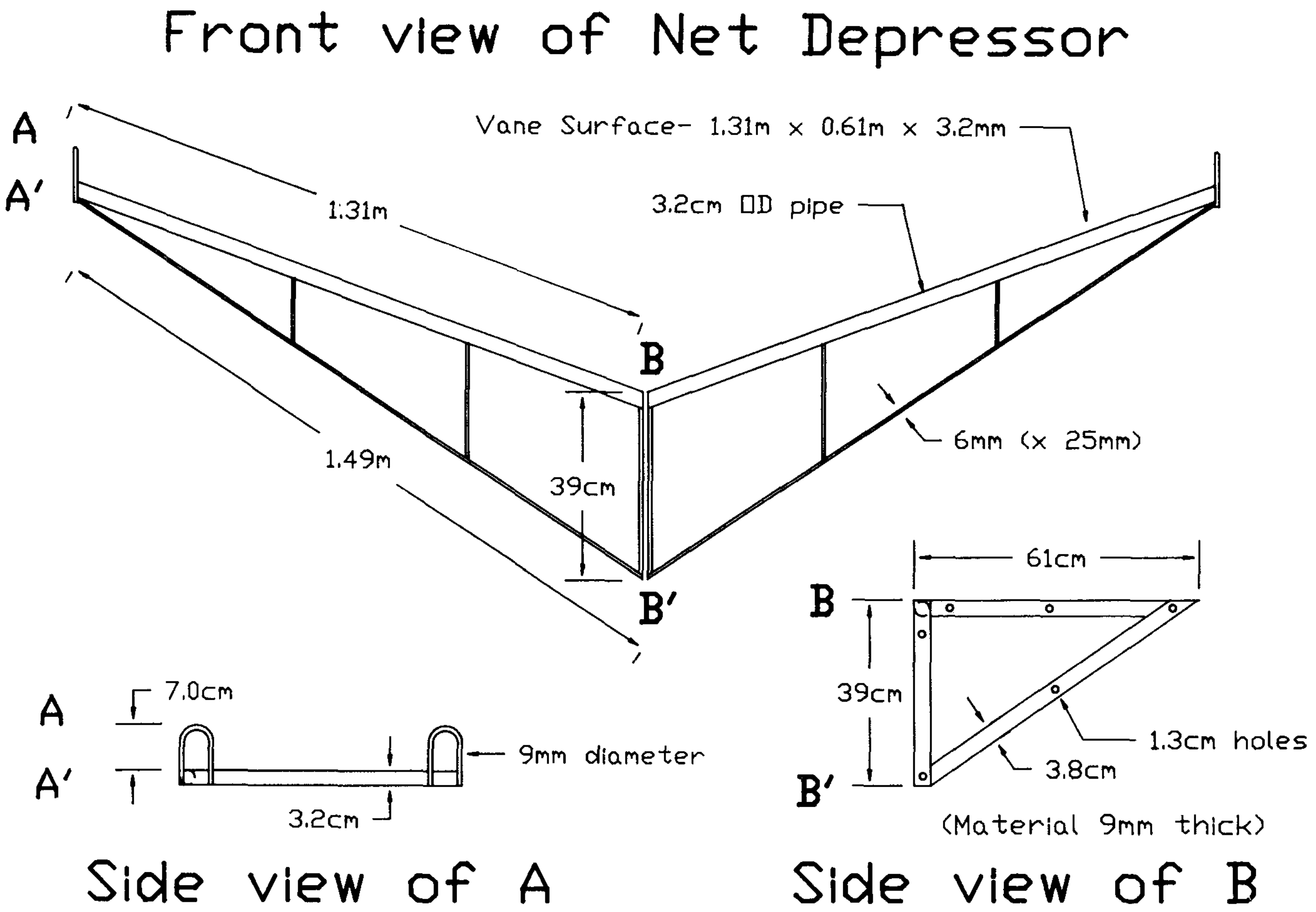

Figure 6. Modified Isaacs-Kidd depressor used with the frame trawl. The hinged asymmetric triangle on the Isaacs-Kidd depressor has been replaced with two U-shaped brackets. The two halves of the frame bolt together with bolt holes shown in side view of B.

As an alternative, we constructed a second, 13-m-long trawl net with 6.4-cm (2.5-inch) stretch mesh and four longitudinal strain members of 16-mm (5/8-inch) rope. An eye was spliced into the forward end of the strain members for attachment to the frame. A liner of 2-mm mesh was installed inside the trawl. IKMT nets built in this manner have proved durable. This alternative net performed well in a brief sea trial, but was significantly heavier than the original design.

SEA TRIALS

The frame trawl has been to sea three times: January, March, and July 1985. For the first two trials we used a prototype version with a rectangular mouth opening ($1.73 \text{ m} \times 1.45 \text{ m} = 2.5 \text{ m}^2$). This frame size was selected to roughly fit the net from a 6-ft IKMT. For the July trial we used the 5-m^2 working version of the frame trawl.

The January trial was designed to test the basic net principle. We made 16 tows to determine the relation between ship's engine RPM, net speed, and net depth. The frame trawl proved to be easy to handle and to have stable tow trajectories. The deployment procedure is as follows:

1. The tow cable is passed through a block at the top of a stern A-frame.
2. The A-frame is tilted forward to lift the block to its highest position.
3. The swivel and forward portion of the bridle are pulled through the block until the frame and depressor are lifted from the deck.
4. The net is tossed into the water.
5. The tow cable is slowly paid out while the A-frame is tilted aft.
6. After the frame is in water and the swivel clears the block, the tow cable can be rapidly paid out.

The March 29-31 trial was the first test of the frame trawl as a sampler. Eighteen tows were made between San Diego, California, and Santa Catalina Island and along the NE shore of the island. All tows were made at night at a speed of 2 m/sec. Four of the tows were made with floats rather than the depressor. Oblique tows to sample the upper 50 m of the water column were made with 200 m of wire out and retrieved at a rate of 10 m/

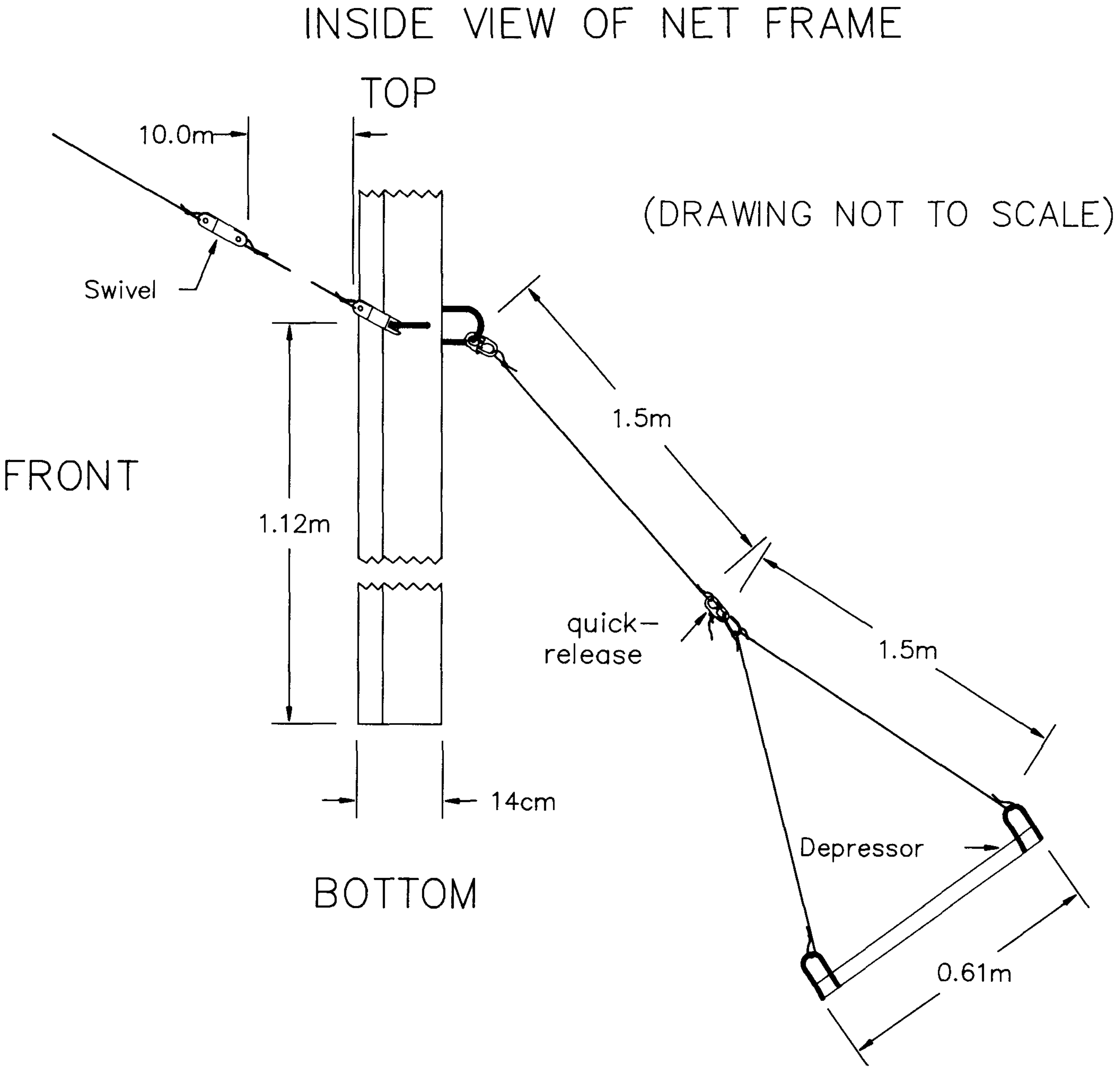

Figure 7. Bridle lengths for the frame trawl. The swivel and anterior portion of the main bridle are designed to be drawn through the block to lift the frame off the deck. The quick-release connectors can be attached either to the depressor or to the floats.

min. Surface tows were made with 100 m of wire out and a duration of 20 min. During surface tows the ship made a slow turn to keep the net to the side of the wake. A flowmeter installed in the mouth of the net indicated that tow speed ranged from 1.88 to 2.36 m/sec (mean = 2.00) and that the volume filtered during the oblique tows ranged from 5,600 to 7,900 m^3 (mean = 7,150).

Large anchovy larvae were consistently collected (Table 1). Most larvae shorter than 10 mm probably were extruded through the 2-mm mesh. The extrusion of small larvae may be reduced if the net is lengthened. This will increase the ratio of pore area to mouth area and decrease the velocity of water through the pores. The high catches of larvae larger than 15 mm are very encouraging; this size range is poorly sampled by plankton nets because of avoidance and low volume filtered.

Catch rates of all size categories were greater in oblique tows than in surface tows among tows 3-9 (Table 1). In the 15-20-mm size range the mean catch was 0.6 larvae per 1,000 m^3 in surface tows and 11.3 per 1,000 m^3 in oblique tows. No larvae larger than 20 mm were

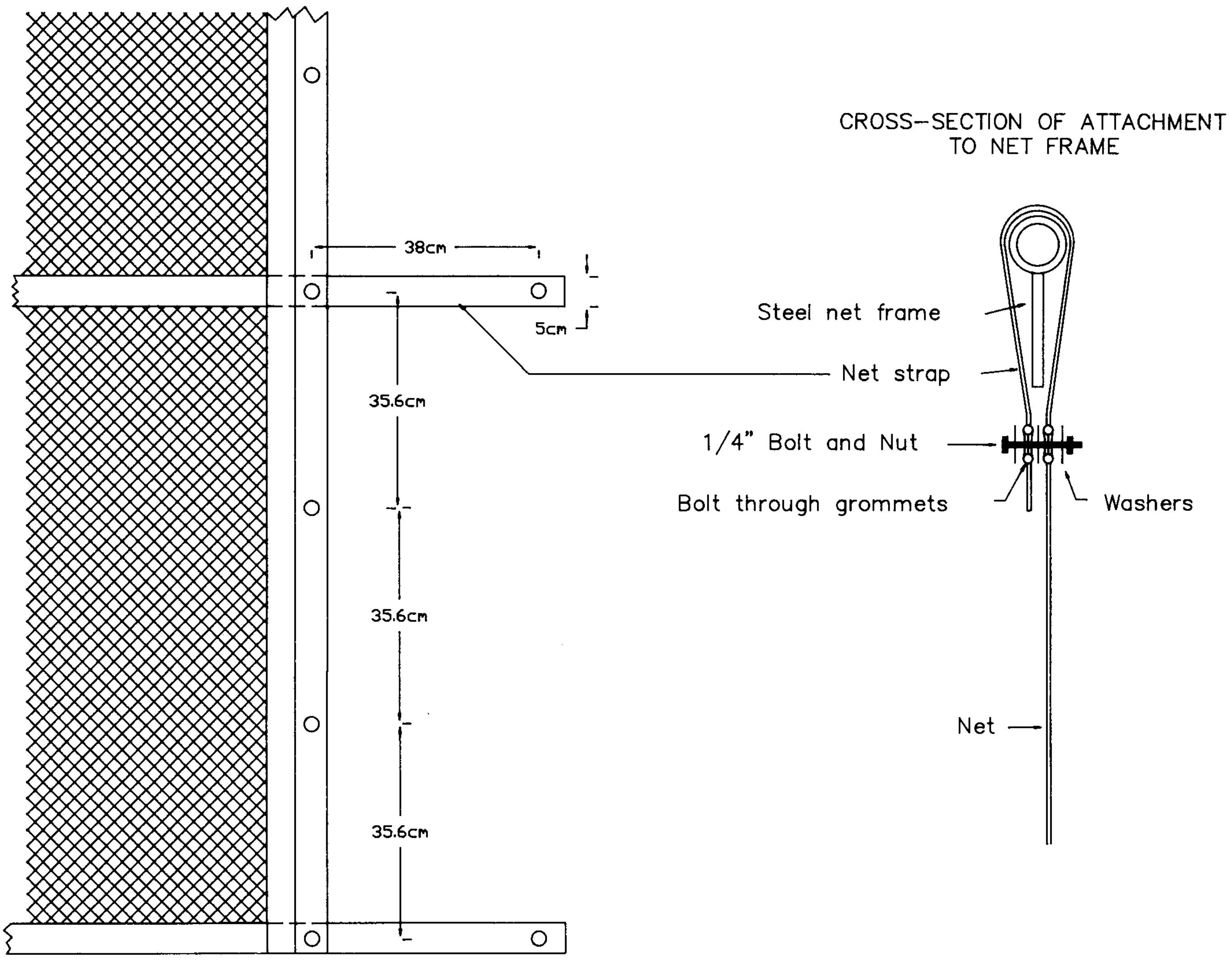

Figure 8. Profile of the anterior portion of the net showing straps used for attachment to the frame.

collected in surface tows. The difference between surface and oblique tows is greater in terms of abundance per unit sea-surface area rather than density. Multiplying the oblique results by 50 m (the maximum depth sampled) and the surface results by 1.45 m (the height of the frame, which is the maximum depth sampled) indicates that abundance of 15-20 mm larvae is 565 per 1,000 m^2 in the upper 50 m, and only 0.87 per 1,000 m^2 in the upper 1.45 m.

Juveniles and adults of other species were commonly collected in excellent physical condition (Table 2). The capture of two *Merluccius* was especially encouraging. The frame trawl was designed to be an effective sampler of age-0 fish, but the *Merluccius* were age 1+.

The 5-m^2 frame trawl was tested on the night of July 29-30, 1985. Ten tows were conducted along the coast north of San Diego. Tows 5 and 6 were over bottom depths of 100 m, and tows 7-15 were over bottom depths of 55-66 m. Surface tows were alternated with oblique tows, and tow procedures duplicated those in the March test of the prototype. Large anchovy larvae were commonly collected (Table 3), and sardine larvae often constituted about 10% of the clupeiform larvae (Table 4). Catch rates of anchovy in surface tows were similar to catch rates in oblique tows (Table 3). Larvae shorter than 10 mm had greater density in surface tows, and larvae longer than 10 mm had greater density in the oblique tows. Only two anchovy larvae longer than 20 mm were collected in surface tows.

DISCUSSION

The average abundance of anchovy larvae collected by the frame trawl is similar to historical catches by the bongo plankton net. Hewitt and Brewer (1983) analyzed bongo collections from the nearshore (<43-m bottom depth) between San Diego and Point Conception. From January to June 1980, the catch of 10-15-

TABLE 1
Catches of Anchovy Larvae in Prototype Frame Trawl, March 1985

Tow number and type	Number of larvae	Abundance per 1,000 m^3					Longest larva (mm)	Location
		<10 mm	10-15 mm	15-20 mm	>20 mm	Total		
1 O	117	4.7	9.3	1.2	0.1	15.3	23.0	San Diego to Santa Catalina
3 O	523	9.3	41.7	15.9	0.0	66.1	19.0	San Diego to Santa Catalina
4 S	63	0.9	7.2	0.0	0.0	8.1	14.0	San Diego to Santa Catalina
5 O	751	33.1	58.1	8.0	2.0	100.2	21.0	San Diego to Santa Catalina
6 S	54	2.0	4.1	0.4	0.0	6.5	18.0	San Diego to Santa Catalina
7 O	432	6.8	49.9	10.9	1.4	68.4	27.0	San Diego to Santa Catalina
8 S	65	2.0	4.5	1.4	0.0	8.0	16.5	San Diego to Santa Catalina
9 O	278	7.5	18.3	10.4	5.4	41.6	23.5	San Diego to Santa Catalina
10 H	87	4.6	4.0	0.8	0.6	10.0	25.0	San Diego to Santa Catalina
11 O	498	12.4	64.7	11.5	0.0	88.6	19.0	3 km offshore N
12 O	1,242	39.1	117.2	6.5	0.0	162.7	17.5	3 km offshore S
13 O	827	31.9	60.3	9.1	1.1	113.8	21.0	2 km offshore N
14 O	1,622	78.0	117.0	8.2	2.1	205.2	22.5	2 km offshore S
15 O	370	17.3	27.6	1.9	0.0	46.8	16.0	1 km offshore N
16 O	353	22.2	22.2	1.9	0.0	46.3	17.0	1 km offshore S
17 O	557	17.9	40.2	27.7	3.6	89.4	24.0	toward San Diego
18 O	744	43.0	48.1	8.2	3.1	102.4	22.0	toward San Diego
Mean for tows 3-9:								
S		1.6	5.3	0.6	0.0			
O		14.2	42.0	11.3	2.2			

O = oblique, S = surface, H = horizontal. Tow 2 was discarded because of the large volume of gelatinous zooplankton. Tows 11-16 were made parallel to the island's shoreline.

mm anchovy larvae averaged 13.8 larvae per tow, and average abundance was 6.7 larvae per m^2 of sea surface. Hewitt and Methot (1982) estimated that the average abundance of 10-15-mm larvae throughout the larval habitat in March 1978 was 8.9 larvae per m^2. In March 1985 the prototype frame trawl collected an average of about 400 10-15-mm larvae per tow, or 2.6 per m^2, and these numbers must be inflated to account for the unmeasured extrusion through the 2-mm mesh. In July 1985 the four nighttime, oblique frame trawl tows

TABLE 2
Fish Other Than Anchovy Collected by Prototype Frame Trawl, March 1985

Tow number and type	Number of larvae	Larger specimens
1 O	57	(2) bathylagidae 87, 90 mm; several myctophidae
3 O	271	(2) bathylagidae 75, 77 mm; many myctophidae
4 S	7	—
5 O	212	(5) bathylagidae 90-105 mm
6 S	15	—
7 O	47	(1) *Porichthys* 120 mm
8 S	13	—
9 O	6	—
10 H	9	—
11 O	105	—
12 O	121	(1) *Merluccius* 160 mm
13 O	174	—
14 O	178	(1) *Merluccius* 170 mm
15 O	52	(1) *Porichthys* 120 mm
16 O	23	(1) *Porichthys* 120 mm; (1) pleuronectidae 31 mm
17 O	123	(6) bathylagidae 37-82 mm; several myctophidae
18 O	111	(4) bathylagidae 87-101 mm; several myctophidae

O = oblique, S = surface, H = horizontal.

TABLE 3
Catches of Anchovy Larvae in the Frame Trawl, July 1985

Tow number and type		Number of larvae	Abundance per 1,000 m^3					Longest larva (mm)
			<10 mm	10-15 mm	15-20 mm	>20 mm	Total	
5	O	9,142	68.2	443.5	170.6	0.0	682.2	17.5
6	S	3,336	42.4	163.9	76.3	0.0	282.7	18.0
7	O	510	6.0	30.7	17.5	0.5	54.8	24.0
9	S	1,956*	67.2	74.7	7.5	0.0	149.3	19.0
10	O	1,462*	18.1	67.3	42.7	1.3	129.4	20.0
11	S	2,311*	81.9	75.4	6.6	0.0	163.9	17.5
12	O	1,699*	7.0	29.5	75.8	28.1	140.4	25.0
13	S	801*	26.4	18.6	3.9	0.0	48.8	18.0
14	O	159	4.0	8.4	3.5	0.2	16.1	21.0
15	S	99	0.7	3.8	2.9	0.2	7.4	20.5
Mean for tows 5-13:								
	S		54.5	83.2	23.6	0.0		
	O		24.8	142.8	76.7	7.5		

*Includes some sardine larvae. O = oblique, S = surface.
Tow 5 began at 32°59.2′N, 117°19.6′W, 100-m bottom depth. Subsequent tows proceeded northward along the coast; tows 7-15 were over bottom depths of 55-66 m. Tow 15 began at 33°14.0′N, 117°29.2′W. Tows 14 and 15 were taken during daylight (0550 and 0719 PDT).

collected an average of 1,600 10-15-mm larvae per tow; average abundance was 7.1 larvae per m^2 (uncorrected for extrusion through the 2-mm mesh). Although the bongo net and frame trawl indicate similar abundances of 10-15-mm anchovy larvae, the frame trawl estimates will be greater when corrected for extrusion, and the frame trawl will be able to detect and quantify much lower larval abundances because it filters over 100 times as much water per tow.

Variance of catch per tow seems lower with the frame trawl than with smaller plankton samplers. Hewitt and Methot (1982) estimate that the coefficient of variation (standard deviation / mean) is about 1.6 for 10-mm larvae collected with the bongo plankton net and 3.5 for 14-mm larvae. The CV for catch of 10-mm larvae by the prototype frame trawl was only 0.6, and the CV was 0.75 for 15-mm larvae. The similarity of catch between replicate frame trawl tows was especially high (Table 1; tow numbers 11-12, 13-14, and 15-16). This low variance must be due to the large volume filtered (about 7,000 m^3) and long distance towed (about 3 km), which integrates much small-scale patchiness.

The frame trawl seems to be a successful and adaptable design. It can be deployed alone, with depressor, or with floats. The model used here had a mouth area of 5 m^2, and frames ranging from 1 to 10 m^2 seem feasible. The frame trawl is superior to the bongo plankton net for sampling large anchovy larvae. Further sea trials will be necessary to determine the overlap in sampling effectiveness between the frame trawl and large midwater trawls.

ACKNOWLEDGMENTS

I am thankful for the suggestions and support provided by Bill Flerx, Reuben Lasker, Paul Smith,

TABLE 4
Fish Other Than Anchovy Collected by Frame Trawl, July 1985

Tow number and type		Number of sardines	Number of others	Larger specimens
5	O	0	139	(1) *Merluccius* 49 mm
6	S	121	16	(2) pipefish 94, 173 mm
7	O	17	20	(3) goby 28-37 mm; (2) *Sebastes* 22-27 mm; sardine 15-17 mm
9	S	220	63	(1) scienidae 140 mm
10	O	present	46	(29) goby 26-43 mm; (1) *Porichthys* 31 mm; (3) pleuronectidae 22-30 mm
11	S	70	61	—
12	O	?	49	(3) goby 22-39 mm; (1) *Sebastes* 22 mm; (7) *Porichthys* 2-27 mm; (3) *Porichthys* 155-185 mm; (8) pleuronectidae 23-28 mm
13	S	?	28	—
14	O	1	4	sardine 17.5 mm
15	S	3	4	sardine 15.0-21.0 mm

O = oblique, S = surface, ( ) number of specimens.

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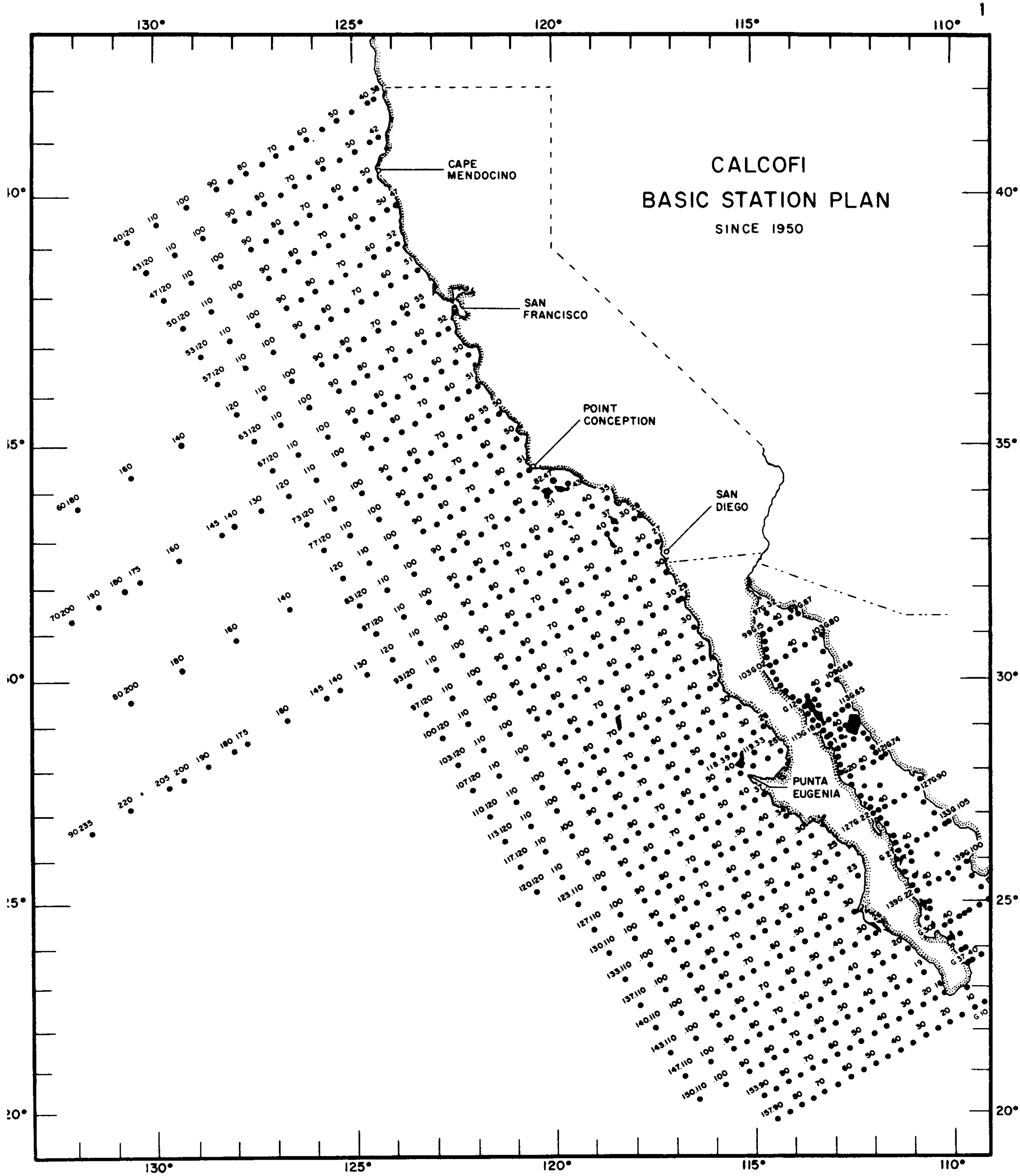

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