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Part I

## REPORTS, REVIEW, AND PUBLICATIONS

### REPORT OF THE CALCOFI COMMITTEE

Sardines are recovering, and for the fourth year in a row, a 1,000-ton quota was opened for sardines on January 1. This year the quota permitted by the California Department of Fish and Game was split, with 200 tons available in the north and 800 tons in the south. The 800-ton quota was landed within two weeks, mostly by San Pedro purse seine vessels. The resurgence of the sardine, well documented by the commercial fishery and sea surveys, is also supported by aerial surveys. Recently, a twenty-five-year review of aerial survey data on populations of adults showed that Pacific sardine and northern anchovy abundance correlated well with changes in the historical abundance of larval sardine and anchovy caught in nets. The larval fish information used in this study was based on CalCOFI egg and larva samples, published in last year's *CalCOFI Reports*. Anchovy larval abundance has fluctuated widely since the mid 1960s; sardine larval abundance declined from the 1950s through the 1970s, rising sharply thereafter.

We estimated northern anchovy biomass this year using data obtained from Mexico on anchovy catch by month, data on the relative length-frequency distribution by month, and information on larval fish abundance from CalCOFI cruises. A paper describing these calculations is published in this volume. We obtained the data on the Mexican anchovy catch under the auspices of the MEXUS-Pacifico agreement, which last year established a U.S.-Mexico Committee to monitor and assess joint fisheries. Cooperative exchange of fisheries research and fishery information, so important in meeting CalCOFI objectives, was the topic of several MEXUS-Pacifico meetings in 1988 with Mexico's Fisheries Secretariat.

To further exchange fisheries information and technology with Mexico, we hosted a four-day workshop on ageing pelagic species. The workshop, which focused on ageing criteria and techniques, resulted in the development of an exchange program for sardine and mackerel otoliths. We presented and participated in a second workshop, held in Mexico, on fishery sampling techniques.

This year, for the first time, we assessed the biomass of Dover sole with the egg production method (EPM) using information about adults, eggs, and larvae that was collected on 1986 and 1987 CalCOFI groundfish cruises. The EPM biomass assessment agreed with the traditional biomass estimate obtained by trawl for the same years. This year CalCOFI completed another 7-week groundfish trawl survey for Dover sole and sablefish; four 2½-week surveys of the California Current; a sardine egg survey that extended from central California to Sebastian Viscaïno Bay, Mexico; a midwater trawl survey for young-of-the-year anchovy, sardine, and mackerel; and two night-light surveys for young Pacific mackerel.

Future plans are to take continuous underway samples on all CalCOFI cruises to obtain more complete spatial coverage. To that end, we used the Doppler acoustic apparatus on one cruise to obtain qualitative information on zooplankton concentrations. An article in this volume describes the diurnal migration, distribution patterns, and relative abundance of these plankters.

At the 1988 CalCOFI Conference, we had a lively exchange in point-counterpoint format on "Can Marine Fisheries Be Enhanced?" The discussants present their evidence for and against enhancement in the Symposium section of this volume. Another highlight at the conference was an evening program and slide show narrated by CalCOFI sea-going technicians to illustrate shipboard collection and processing activities.

To encourage student participation at the annual conference, we established two scholarship funds this year. We endowed The Reuben Lasker Memorial Fund and will use the annual yield to fund fellowships for students taking part in the conference. Contributions to the Lasker Fund are exempt from taxation. Additional contributions, graciously donated by the Redondo Beach Sister City Program, will fund the attendance of one student from La Paz and one from Ensenada each year.

To increase and broaden participation in the annual CalCOFI Conference and to recognize the in-

creasing importance of groundfish, the CalCOFI Committee decided to convene the conference in northern California in 1990, and thereafter to alternate the location between south and north.

Visibility of *CalCOFI Reports* was increased last year with the publication of manuscript abstracts in *Aquatic Sciences and Fisheries Abstracts* and in *Oceanic Abstracts*; *CalCOFI Reports* also is now indexed in *Current Contents*. We learned from the Institute for Scientific Information (ISI), publishers of *Current Contents*, that in 1988 *CalCOFI Reports* was cited 57 times in other scientific journals. It is because of this high citation rate that ISI granted our request for indexing.

*CalCOFI Reports* has a new look this year. We are beginning our next forty years with a new cover design. Included in this volume are author-title and subject indexes for 1983 through 1988. The last index, in volume XXIV, encompassed 1950 through 1982.

Many thanks to the officers and crews who assist us in our work on the University of California RV *New Horizon*, the National Oceanic and Atmospheric Administration Ship *David Starr Jordan*, the Southern California Ocean Studies Consortium RV *Yellowfin*, the RV *Point Loma*, the RV *Shana Rae*, and the RV *Westwind*.

The Committee also thanks all of those who have worked so hard on this thirtieth volume: *CalCOFI Reports* editor Julie Olfe for her patient, professional assistance and her continuing vigil over rising publishing costs; Spanish editors Carina Lange and Maria Vernet; Coordinator Gail Theilacker; and the following reviewers who assisted in making this an excellent report: Angeles Alvariño, Jay Barlow, Peter Boveng, Richard Brusca, Richard Deriso, Joris Gieskes, Edward Goldberg, Loren Haury, George Hemingway, William Hettler, D. Van Holliday, John Hunter, Margaret Knight, Donald Kobuyaski, Garth Murphy, Mark Ohman, Susan Picquelle, Kurt Schaefer, and William Shelton.

Finally, the Committee extends thanks and sincere appreciation to Gail Theilacker, not only for her dedicated work as CalCOFI Coordinator from 1987 through 1989, but also for her outstanding efforts in establishing the Lasker Memorial Fund, and her initiative in winning increasing professional visibility for *CalCOFI Reports*.

*The CalCOFI Committee:*

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## REVIEW OF SOME CALIFORNIA FISHERIES FOR 1988

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Total landings of fishes, crustaceans, and mollusks increased (10%) for the third year in a row, following a decline from 1981 to 1985. Although still below the average of the last 10 years, 1988 landings considerably exceeded (33%) the 1983 low.

Pelagic wetfish landings continued the upward trend that began in 1985, with a gain of 19% over last year (table 1). The increase was due to a record squid catch, which ranks as the highest annual total in the history of the fishery, and exceeds the previous (1981) high by nearly 60%. Landings of Pacific and jack mackerel decreased, while the take of anchovy and Pacific herring increased slightly. Recovery of the Pacific sardine continued, although slowly; landings rose substantially over last year.

A slight decrease in groundfish landings was again noted, though it was probably due more to a decrease in effort than availability. California halibut landings also declined slightly, but still exceeded the 10-year average. Similarly, the lobster catch, though down from last year, was well above the average for the past 20 years.

Pacific ocean shrimp landings improved greatly. Dungeness crab landings also showed an increase, though slight. Albacore landings declined, for the third consecutive year, to the lowest annual total since 1934.

The sportfish catch, which increased overall, reflected an increase in rockfish and nearshore species, and a decrease in pelagic species.

### PACIFIC SARDINE

The California Department of Fish and Game (CDFG) conducted sea surveys in July 1987 to determine the spawning biomass of Pacific sardines (*Sardinops sagax*). These surveys consisted of (1) evaluating the spawning biomass relative to 20,000 short tons, based on the spawning area as determined from the occurrence of sardine eggs (egg production area method), and (2) estimating adult reproductive parameters for use in an egg production method (EPM) of biomass estimation. The observed spawning area was about 1,850 nautical miles<sup>2</sup> (n.mi.<sup>2</sup>). Eggs were found off the San Diego

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
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	653	1,792	38,150	10,318	8,801	11,326	71,040
1986	1,283	2,105	45,503	12,188	8,405	23,454	92,938
1987	2,309	1,595	45,890	13,055	9,258	22,055	94,162
1988*	4,170	1,618	44,510	10,813	9,721	40,865	111,697

\*Preliminary

coast and near Tanner and Cortez banks (figure 1), where they had not been collected in surveys conducted since 1985. The critical spawning area indicative of a 20,000-ton biomass was estimated to be 500 n.mi.<sup>2</sup> in 1987. The results of the egg production area survey thus provided for the opening of a 1,000-ton directed fishery on January 1, 1988. This was the third consecutive year of directed fishing allowed since the moratorium on fishing sardines was enacted in 1974.

The character of the directed fishery was very different in 1988 than in the previous two years. This year, the fishery was closed on January 15, whereas the fishery extended until April 17 in 1987, and July 11 in 1986. An estimated 1,085 tons were landed in the 1988 fishery, and 81% consisted of pure loads brought in by the southern California mackerel purse seine fleet. The fish were canned and test-marketed for human consumption and as pet food. In the previous years' fisheries, over 60% of the landings were made by a single lampara vessel, and the primary use was as dead bait for the central California striped bass recreational fishery.

Incidental landings of sardines in the mackerel fishery totaled 3,085 tons in 1988; this represents increases of 64% over landings in 1987, and 267% over 1986. Sardines constituted 5% of the mackerel catch for the year, as compared to 3% in 1987 and 1% in 1986. In 1988 fishermen complained that abundant sardines were eliminating some traditional mackerel fishing grounds, particularly around some of the northern Channel Islands. Landings of sardines from all sources totaled 4,170 tons, as compared to 2,310 tons in 1987.

Young-of-the-year sardines did not make a strong showing in the 1988 live bait fishery. Most of the sardines in the live bait were at least one year old. A total of 55 tons was reported by fishermen, with a total of 155 tons estimated by Department observers on partyboats. This compares to a reported total of 240 tons, and an estimated total of 855 tons, landed in 1987.

Several legislative changes during 1988 affect the take of sardines: the tolerance limit for incidentally taken sardines mixed with other species was increased from 25% to 35% by weight; adjustments to the tolerance limit will now be based on fish taken or wrapped, rather than fish landed; 20% of the directed fishery quota will be reserved for ports of landing north of Point Buchon (figure 1); and a special quota of 250 tons (500 tons if the directed fishery quota increases to 2,500 tons or more), established specifically for dead bait purposes, will open on March 1 of each year.

Results of the 1987 EPM biomass estimate were finalized in early 1988. Estimates of adult reproductive parameters were similar to those obtained in 1986, warranting incorporation of these new estimates into the egg production area method. The new estimate of critical spawning area is 2,300 n.mi.<sup>2</sup> The biomass estimate for 1987 was 17,290 tons, with a coefficient of variation of over 90%, due primarily to the variance in the estimate of egg production rate.

Biomass estimation cruises were again conducted in May and June 1988. Surveys were made off central California (north of Monterey Bay to Point Conception), and also off southern California (Point Conception to the Mexican border), with increased coverage of the offshore banks. No eggs were collected off central California, and the adult females collected were in nonspawning or pre-spawning states. Spawning observed off southern California was less extensive around the northern Channel Islands than in 1987, probably because of intense upwelling and low water temperatures coinciding with the survey. However, spawning along the southern coastal portion of the survey (San Onofre to San Diego) and over the offshore banks was more extensive in 1988. The observed spawning area for 1988 was 2,560 n.mi.<sup>2</sup> As a result, a directed fishery was opened on January 1, 1989.

A sardine management workshop, involving state, federal, and industrial biologists, was held by the CDFG in September 1988. A review of information on the status of the sardine resource led to the consensus that an increase in current quotas was not warranted. An EPM estimate of the spawning biomass measured in 1988 was completed by May 1989. In June 1989, egg cruises were conducted in an expanded area off southern California, and off northern Baja California as far south as Bahía de San Quintin.

## NORTHERN ANCHOVY

Landings of northern anchovy (*Engraulis mordax*) for reduction purposes in 1988 were limited primarily by poor market conditions. Although fish meal prices rose dramatically during the 1987-88 reduction season, as a result of the drought-impacted domestic soybean market and the inability of local processors to obtain anchovy from South America, this increase was not reflected in the price of \$25-\$30 per ton offered to local fishermen. Northern processors issued no orders during the latter half of the 1987-88 season. Although processors in the southern region issued orders for anchovy, local purse seine fishermen continued to concentrate on

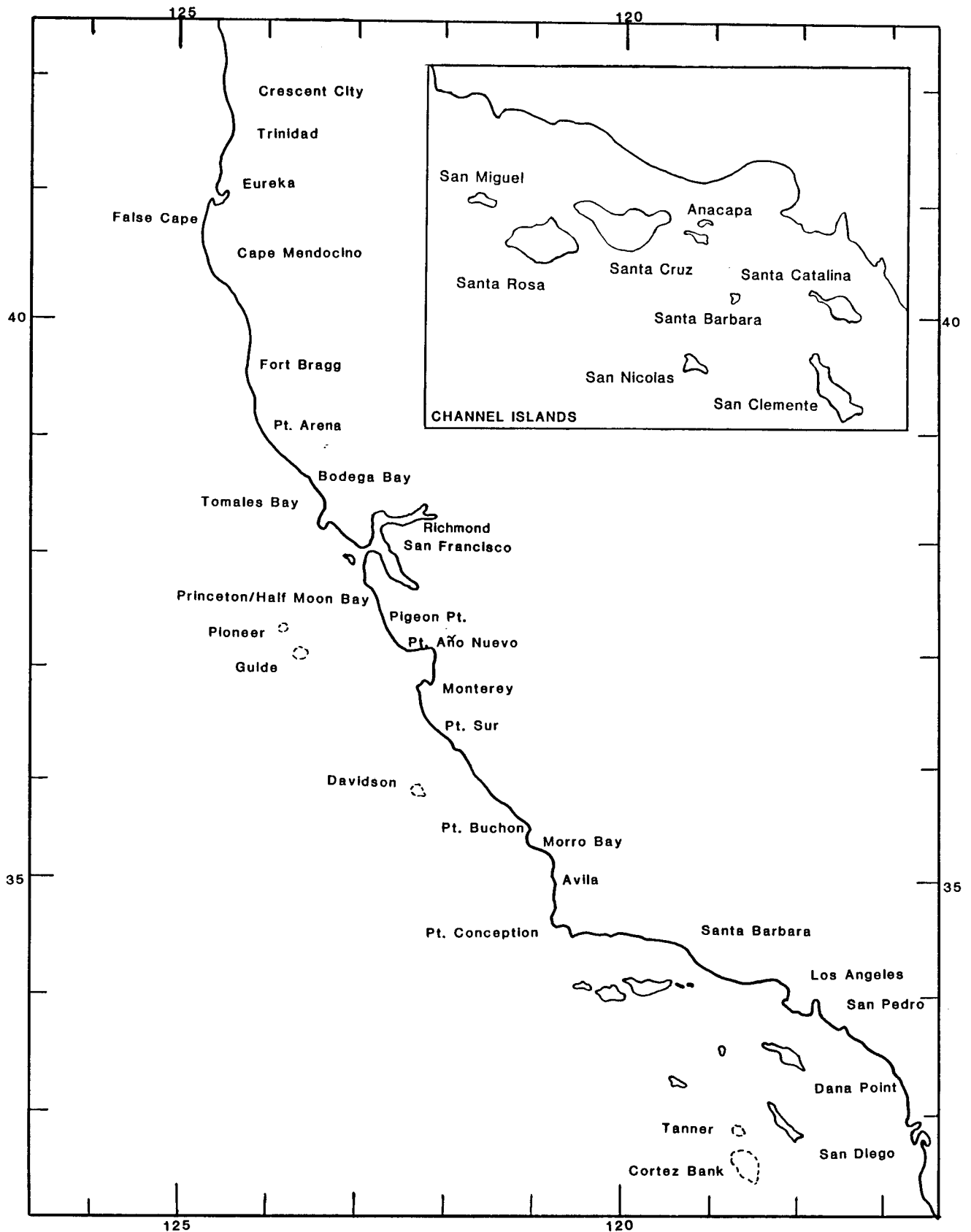


Figure 1. California ports and fishing areas.

more lucrative mackerel and squid. Consequently, no reduction landings took place in either the northern or southern regions. The 1987–88 season closed on June 30 with only one landing of 122 tons (table 2), which occurred in 1987.

National Marine Fisheries Service biologists estimated the 1988 spawning biomass of northern anchovy to be at least 1,111,119 short tons (1,008,000 MT), based on a stock synthesis model. The U.S. harvest quota for reduction was set at 154,350 tons, with allocations of 10,000 tons for the northern permit region and 144,350 tons for the southern. The 1988–89 fishery opened on August 1 in the north and on September 15 in the south. Landings totaling 258 tons were made during October and November in the northern permit area, and were delivered to the Salinas reduction facility at \$35 per ton. In October, an unknown quantity of anchovy was sold to the reduction facility in Richmond by the Salinas processor because of insufficient capabilities to process the fish. Both processors indicated that they might issue orders for anchovy in the latter half of the 1988–89 season. No landings were made in the southern area through December 1988, reportedly because fishermen were unable to find anchovy large enough for reduction purposes.

Total landings of anchovy during 1988 included 258 tons for reduction, 1,360 tons for nonreduction purposes (table 1), and 4,664 tons for live bait. The live bait fishery benefited from the good availability

of anchovy close to shore for much of 1988; most bait haulers considered it a good year.

### JACK MACKEREL

Approximately 19,815 tons of jack mackerel (*Trachurus symmetricus*) were landed during 1988. Jack mackerel constituted 19% of total mackerel landings, a slight decrease from 21% during each of the previous three years. Since 1979, jack mackerel have contributed less than Pacific mackerel to the California mackerel fishery. Over the last five years, the jack mackerel proportion of total annual mackerel landings has been the lowest since the fishery began in the late 1940s.

During 1988, as in the previous two years, jack mackerel never dominated statewide landings. This is probably due to unrestricted Pacific mackerel landings since 1986. In northern California, jack mackerel dominated the mackerel landings about half the time, but only 1% of the statewide jack mackerel catch was landed in northern California. The monthly proportion of jack mackerel in the total 1988 mackerel landings ranged from 4% to 42%, which is similar to the previous two years. Over the last three years, 94%, 97%, and, most recently, 99% of all jack mackerel landings occurred in southern California. Calculated throughout the year, jack mackerel made up 66% of the total mackerel landings in northern California, and 18% in southern California. This represents a change in northern California, where the catch has typically been 20%–30% jack mackerel over recent years, but is very similar to the last three years in southern California.

A sea survey conducted during October 1988 suggested fair recruitment of the 1988 year class of jack mackerel. In comparison with surveys in earlier years, the 1987 year class appears weak, and the 1986 year class appears fairly strong.

### PACIFIC MACKEREL

The year began with 24,030 tons of Pacific mackerel (*Scomber japonicus*) already landed through the first half of the 1987–88 season (July 1 through June 30). Current law allows an open fishery when the biomass exceeds 150,000 tons. Since the biomass was estimated to be 285,000 tons, no quota restrictions were established.

During the first three months of the year, mackerel landings were only fair, because weather was often rough and commercial-sized schools of mackerel were difficult to locate. Landings improved considerably during the second quarter, when the

TABLE 2  
**Anchovy Landings for Reduction Seasons in the Southern and Northern Areas (Short Tons)**

Season	Southern area	Northern area	Total
1967–68	852	5,651	6,503
1968–69	25,314	2,736	28,050
1969–70	81,453	2,020	83,473
1970–71	80,095	657	80,752
1971–72	52,052	1,314	53,366
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	68,467	7,212	75,679
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	78	0	78
1985–86	0	1,595	1,595
1986–87	0	42	42
1987–88*	0	122	122

\*Preliminary

weather was only occasionally poor. During the first half of the year, particularly when mackerel were not available, fishermen complained that abundant sardines interfered with mackerel fishing. The 1987–88 season closed on June 30, 1988, with a total catch of 49,420 tons of Pacific mackerel. This is the highest seasonal total since the fishery reopened in 1977. Pacific mackerel contributed 73% to statewide landings of mackerel, and 98% of all Pacific mackerel landings were made in southern California.

The 1988–89 season opened on July 1, 1988, with no quota restrictions, based on a biomass estimated to be about 290,000 tons. Landings during July, August, and September were fair, although effort in July was often redirected to more profitable bonito and bluefin tuna. Record-size bluefin tuna again captured the interest of the purse seine fleet in November and December; this, in combination with rough weather, resulted in lower landings during the last quarter. By the end of the year, 19,120 tons of Pacific mackerel had been landed toward the 1988–89 season total. This is only 80% of the landings made during the first half of the 1987–88 season. Landings of Pacific mackerel for the year totaled 44,510 tons. Although slightly less than the 1987 total, the 1988 catch still exceeds the annual average landings for the previous five years. Northern California landings contributed only 2% to the year's total. The proportion of the Pacific mackerel catch occurring in Monterey has declined steadily over the last several years.

Market demand remained constant throughout the year, and processors continued to impose landing limits (40–50 tons per boat per day, on average). The ex-vessel price, \$155 per ton, has not changed since 1985.

Although the 1986 year class is strong and contributed 40% (by weight) of the fish landed during the year, the 1987 year class made a weak appearance as one-year-olds, and constituted only 14% of the landings. The 1988 year class dominated landings in December and may be strong. It is difficult, however, to accurately assess the strength of the incoming year class. If the 1988 year class does not prove to be substantial, the fishery will be sustained primarily by 1985 and 1986 year-class fish.

“Night-light” surveys, in which mackerel were sampled by hook and line both at night (random stations) and during the day (random and visually located stations), were conducted in 1988. Results indicated that this technique may be useful as an early, fishery-independent index of year-class strength.

## MARKET SQUID

Landings of market squid (*Loligo opalescens*) in 1988 totaled 40,865 short tons. These landings greatly exceed the previous fishery high in 1981 of 25,915 tons, and are 2.5 times the previous 10-year average of 16,122 tons (table 1).

The northern California (or Monterey) fishery landed only 5,000 tons this year. Since the 1982–83 El Niño event, Monterey landings have never returned to the previous levels of 10,000 to 14,000 tons; instead, landings have ranged between 4,300 and 6,500 tons. This year, however, the proportion of landings dropped, with only 12% of the total catch landed in northern California. As is typical, most of northern California's squid was caught in the Monterey area. Unlike last year, only a small amount of squid was taken from the Año Nuevo and Pigeon Point area (figure 1).

The price in Monterey remained at \$200 per ton until midseason, when a two-day strike by fishermen raised the price to \$240 per ton. With the increased price, however, came buyer-imposed trip limits.

Fishing under experimental gear permits took place in Monterey Bay in 1987 and 1988. The purse seine and half-purse drum seine gear had a leadcore footrope instead of chain, and the purse rings were attached to the footrope with lines containing no metal. A Department observation program evaluated the effectiveness of this gear and the typical lampara gear relative to egg-case mortality. The results indicated that the new nets would not have a serious impact on squid eggs, and the Department recommended that fishermen be permitted to use this gear throughout Monterey Bay. Fishing with lights, which concentrates the squid at the surface, was authorized in all of Monterey Bay this year. The observation program suggested that the use of lights with the new gear could result in fewer squid egg cases being taken. In addition, the observations indicated that the use of balloons or suspenders to raise the lead line could prevent the scraping of eggs off the bottom. This gear, however, is not in widespread use. For the 1989 season, it was recommended that the experimental gear vessels not be allowed to fish during April and May. This would allow some spawning to occur in the spring, and keep the peak fishing season open during the summer and fall.

In marked contrast to the northern fishery this year, the southern fishery had tremendous success, landing 35,865 tons. Spawning squid were reported in many locations where they are not traditionally seen. The southern fishery typically follows a fall-

winter season, but this year, significant landings occurred through July. Major squid landings began again in October at much higher levels than typically seen, and continued through the end of the year. The price remained stable at \$200 per ton until the end of the year, when it dropped to \$180 per ton.

### PACIFIC HERRING

The herring (*Clupea harengus pallasii*) roe fishery experienced a successful 1987–88 season (December–March). The statewide seasonal catch was 9,622 tons, and the 1988 annual catch was 9,721 tons (table 1). Both seasonal and annual catches are post-El Niño highs.

The economics of this fishery are complex, and are influenced by Japanese demand for herring roe. The ex-vessel value of the 1987–88 catch increased substantially from \$8 million last season to over \$13 million in the 1987–88 season. Japanese herring buyers offered \$800 to \$1,200 per ton base price for 10% roe recovery; a 25% increase in price from the 1986–87 season.

In San Francisco Bay, surveys of spawning grounds indicated a 1987–88 spawning population of 69,000 tons. This was substantiated by an independent acoustical survey, which estimated 71,000 tons of spawning biomass. The San Francisco Bay herring population increased about 20% from 1986–87. The continued increase of the population is attributed to five successive good year classes (1982–86).

The Tomales Bay population estimate declined to 2,000 tons in the 1987–88 season. Over the past five seasons, the Tomales Bay herring biomass estimates have shown an alarming variation, alternating between good years and poor years. Because there are eight year classes in the population, this pattern of sudden declines to low population levels, followed by quick recoveries, requires explanation. At this time, it is believed that herring are not using the historic spawning areas in Tomales Bay, and that this behavior was initiated by the 1983 El Niño. Abandonment of spawning grounds by herring, which has been documented in the Pacific Northwest, poses a threat to the future of the Tomales Bay fishery.

Based on biomass estimates in the 1987–88 season, catch quotas were adjusted for the 1987–88 season. The San Francisco Bay quota was raised 1,000 tons, to 9,500 tons; Tomales Bay was reduced 350 tons, to 400 tons.

The 1988–89 season began quickly, with over 2,000 tons taken in December. Herring buyers were

offering \$1,000 per ton for 10% roe recovery at the beginning of the season.

### GROUND FISH

California's 1988 commercial groundfish harvest was 39,946 metric tons (MT), with an ex-vessel value of \$30,765,000. The 1988 catch decreased by 5%, or 960 MT, from the 1987 total, primarily as a result of decreased effort. In particular, setnet effort for groundfish decreased substantially during the year. The major share of the landings, 82.5% (32,967 MT), was harvested by trawl gear. Setnet landings constituted 8.8% (3,502 MT) of the total, followed by line gears at 6.9% (2,747 MT), and other gears at 1.8% (730 MT).

Rockfish (a multispecies group), Dover sole (*Microstomus pacificus*), Pacific whiting (*Merluccius productus*), and sablefish (*Anoplopoma fimbria*) were the leading species harvested in 1988 (table 3). Trawl landings of Dover sole dropped by 24%, partly because of a notable drop in demand from spring through fall of 1988. Trawl rockfish landings and value also suffered from a drop in demand, due to very large Canadian rockfish exports to West Coast markets in the first two quarters of the year. Continued high demand in Japan for sablefish fueled an 11% increase in ex-vessel prices, which appeared to attract additional fishing effort for this species. Demand for thornyheads (*Sebastolobus* spp.) also remained at high levels in Asian markets; 1988 landings increased by 53% to 4,524 MT.

Line catches of groundfish in 1988 remained relatively unchanged. Setnet catches, however, dropped by 13.4% from the previous year's level. Rockfish dominated both line and setnet landings, accounting for 74% and 78% of the totals, respectively.

TABLE 3  
 California Groundfish Landings (Metric Tons)

Species	1987	1988	Percent change
Dover sole	10,759	8,176	-24.0%
English sole	1,322	1,059	-19.9%
Petrale sole	824	780	-5.3%
Rex sole	825	839	1.7%
Thornyheads	2,955	4,524	53.1%
Widow rockfish	2,274	1,847	-18.8%
Other rockfish	11,419	9,776	-14.4%
Lingcod	841	863	2.6%
Sablefish	4,345	3,782	-13.0%
Pacific whiting	4,518	6,541	44.8%
California halibut	539	515	-4.5%
Other groundfish	1,322	1,244	-5.9%

Federal and state groundfish regulations for 1988 reduced the California harvest of sablefish and widow rockfish (*Sebastes entomelas*). Coastwide numerical optimum yield (OY) levels for sablefish were 9,200–10,800 MT; for widow rockfish they were 12,100 MT. The sablefish OY was allocated to two gear quotas: 5,200 MT for trawl and 4,800 MT for nontrawls gears. An additional 800-MT reserve was established in case the trawl fishery unavoidably exceeded its allocation. For the first time, trawl sablefish trip limits were imposed on January 1, with the objective of extending the fishery throughout the year. A trip limit of 6,000 pounds or 20% of the fish on board, whichever was greater, was employed from January 1 until August 2.

Trawl landings remained high despite these restrictions, necessitating a 2,000-pound, once-per-week trip limit effective August 3, and release of the 800-MT reserve. Although this regime slowed landings, sablefish discards increased significantly. Projections indicated that the 2,000-pound, once-per-week trip limit had slowed landings to the extent that the original 5,200-MT quota would not be achieved. The Pacific Fishery Management Council removed the trip-frequency restriction in early October, in an attempt to reduce the regulation-caused discarding. Total 1988 trawl sablefish landings were 5,483 MT, of which California landed 2,640 MT.

Unlike the trawl sablefish fishery, most non-trawl-caught sablefish do not supply fresh fish markets; thus no effort was made to extend the nontrawl fishery. As a result, the nontrawl fishery was closed on August 25, with a total catch of 5,295 MT (California portion: 1,144 MT).

The 1988 widow rockfish fishery began with a trip limit of 30,000 pounds. By September, a reduction to 3,000 pounds was necessary to keep widow rockfish landings within the OY. California accounted for 1,847 MT of the 12,100 MT landed coastwide.

### DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1987–88 season totaled 8.7 million pounds, a slight increase over 1986–87 landings of 8.4 million pounds.

The northern California ports of Crescent City, Trinidad, Eureka, and Fort Bragg (figure 1) received 2.84, 0.69, 1.41, and 0.68 million pounds, respectively, for a total of 4.94 million pounds. This is about 1.85 million pounds below the previous season.

The season opened December 1, after a price settlement of \$1.25 per pound. A severe storm during

the first week of the season destroyed large quantities of gear and trapped crabs. The season closed July 15; a total of 316 vessels participated in the fishery.

Commercial fishermen in the San Francisco region caught 3.1 million pounds of Dungeness crab during the 1987–88 season. This is the largest season total since the 1959–60 season, when 4.8 million pounds were landed. Landings for Bodega Bay, San Francisco, and Half Moon Bay were 1.28, 0.83, and 0.93 million pounds, respectively. Landings for November and December 1987, the first two months of the season, were 1.7 million pounds for the San Francisco region, 56% of the seasonal total. Effort remained strong until May, when many fishermen switched to salmon fishing.

### PACIFIC OCEAN SHRIMP

Statewide landings of Pacific ocean shrimp in 1988 increased to 11.1 million pounds from the 7.8 million pounds landed in 1987. This was the fifth consecutive annual increase in statewide landings and the third largest ever. Areas of production were Area A (Oregon border to False Cape), Area B-1 (False Cape to Point Arena), and Area C (Pigeon Point to Mexican border; figure 1). The season was open from April 1 through October 31.

Shrimp landings from Area A waters totaled 9.3 million pounds, a substantial increase over the 5.6 million pounds landed during the 1987 season. An additional 1 million pounds, which had been caught in other areas, were landed in Area A ports. The majority, 0.77 million pounds, came from Oregon waters; the remaining 0.24 million pounds came from Area B-1.

The season began with a two-week strike over price. A price of \$0.50 per pound was initially agreed upon, but with the first landing, the price was changed to a \$0.50 and \$0.25 per pound split, with the break at 140 shrimp per pound. This was due to the large volume of small shrimp (more than 170 per pound). Another two-week strike started the first of May, when the dealers dropped the price to a \$0.40 and \$0.25 per pound split. The strike ended when a single price of \$0.40 per pound for legal-count (160 per pound) shrimp was agreed upon. The price climbed to \$0.50 per pound during October. One dealer maintained a split price throughout the season.

A total of 57 boats (40 single-rigged and 17 double-rigged) delivered shrimp to Area A ports during 1988, down 3 single-rigged vessels from 1987. Single-rigged vessels had an average seasonal catch rate of 488 lb/hr, which is an increase of 195 lb/hr over

1987. Double-rigged vessels averaged 758 lb/hr, as compared to 460 lb/hr during 1987.

One-year-old shrimp constituted a very high proportion by number (75%–95%) of the catch throughout the season. The incoming year class (0's) constituted 18.7% by number of the catch in October; this is a decrease from the 21.1% present during October 1987.

Area B-1 shrimpers landed 0.38 million pounds during 1988, about half the 1987 catch of 0.74 million pounds. Price negotiations, with strikes and settlements, followed those in Area A. Four single-rigged vessels made deliveries to Fort Bragg during 1988.

A total of 0.38 million pounds of ocean shrimp was landed in Morro Bay and Avila (Area C) during the 1988 season. This represents 57% of the 1987 shrimp total. As in past years, large amounts of salps fouled the nets, making tows unprofitable in the late summer, and causing fishermen to leave the fishery.

Fishing was delayed until the middle of April because of price negotiations. The count-per-pound in the market samples ranged from 38 to 118, with an average well below 100. Females dominated the early samples (53%), but dropped to 20% in August and 34% in September.

#### PELAGIC SHARK AND SWORDFISH

During 1988, 202 permits were issued for harpooning swordfish (*Xiphias gladius*), and 231 drift gill net permits were issued for taking pelagic sharks and swordfish.

Harpoon fishermen reported landing 1,187 swordfish, making 1988 the third year of declining catches. On the other hand, drift gillnetters reported 11,138 swordfish taken during 1988, nearly equal to 1987, but still far below the peak of 25,367 fish reported for 1985. The reported average size of swordfish, taken by all gears, increased this year to approximately 190 pounds dressed weight. Variation in the annual average size and the inconsistent direction of shift in size from one year to the next seem to indicate that local availability depends strongly on fluctuating immigration rates from waters outside the California fishing grounds. The exact nature of this annual immigration and, in general, the migration of swordfish throughout the eastern Pacific Ocean, is unknown.

Common thresher shark (*Alopias vulpinus*) landings off California remained low during 1988, amounting to 0.52 million pounds. Although Oregon and Washington again allowed an experimental fishery for thresher shark during 1988, landings

were low (110,084 pounds), partially because of commercial fishermen's lack of interest.

Shortfin mako sharks (*Isurus oxyrinchus*) were pursued with both drift gill nets and drift longlines; the latter gear was authorized by the California Fish and Game Commission as an experimental fishery limited to 10 permit vessels. Total landings were 481,586 pounds. Of that, 231,380 pounds were taken by the 10 permitted longline vessels.

Market sampling indicates that the mako fishery takes primarily immature one- and two-year-old fish off California. Concerns over the development of another gear, in an area that appears to be a mako shark nursery grounds, has led the Fish and Game Commission to call for a shift in emphasis by drift longline vessels from pursuit of shortfin mako to blue sharks (*Prionace glauca*). If a substantial market for blue sharks is not developed during 1989, the Commission will reevaluate the experimental fishery.

#### CALIFORNIA HALIBUT

California halibut (*Paralichthys californicus*) landings totaled 522 MT for 1988, 1.6% less than the 530 MT recorded for 1987. Following a low catch of 122 MT in 1973, catches have steadily increased, averaging 456 MT for the last 10 years (table 4). Landings for 1988 exceed the 10-year average by 66 MT (6.8%). During 1988, 52% of the halibut landings occurred south of Point Conception. Southern California generally lands over 50% of the state's catch. Exceptions to this occurred during the warm-water year of 1982, when southern California's landings dropped to 47.5%.

The traditional winter-spring and summer-fall fishing seasons were again followed in 1988 by both northern and southern California halibut fishermen, with peak landings in March (44.5 MT) and

TABLE 4  
 California Halibut Landings (Metric Tons)

Year	North of Pt. Conception	South of Pt. Conception	Total
1977	25	186	211
1978	34	165	199
1979	54	205	259
1980	90	231	321
1981	163	409	572
1982	206	339	545
1983	256	248	504
1984	153	345	498
1985	144	429	573
1986	240	312	552
1987	192	347	530
1988*	249	273	522

\*Preliminary values as of March 15, 1989



October (36.9 MT). Entangling nets (trammel and set gill nets) accounted for 48.2% of all halibut taken, followed by trawl (30.4%), unknown gear (13.6%), and hook and line (7.8%). In northern California, the majority of the halibut are taken by trawl (57.6%); in southern California, entangling nets account for 75.8%. Average ex-vessel prices ranged from \$1.00 per pound in Bodega Bay to \$5.00 per pound in Princeton/Half Moon Bay, and averaged \$2.20 per pound statewide.

### CALIFORNIA SPINY LOBSTER

The 1987–88 (first Wednesday in October to first Wednesday after March 15) commercial fishery for California spiny lobster in southern California was well above the average for the past 20 years. A total of 477,000 pounds was landed, representing only a 3.5% decrease from the previous season.

Forty-two percent of the catch was made in October, and 23% in November. December effort was reduced by stormy weather, and the month produced only 11% of the season's catch. January accounted for 16%, and 8% was landed in February and March combined. The San Diego County area accounted for about 39% of the landings, with the Los Angeles–Orange and Santa Barbara–Ventura county areas contributing about 37% and 24%, respectively.

The ex-vessel price was up 15% from the previous season. At an average value of \$5.25 per pound, fishermen received an estimated \$2.5 million for the 1987–88 season. During the season, 321 permittees participated in the fishery, representing a 15% decrease from the 1986–87 season.

### ALBACORE

Albacore (*Thunnus alalunga*) landings for 1988 totaled 1,330 tons, the lowest annual total since 1934. Historically, California contributed 53% of all albacore landed in Washington, Oregon, and California. In 1988, the California total fell 30%, while Oregon and Washington totals rose substantially.

The season started in late July when several fishing vessels landed albacore from the Midway Islands. A few albacore were caught in southern California; they were not, however, abundant enough to sustain a commercial or sport fishery. In August the albacore fleet moved northward to Oregon and Washington, where the fish were more available. Limited activity occurred in central California, where albacore were caught incidentally by drift gill net boats (DGN) fishing for swordfish at Davidson and Pioneer seamounts (figure 1). By September, fishing in California was focused off the

central coasts between Monterey and Morro Bay. DGN boats and the few jig boats that remained in the area continued to take small catches of medium-to-large albacore. There was no albacore fishing effort south of Point Conception.

The sportfishing season had a slow start as well. Sportboats in San Diego began looking in July, but turned to other species when it became apparent that there were no albacore in the area. Sportboats in central California scored fair catches of albacore during September and October. These boats fished 50–100 miles west of Point Sur and around Davidson, Pioneer, and Guide seamounts.

The Western Fishboat Owners Association and Pan Pacific cannery agreed on \$1,700 per ton for fish over nine pounds, and \$1,200 per ton for fish nine pounds and under. This is a 15% increase over last year's price. Fishermen who sold directly to the public charged between \$1.00 and \$1.25 per pound; approximately 2% of all albacore landed was sold in this manner.

The disappointing 1988 season can be attributed to three factors. First, there was a good run of salmon in the north Pacific; consequently, fishermen did not fish for albacore. Second, although there were favorable water conditions (weak upwelling and cool surface temperatures) off the central and southern coasts, the albacore never appeared as expected. Lastly, the abundance of albacore off Oregon and Washington drew the California fleet northward and away from the few scattered schools of albacore off the central coast.

### RIDGEBACK AND SPOT PRAWN

Ridgeback prawn (*Sicyonia ingentis*) landings for 1988 fell to 131,000 pounds, the lowest since 1982 (table 5). Nearly all the catches occurred in the Santa Barbara Channel; some were made off Santa Monica Bay. During 1988, 15 trawlers were involved in the fishery. Catch-per-unit-effort declined from 82

TABLE 5  
 Ridgeback Prawn and Spot Prawn Landings  
 (1,000s of Pounds)

Year	Ridgeback prawn	Spot prawn
1979	356	48
1980	276	69
1981	193	369
1982	141	300
1983	157	109
1984	623	49
1985	905	64
1986	672	102
1987	242	88
1988	131	163

pounds per hour in 1987 to 64 pounds per hour in 1988. Even though the 1988 prawn recruitment survey indicated signs of an abundant year class, recruitment to the fishery was poor.

Spot prawn (*Pandalus platyceros*) landings increased from 88,000 pounds in 1987 to 163,000 pounds in 1988 (table 5). Most of the landings occurred off Santa Barbara, San Pedro, and San Diego. Approximately 55% was taken by trap, 30% by trawl, and the remainder by unidentified gear.

Management measures over the trawl fishery, improved environmental conditions, and development of the trap fishery have all contributed to increased landings in recent years.

### SEA URCHIN

The 1988 California red sea urchin (*Strongylocentrotus franciscanus*) fishery landings represent a historical high (table 6). The statewide total of 49,395,000 pounds marks a 7% increase over 1987 landings. The northern California harvest increased 22% over the previous year, while southern California landings dropped by 8%. The 1987 northern California totals represent a 250% increase over the 1986 landings for that area. August provided the highest monthly statewide catch of 6.3 million pounds, despite a one-week-per-month coastwide fishery closure that was in effect from May through September. Fort Bragg led all ports, with 36% of the landings.

Divers, using surface-supplied air, harvest sea urchins by raking them into mesh bags, which are then air lifted to the surface. Catch-per-unit-of-effort

(CPUE) can be measured as pounds harvested per diving hour. Northern California CPUE was 579 pounds per hour in 1987, compared to 505 pounds in 1988, as indicated by interviews with fishermen. This compares to a southern California CPUE ranging from less than 200 pounds per hour in the San Diego area fishery to just over 400 pounds per hour in the San Nicolas Island area.

There were 206 vessels participating in the northern California fishery in 1988, up from 159 in 1987. Only 34 vessels harvested 50% of this area's catch. About 3,600 pounds were landed per trip, which is 48% higher than the average in southern California. Higher catch rates in northern California were partly due to the relatively unexploited state of stocks. In the Point Arena area, in particular, individual single-day trip landings of 10,000 to 15,000 pounds were not unusual during the summer, when fishing conditions were optimal.

Although the southern California fishery has averaged about 20 million pounds per year since 1980, effort has shifted from the northern Channel Islands, where stocks have been fished down, to the southern islands and to northern California. The average test diameter of harvested urchins in southern California is about 20 mm smaller than in northern California, where harvested urchins averaged 107 mm in 1988. In March 1989, the Department instituted a 3-inch (76-mm) minimum size limit, partially in response to the increasing percentage of smaller urchins observed in the harvest. In the Santa Barbara area, where the fishery has a long history, urchins under 3 inches made up 35% of the sampled landings in 1988, compared to only 3% of the harvest from the southern Channel Islands and from northern California, where the fishery is relatively new.

Other management and research efforts include the establishment of a limited entry system for sea urchin diving permits in 1989, as well as the continuation of underwater studies to assess stock size composition and relative abundance. These studies were begun by the Department in 1988 in northern California.

### RECREATIONAL FISHERY

Catches from the California commercial passenger fishing vessel (CPFV, or partyboat) fleet can generally be considered indicative of nearshore and offshore sport angler success. The CPFV fleet is capable of locating and catching any species available within the fishing area. Catches can vary widely for latitudinally migratory species, such as barracuda (*Sphyraena argentea*) and yellowtail (*Seriola lalandi*), and for highly migratory transoceanic

TABLE 6  
 Sea Urchin Landings (1,000s of Pounds)

Year	Northern California	Southern California	Total
1971	0	<1	<1
1972	<1	76	76
1973	18	3,594	3,612
1974	51	7,056	7,107
1975	3	7,323	7,326
1976	95	11,012	11,107
1977	386	16,208	16,594
1978	34	14,394	14,428
1979	237	20,307	20,544
1980	103	21,196	21,299
1981	194	24,720	24,914
1982	92	19,347	19,439
1983	61	17,207	17,268
1984	59	14,920	14,979
1985	1,921	18,074	19,995
1986	10,174	23,957	34,131
1987	23,600	22,500	46,100
1988	28,660	20,735	49,395

TABLE 7  
 1988 Commercial Passenger Fishing Vessel Catch

Species/species group	Number of fish (thousands)	Rank
Rockfish	1,851	1
Kelp/sand bass	730	2
Pacific mackerel	406	3
Bonito	245	4
Barracuda	140	5
Sculpin	128	6
White croaker	121	7
Salmon	113	8
Halfmoon	80	9
Yellowtail	66	10
Lingcod	63	11
Ocean whitefish	56	12
Queenfish	33	13
Sheephead	31	14
Jack mackerel	21	15
Yellowfin tuna	20	16
Pacific hake	19	17
Flatfish (misc.)	16	18
California halibut	12	19
Striped bass	9	20
Others	43	
Total	4,203	

species like albacore (*Thunnus alalunga*). Catches of resident species in nearshore areas may also show fluctuations associated with warmer oceanic regimes.

The total 1988 partyboat landings, 4.2 million fish, were slightly higher than in 1987 (table 7). Rockfish (a multispecies group) maintained its first-rank position, with 1.9 million fish caught; this is about a 12% increase over the previous year.

The kelp/sand bass complex (730,000 fish) remained at about the 1987 level. Within this group, sand bass (*Paralabrax nebulifer*) landings again increased and exceeded the kelp bass (*Paralabrax clathratus*) catch, which showed a slight decline. Pacific mackerel (*Scomber japonicus*) and bonito (*Sarda chiliensis*) exchanged rankings in 1988, with 406,000 and 245,000 fish taken, respectively. The bonito catch decreased more than 50% from last year.

The barracuda catch, 140,000 fish, was fair and ranked fifth. This is still well above the landings of

50,000–90,000 fish during the 15 years preceding 1987. Sculpin (*Scorpaena guttata*) landings were exceptional, with 128,000 fish logged; this is more than double the 1987 catch, and this species ranked sixth in 1988. White croaker showed a dramatic increase of over 3000% in 1988, with 121,000 fish landed. The highly prized salmon group provided another good season, with landings of 113,000 fish. This is slightly less than in 1987, but still relatively high. The catch of halfmoon, a nearshore resident species, more than doubled in 1987; it ranked ninth, with 80,000 fish. The popular yellowtail ranked tenth, with 66,000 fish recorded; this is a 15% increase over 1987. The highly desirable California halibut ranked nineteenth, experiencing a 52% increase for 1988 (11,501 fish). This is the highest catch since 1982 (11,804 fish), and the second highest since 1970.

Probably the highlight of 1988, albeit a negative one, was the virtual failure of the albacore fishery, with only 559 fish logged. This is the lowest catch since 1959, when the CPFVs caught only 39 albacore.

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## SPAWNING BIOMASS OF THE NORTHERN ANCHOVY IN 1988

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### ABSTRACT

The spawning biomass estimate of the northern anchovy in 1988 is 1,009,000 MT. The estimate was made with the stock synthesis (SS) model, which uses time series of abundance data and age composition data, anchovy landings from the United States and Mexico, and sea-surface temperature. New data incorporated in the 1988 estimate were an egg production index derived from CalCOFI plankton samples of January–February 1988, monthly sea-surface temperatures taken at the pier of the Scripps Institution of Oceanography, and the age composition from the Mexican fishery in Ensenada during 1987. The spawning biomass of anchovy in 1988 remained at a level similar to that in 1987.

### RESUMEN

La estimación de la biomasa del desove de la anchoveta del norte es de 1,009,000 toneladas métricas para 1988. Esta estimación se realizó por medio del modelo de síntesis del stock ("stock synthesis", SS), que utiliza una combinación de datos distribuidos en el tiempo de abundancia y composición por edad, datos de desembarque de capturas de los Estados Unidos y México, y datos de temperatura de la superficie del mar. Se incorporaron a la estimación de la biomasa del desove para 1988 datos nuevos, tales como el índice de producción de huevos obtenido de las muestras de plancton recolectadas en los meses de enero y febrero de 1988 por la campaña de la CalCOFI, los valores de temperatura de las aguas de superficie obtenidos desde el muelle del Scripps Institution of Oceanography, y los datos de composición por edad obtenidos por la pesquería de Ensenada durante el año 1987. La biomasa del desove de la anchoveta para 1988 es similar a la del año 1987.

### INTRODUCTION

This is a report on the estimate of the 1988 spawning biomass of the central subpopulation of the

northern anchovy (*Engraulis mordax*). The Southwest Fisheries Center is required to estimate the spawning biomass according to the provisions of the Anchovy Management Plan of the Pacific Fishery Management Council (PFMC 1983). In 1980–85, the spawning biomass was estimated by the egg production method (EPM) (Lasker 1985). Beginning in 1986, the estimate was computed by the stock synthesis (SS) model (Methot 1986; Methot and Lo 1987). The SS model integrates the EPM observation with other data. These data include other biomass indexes, age composition from U.S. and Mexican fisheries, age composition from California Department of Fish and Game surveys, and environmental data. Although four time series of abundance data are used in the historical model, the new data points in 1988 are only (1) the modified historical egg production computed from plankton samples in the California Cooperative Oceanic Fisheries Investigation (CalCOFI) survey; (2) the 1987 age composition data from the Mexican fishery in Ensenada (pers. comm. Walterio Garcia Franco, Centro Regional Investigación de Pesquera [CRIP], Instituto Nacional de Pesca); and (3) the sea-surface temperature at the pier of the Scripps Institution of Oceanography.

### MODEL

The SS model (figure 1) developed by Methot (1986) and revised by Methot and Lo (1987) and Methot (in press) used data on age composition and various biomass time series to construct time series of age-structured populations. The age-composition data provide information on recruitment variability and describe year-to-year changes in relative abundance; biomass time series establish the trend in abundance. The population from the model is characterized by a set of biological parameters, e.g., recruitment, natural mortality, age-specific availability to the fishery, and temperature-dependent fraction of age 1 anchovy that are mature. Other parameters are associated with fishery-independent biomass estimates. Parameter estimates are chosen so that the age compositions and biomass indexes

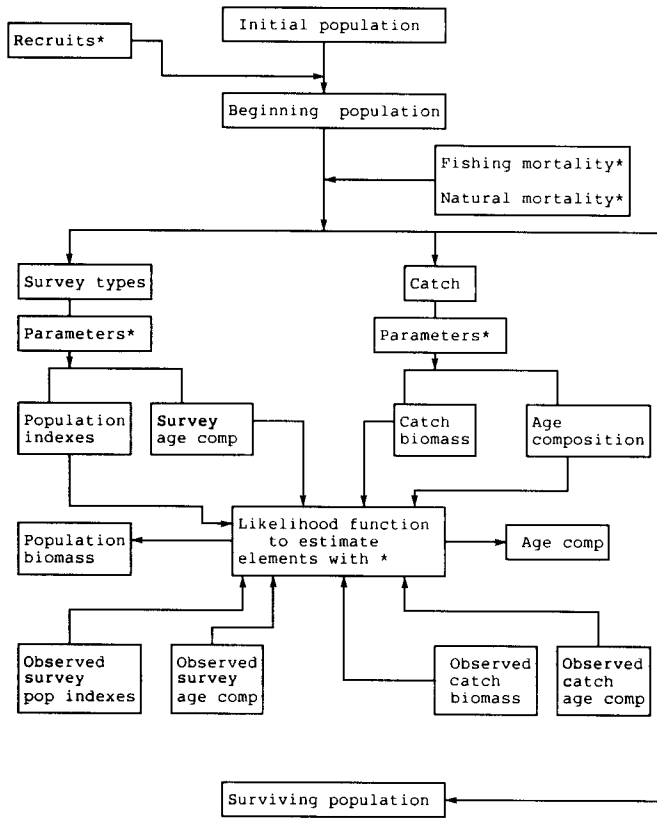


Figure 1. Schematic stock synthesis model. Asterisks indicate parameters to be estimated by the model.

computed from the model closely match the “observed” values. The best estimates are those that maximize a composite likelihood function. These estimates are then used in the population model to compute biomass at age and the spawning biomass (figure 1).

The observed age compositions are obtained from commercial catches of the U.S. and Mexican fisheries and from U.S. sea surveys. The observed biomass may be any existing biomass time series. The current SS model uses spawning biomass time series (table 1) from the egg production method (Lasker 1985; Bindman 1985), historical egg production (HEP) (Lo 1985), sonar (Mais 1974), and modified HEP (Methot and Lo 1987). The environmental variable, sea-surface temperature (George Anderson, SIO, pers. comm.), is included to model the availability to the fishery, the fraction of one-year-olds that are mature, and the fraction of one-year-olds that are actively spawning (Methot, in press). The natural mortality was fixed at the value 0.6, which is consistent with the literature (MacCall 1974) and earlier investigation with the SS model (Methot 1986).

TABLE 1  
 Fishery-Independent Spawning Biomass Estimate  
 for Northern Anchovy

Year	EPM	HEP	MHEP	Z	Sonar
1951	—	0.012 (0.12)	0.011 (0.06)	0.23 (2.18)	—
1952	—	0.017 (0.11)	0.024 (0.14)	.09 (1.27)	—
1953	—	0.066 (0.18)	0.035 (0.08)	.19 (0.54)	—
1954	—	0.168 (0.19)	0.177 (0.18)	.12 (0.24)	—
1955	—	0.316 (0.34)	0.360 (0.41)	.07 (0.26)	—
1956	—	0.146 (0.65)	0.476 (2.21)	.33 (0.88)	—
1957	—	0.364 (0.42)	0.444 (0.47)	.20 (0.25)	—
1958	—	1.274 (1.18)	1.718 (1.23)	.43 (0.23)	—
1959	—	0.992 (0.82)	1.777 (1.31)	.23 (0.20)	—
1960	—	1.765 (0.77)	2.443 (1.20)	.24 (0.10)	—
1961	—	0.653 (0.64)	0.706 (0.61)	.29 (0.22)	—
1962	—	1.314 (1.17)	2.248 (1.66)	.19 (0.18)	—
1963	—	2.275 (0.99)	2.967 (1.39)	.28 (0.09)	—
1964	—	4.147 (2.68)	8.643 (4.59)	.42 (0.13)	—
1965	—	4.019 (1.18)	8.177 (2.91)	.19 (0.06)	—
1966	—	5.256 (1.80)	12.851 (5.12)	.42 (0.07)	—
1967	—	—	—	—	—
1968	—	—	—	—	—
1969	—	3.821 (1.06)	5.431 (1.55)	.19 (0.06)	438
1970	—	—	—	—	275
1971	—	—	—	—	233
1972	—	1.657 (0.80)	3.450 (0.83)	.25 (0.11)	822
1973	—	—	—	—	1671
1974	—	—	—	—	947
1975	—	19.691 (10.36)	16.707 (3.96)	.44 (0.11)	3086
1976	—	—	—	—	—
1977	—	—	—	—	1984
1978	—	2.33 (4.48)	14.657 (6.53)	.59 (0.10)	392
1979	—	5.426 (2.62)	5.070 (2.19)	.48 (0.10)	292
1980	870	2.671 (1.26)	2.548 (0.99)	.36 (0.08)	604
1981	635	4.376 (2.08)	4.738 (1.78)	.38 (0.08)	567
1982	415	3.29 (1.36)	1.684 (2.03)	.36 (0.09)	250
1983	652	3.91 (1.17)	1.654 (1.27)	.46 (0.06)	532
1984	309	2.85 (1.06)	2.567 (1.76)	.36 (0.08)	573
1985	521	2.62 (0.67)	5.160 (2.16)	.28 (0.05)	1015
1986	—	—	7.558 (3.34)	.34 (0.12) <sup>a</sup>	—
1987	—	—	7.234 (2.57)	.19 (0.08) <sup>a</sup>	—
1988	—	—	6.891 (3.42)	.53 (0.09) <sup>a</sup>	—

<sup>a</sup>Z for 1986–88 computed from the condensed CalCOFI area.

EPM is spawning biomass (thousand MT) estimated by the egg production method; HEP is the historical egg production index of spawning biomass (Lo 1985); MHEP is HEP as modified to account for the reduced CalCOFI sampling pattern. Z is the daily egg mortality associated with the HEP estimate and was used in making the MHEP estimate. Sonar is based on the acoustic surveys conducted by CDFG. Standard errors are in parentheses.

## DATA

### Fishery Data

The total landings from the U.S. fishery in 1987 were 5,024 MT, compared to 5,500 MT in 1986 (table 2). The total landings included 149 MT for reduction to oil and meal, and 4,875 MT for live bait and other uses (Thomson et al. 1988). The total landings at Ensenada, Baja California, Mexico, during 1987 were 124,457 MT (Secretaria de Pesca de México 1988; W. Garcia F., pers. comm.) compared to 96,000 MT in 1986. The 1987 landings are

TABLE 2  
 United States Fishery Landings and Weight at Age

Year	Month	Landings (MT)	Weight at age (g)					
			0	1	2	3	4	5+
1964	1-2	0						
	3-6	3482	0.0	12.9	17.5	21.0	24.5	28.8
	7-8							
	9-12	3484	11.2	16.6	19.4	21.8	24.4	26.3
1965	1-2							
	3-6	4122	0.0	12.9	17.5	21.0	24.5	28.8
	7-8							
1966	9-12	4124	11.2	16.6	19.4	21.8	24.4	26.3
	1-3	4518	2.7	12.1	15.8	19.4	23.4	28.5
	4-6	14440	6.7	13.6	17.4	20.1	22.9	28.0
	7-9	4958	10.8	15.1	18.4	20.0	22.3	26.9
1967	10-11	3851	12.3	17.1	19.4	21.7	23.9	26.3
	12-2	16982	1.8	11.4	16.6	19.5	22.4	26.0
	3-6	16934	5.9	11.7	17.7	22.3	28.1	33.3
	7-9	3876	10.9	15.2	18.4	19.9	22.3	26.8
1968	10-12	5307	12.1	16.9	19.5	21.8	24.1	26.8
	1-3	979	2.8	12.1	15.7	19.2	23.2	28.5
	4-6	3308	6.9	13.6	17.5	20.0	22.7	28.0
	7-9	4487	10.9	15.2	18.4	19.9	22.3	26.8
1969	10-1	13868	14.9	17.4	20.2	23.1	27.1	31.3
	2-3	2445	3.8	14.2	16.0	21.0	20.7	24.1
	4-5	10134	5.9	14.3	16.2	20.4	24.7	27.1
	6-8	4676	9.1	13.7	18.3	20.1	22.1	27.8
1970	9-12	47099	12.7	17.7	21.4	25.1	29.0	32.7
	1	6089	1.3	13.8	17.8	20.0	26.1	27.8
	2-5	23663	5.1	12.7	17.8	20.8	27.4	33.1
	6-10	30437	11.8	17.5	21.6	24.3	29.3	27.8
1971	11-12	32664	14.1	17.6	21.9	25.3	31.7	35.4
	1	9128	1.3	13.5	18.7	22.5	25.9	32.5
	2-5	10881	5.8	13.9	18.2	24.9	27.3	31.4
	6-9	7359	9.9	14.5	18.3	20.0	22.2	27.1
1972	10-12	19117	13.4	14.8	17.1	22.5	24.2	25.3
	1-2	11734	1.9	12.5	15.1	18.2	24.3	27.8
	3-5	16426	5.7	12.2	15.5	19.0	24.8	27.1
	6-9	9508	9.9	14.6	18.3	20.0	22.2	27.0
1973	10-12	30325	12.8	13.8	16.5	19.0	24.8	26.0
	1-2	3483	1.7	8.9	11.1	13.7	14.0	27.9
	3-6	36629	6.2	12.8	14.3	17.0	21.1	28.5
	7-10	38266	8.5	14.0	16.2	18.5	21.6	29.3
1974	11-12	47587	13.7	15.8	18.9	22.1	25.7	29.9
	1-2	11824	2.0	10.7	12.9	15.4	17.7	25.0
	3-6	18989	6.1	13.0	15.6	18.3	22.0	26.4
	7-9	5084	11.1	15.4	18.4	19.9	22.3	26.6
1975	10-1	61075	10.7	17.1	18.0	20.8	22.7	24.7
	2-3	13491	3.2	13.7	17.6	18.7	21.4	26.1
	4-6	34132	6.1	17.1	20.7	21.7	24.2	27.4
	7-10	42862	15.1	18.1	19.5	20.3	22.6	23.6
1976	11-1	60267	9.0	18.3	20.6	22.3	26.9	27.3
	2-3	12557	3.9	10.4	19.6	22.9	25.0	30.4
	4-6	19887	5.7	14.5	20.5	23.0	23.9	28.0
	7-9	10229	11.6	17.1	19.1	20.7	22.2	24.6
1977	10-1	61069	10.4	15.8	20.4	22.0	23.7	25.2
	2	503	2.7	11.7	15.2	17.4	21.1	27.7
	3-6	32294	4.7	13.9	15.5	19.1	22.5	26.5
	7-9	13483	12.8	18.0	19.3	21.0	22.4	25.7
1978	10-12	58869	12.2	18.4	20.3	22.1	22.9	26.2
	1-3	832	3.0	12.1	15.7	19.2	23.2	28.5
	4-6	3052	6.7	13.6	17.4	20.0	22.9	28.0
	7-9	6031	12.2	17.0	18.9	25.0	22.3	26.4
1979	10-12	7556	11.0	18.3	19.8	23.7	20.3	28.6
	1-3	625	2.6	12.0	15.7	19.1	23.1	28.4
	4-6	41754	6.5	14.3	18.6	22.5	24.8	24.9
	7-9	4563	11.3	15.6	18.4	19.9	22.3	26.4
	10-1	8591	8.8	19.2	23.0	20.0	24.9	26.6

(continued on next page)

TABLE 2 (continued)  
 United States Fishery Landings and Weight at Age

Year	Month	Landings (MT)	Weight at age (g)					
			0	1	2	3	4	5+
1980	2-3	207	3.5	12.2	15.7	19.1	23.1	28.6
	4-6	26730	6.8	11.2	18.4	20.8	24.1	27.7
	7-9	3374	11.0	15.2	18.4	19.9	22.3	26.8
	10-1	27401	9.5	14.2	19.2	21.5	22.8	27.6
1981	2-3	432	3.4	12.2	15.6	18.9	22.9	28.5
	4-6	34699	6.5	14.0	15.8	19.7	21.9	28.6
	7-9	2878	11.0	15.3	18.4	19.9	22.3	26.7
	10-1	9151	7.6	17.0	18.3	20.4	25.1	26.8
1982	2-3	375	3.4	12.2	15.6	19.0	23.0	28.6
	4-6	40808	7.3	14.4	18.5	20.2	22.2	25.2
	7-9	3044	10.6	14.8	18.4	20.0	22.3	27.2
	10-12	2872	11.9	16.8	19.4	21.5	23.7	26.5
1983	1-3	526	3.2	12.2	15.8	19.4	23.5	28.7
	4-6	4561	7.4	13.4	17.8	20.1	22.4	27.9
	7-9	2218	10.6	14.9	18.4	20.0	22.3	27.2
	10-12	1182	12.2	17.0	19.4	21.7	23.9	26.5
1984	1-3	427	2.5	11.9	15.7	19.0	22.9	28.3
	4-6	3680	6.8	13.6	17.4	20.0	22.8	28.0
	7-9	2266	10.5	14.9	18.4	20.0	22.3	27.2
	10-12	929	12.0	16.8	19.4	21.5	23.8	26.5
1985	1-3	503	2.8	12.0	15.6	18.8	22.7	28.3
	4-6	1064	7.3	13.5	17.7	20.1	22.5	28.0
	7-9	2727	10.7	15.0	18.4	20.0	22.3	27.1
	10-12	1490	12.1	16.9	19.5	21.7	24.0	26.7
1986	1-3	456	2.7	12.1	15.8	19.3	23.2	28.5
	4-6	1648	6.4	13.8	17.2	19.9	23.1	28.1
	7-9	2519	10.6	14.9	18.4	20.0	22.3	27.2
	10-12	881	12.1	16.9	19.4	21.6	23.9	26.6
1987	1-3	370	2.9	12.1	15.7	19.0	23.0	28.4
	4-6	1013	6.7	13.5	17.5	20.1	22.9	28.0
	7-10	2965	10.9	15.4	18.6	20.2	22.5	26.9
	11-12	527	12.4	17.1	19.6	22.2	24.5	26.8

62% of the 200,000-MT optimum yield. The landings data are necessary for calculating survivorship from the previous year's biomass estimate. Monthly landings, age composition, and weight-at-age data for 1987 were obtained from CRIP (tables 3-5. For data sources for years before 1987, see

Methot 1986). The CRIP port sampling program collected monthly anchovy samples from randomly selected fishing boats. Hundreds to thousands of fish were measured, and age was determined from otolith readings (W. Garcia F., pers. comm.). The age composition from the autumn fishery reveals

TABLE 3  
 Mexican Fishery Data, 1987

Month	Landings (MT)	Age composition						N aged	Weight at age (g) × 10						
		0	1	2	3	4	5+		0	1	2	3	4	5+	
1	73	0	0	0	0	0	0	0	0*	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	95	0	468	33	7	4	0	512	0	63	120	120	130	0	0
4	4359	0	684	241	60	12	8	1005	0	99	104	133	186	178	0
5	23041	0	1105	189	74	28	15	1411	0	104	106	174	199	218	0
6	16455	368	491	43	45	11	23	981	40	152	133	221	232	246	0
7	22298	512	476	122	39	3	4	1156	47	125	128	144	195	214	0
8	29768	338	201	251	14	2	0	806	71	135	130	155	223	0	0
9	16291	1359	180	668	91	3	0	2301	67	121	111	118	117	0	0
10	11030	493	33	332	187	36	8	1089	75	127	134	128	129	159	0
11	1065	253	44	82	12	0	0	391	90	109	127	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

\*In Weight at age section, 0 indicates that no samples were taken.

TABLE 4  
 Mexican Fishery Landings and Weight at Age

Year	Month	Landings (MT)	Weight at age (g)					
			0	1	2	3	4	5+
<b>Yearly data</b>								
1964	3	4599	8.5	12.5	14.4	16.0	17.6	18.6
1965	3	9171	8.5	12.5	14.4	16.0	17.6	18.6
1966	3	13243	8.5	12.5	14.4	16.0	17.6	18.6
1967	3	20104	8.5	12.5	14.4	16.0	17.6	18.6
1968	3	14267	8.5	12.5	14.4	16.0	17.6	18.6
1969	3	3871	8.5	12.5	14.4	16.0	17.6	18.6
1970	3	27977	8.5	12.5	14.4	16.0	17.6	18.6
1971	3	20079	8.5	12.5	14.4	16.0	17.6	18.6
1972	3	30047	8.5	12.5	14.4	16.0	17.6	18.6
1973	3	15424	8.5	12.5	14.4	16.0	17.6	18.6
<b>Seasonal data</b>								
1974	1-3	0						
	4-6	12552	0.0	9.5	11.2	13.4	15.0	16.5
	7-9	19115	8.5	12.5	14.4	16.0	17.6	18.6
	10-12	11143	8.2	12.8	14.6	18.1	19.2	18.6
1975	1-3	6897	1.5	8.7	13.2	15.9	17.0	20.8
	4-6	21191	7.0	10.8	13.9	15.5	16.8	20.8
	7-8	20733	6.3	11.8	14.7	15.6	17.4	20.8
	9-12	8056	6.0	11.3	14.1	15.2	17.9	20.8
1976	1-3	253	2.2	8.9	13.3	15.8	17.0	20.8
	4-5	2492	5.0	10.0	13.5	15.6	16.8	20.8
	6-9	36686	6.4	11.5	14.6	15.5	17.7	20.8
	10-1	38745	7.7	11.3	14.3	15.6	17.5	20.8
1977	2-3	2204	2.7	9.4	13.4	15.8	17.0	20.8
	4-5	9884	5.0	10.0	13.5	15.6	16.8	20.8
	6-8	90522	6.3	11.6	14.6	15.6	17.5	20.8
	9-1	37692	6.5	11.5	14.2	15.7	17.7	20.8
1978	2-3	0	0.0	0.0	0.0	0.0	0.0	0.0
	4-5	12089	5.2	10.0	13.5	15.5	16.7	20.8
	6-8	72637	9.2	13.6	15.4	17.3	18.8	20.8
	9-1	56261	10.4	14.6	16.3	19.2	18.0	20.8
1979	2-3	0	0.0	0.0	0.0	0.0	0.0	0.0
	4-6	78899	6.9	11.6	12.8	15.0	17.2	20.7
	7-8	45929	7.4	11.8	13.3	16.6	17.5	20.8
	9-1	81238	7.1	12.0	13.6	16.9	17.9	20.8
1980	2-3	139	2.8	9.4	13.4	15.8	17.0	20.8
	4-5	4611	5.4	10.2	13.9	15.7	17.0	20.8
	6-8	130810	7.7	12.9	16.1	17.0	18.7	20.8
	9-1	110940	8.5	13.0	16.0	17.7	18.8	20.8
1981	2-3	0	0.0	0.0	0.0	0.0	0.0	0.0
	4-6	71423	7.4	10.7	12.6	14.3	15.4	20.8
	7-9	144543	7.6	10.7	12.6	14.0	16.2	20.8
	10-1	39420	8.4	11.4	13.3	14.7	14.9	20.8
1982	2-3	0	0.0	0.0	0.0	0.0	0.0	0.0
	4-5	27240	5.3	12.4	14.3	15.9	16.5	21.5
	6-8	105296	8.2	12.1	13.5	14.8	15.3	23.4
	9-10	24695	7.3	11.9	13.5	14.7	15.4	22.5
1983	11-3	24418	1.1	6.7	9.0	10.1	12.1	18.6
	4-5	35725	5.3	7.1	8.7	9.1	17.6	21.0
	6-8	18308	6.7	8.7	10.2	11.0	17.8	23.8
	9-2	21341	3.3	7.1	8.0	9.7	13.9	22.5
1984	3-4	590	4.4	6.9	8.1	11.1	17.4	18.2
	5-6	36495	5.6	8.6	13.7	16.0	17.5	23.7
	7	25465	4.9	9.2	12.7	12.1	17.3	22.5
	8-1	38546	5.0	8.5	12.0	15.2	15.8	22.5
1985	2	0	0.0	0.0	0.0	0.0	0.0	0.0
	3-6	59348	5.1	14.1	15.7	18.3	18.7	20.6
	7	17894	6.4	18.8	20.1	26.2	25.0	22.5
	8-1	44547	7.1	18.5	20.9	22.3	22.6	22.5
1986	2-3	211	2.7	6.5	12.4	15.4	17.0	18.2
	4-5	7334	4.7	8.4	13.8	16.4	16.6	20.2
	6-7	36648	8.1	13.1	16.0	20.7	20.9	23.7
	8-12	51478	5.3	12.9	15.5	19.7	18.6	22.5

(continued on next page)



TABLE 4 (continued)  
 Mexican Fishery Landings and Weight at Age

Year	Month	Landings (MT)	Weight at age (g)					
			0	1	2	3	4	5+
1987	1-3	168	2.2	6.3	12.2	13.7	15.3	18.2
	4-5	27400	5.3	10.3	10.5	16.7	19.8	21.3
	6-7	38753	4.4	13.8	12.9	18.3	22.3	24.1
	8-12	58154	7.1	13.2	12.6	13.1	14.4	21.5

TABLE 5  
 Age Composition for U.S. Fishery, Mexican Fishery, and U.S. Survey

Year	Qtr.	Type	Age					N aged	
			0	1	2	3	4		5+
1967	1	US-F	0.0	39.0	224.3	662.3	704.0	239.0	1870
	2	US-F	0.0	42.3	167.0	265.6	165.7	96.4	739
1968	1	US-S	0.0	422.0	305.0	149.0	111.0	14.0	105
	2	US-S	0.0	144.0	248.0	189.0	259.0	161.0	245
1969	4	US-F	39.1	358.1	285.0	92.4	60.8	6.2	845
	1	US-F	0.0	62.7	73.7	26.0	6.6	10.1	179
1970	2	US-F	0.0	200.8	389.9	119.7	50.1	30.5	789
	4	US-F	101.2	722.6	1664.8	423.3	80.1	12.0	3003
1971	1	US-F	0.0	167.0	352.0	207.0	44.0	16.0	786
	1	US-S	0.0	359.0	322.0	250.0	47.0	22.0	206
	2	US-F	0.0	1191.0	528.9	338.3	73.7	18.1	2153
	3	US-F	4.5	411.3	902.0	302.9	34.3	3.0	1657
1972	4	US-F	42.0	682.0	756.0	480.0	57.0	9.0	2024
	1	US-F	0.0	69.0	367.0	304.0	243.0	67.0	1050
	1	US-S	0.0	196.0	301.0	307.0	164.0	33.0	173
	2	US-F	0.0	54.4	89.6	95.8	51.7	20.5	312
1973	2	US-S	0.0	223.0	281.0	300.0	132.0	64.0	171
	4	US-F	62.5	477.2	365.7	94.5	24.1	0.7	1029
	1	US-F	0.0	106.8	890.9	366.4	147.7	44.0	1557
	2	US-F	0.0	154.5	424.9	192.8	79.1	15.6	867
1974	2	US-S	0.0	122.0	412.0	253.0	119.0	94.0	190
	4	US-F	74.1	500.2	1561.2	431.6	37.8	9.1	2616
	1	US-S	0.0	43.0	377.0	457.0	112.0	11.0	249
	2	US-F	0.0	425.9	864.5	1237.8	455.6	134.1	3116
1975	2	US-S	0.0	35.0	219.0	406.0	255.0	86.0	190
	3	US-F	6.0	319.3	985.6	907.5	153.8	10.8	2383
	4	US-F	27.6	269.5	935.9	1027.4	264.5	24.0	2548
	1	US-F	0.0	263.9	607.5	471.9	260.1	37.8	1640
1976	2	US-F	0.0	157.0	274.7	174.2	134.0	42.1	782
	2	US-S	0.0	28.0	144.0	333.0	396.0	100.0	290
	4	US-F	43.2	579.7	1694.7	966.9	301.0	18.9	3611
	1	US-F	0.0	154.9	231.0	252.1	170.2	83.8	892
1977	1	MX-F	0.0	49.8	65.2	186.6	60.7	9.7	372
	1	US-S	0.0	84.0	153.0	273.0	262.0	228.0	220
	2	US-F	0.0	52.9	317.3	656.8	598.6	343.5	1970
	2	MX-F	1.3	8.0	77.2	144.4	49.5	7.7	288
1978	3	US-F	13.0	369.7	1187.9	738.5	162.9	27.2	2498
	3	MX-F	4.3	16.5	70.9	114.0	37.5	5.7	249
	4	US-F	59.9	297.0	1345.2	1342.5	531.7	46.5	3625
	4	MX-F	21.5	24.5	37.0	62.0	25.2	5.8	176
1979	1	US-F	0.0	52.1	57.7	180.1	263.0	257.7	809
	2	US-F	0.0	7.0	89.1	299.9	467.2	286.8	1151
	2	MX-F	0.0	27.4	100.3	189.1	66.7	8.5	392
	2	US-S	0.0	16.0	24.0	151.0	430.0	380.0	320
1980	3	US-F	0.0	36.0	67.0	76.0	13.0	1.0	193
	3	MX-F	170.3	144.2	151.1	175.1	78.5	10.7	730
	4	US-F	306.2	255.2	579.8	1086.1	535.3	93.3	2856
	4	MX-F	376.2	59.9	81.5	36.8	10.6	0.0	565

(continued on next page)

TABLE 5 (continued)  
 Age Composition for U.S. Fishery, Mexican Fishery, and U.S. Survey

Year	Qtr.	Type	Age					N aged	
			0	1	2	3	4		5+
1977	1	MX-F	0.0	93.0	39.5	113.2	51.3	0.0	297
	1	US-S	0.0	450.0	47.0	96.0	216.0	191.0	470
	2	US-F	0.0	908.7	250.2	187.8	264.1	212.2	1823
	2	MX-F	0.0	98.4	47.3	66.1	55.4	24.8	292
	3	US-F	5.0	158.0	76.0	40.0	50.0	10.0	339
	3	MX-F	34.1	215.2	166.3	233.0	182.1	40.2	871
	4	US-F	262.9	886.3	506.8	379.6	358.3	77.0	2471
	4	MX-F	115.2	183.1	115.4	112.2	51.9	15.2	593
1978	1	US-S	0.0	96.0	459.0	160.0	149.0	135.0	396
	3	MX-F	146.5	151.4	1043.1	62.8	39.0	23.2	1466
	4	US-F	71.4	107.3	114.5	4.9	7.3	1.7	307
	4	MX-F	1353.8	170.6	303.6	9.4	8.1	3.5	1849
1979	1	US-S	0.0	652.0	95.0	180.0	64.0	8.0	508
	2	US-F	0.0	2453.2	720.9	432.7	63.8	18.5	3688
	2	MX-F	6.9	1096.8	430.2	146.3	7.0	1.9	1689
	2	US-S	0.0	727.0	132.0	97.0	25.0	18.0	328
	3	MX-F	48.1	799.9	155.1	49.6	2.2	0.0	1055
	4	MX-F	744.1	1112.4	135.7	45.1	1.6	0.0	2039
1980	1	US-S	0.0	348.0	501.0	120.0	22.0	8.0	610
	2	US-F	0.0	915.6	1170.1	159.6	23.2	2.4	2270
	2	MX-F	0.0	241.0	202.7	21.5	14.8	0.0	480
	3	MX-F	15.9	763.2	1089.2	107.3	20.5	0.0	1996
	4	US-F	135.2	1008.6	736.6	77.6	10.0	0.0	1966
	4	MX-F	750.5	723.5	607.9	57.5	3.7	0.0	2143
1981	1	US-S	0.0	453.0	305.0	205.0	34.0	2.0	555
	2	US-F	0.0	1177.1	902.8	583.3	59.4	2.0	2724
	2	MX-F	12.0	1490.3	789.6	282.1	24.1	0.0	2598
	2	US-S	0.0	297.0	316.0	379.0	8.0	0.0	460
	3	MX-F	130.8	1246.4	583.0	215.2	21.6	0.0	2197
	4	US-F	8.3	125.5	168.8	29.4	0.0	0.0	332
	4	MX-F	441.2	737.6	411.7	148.4	14.6	3.5	1757
1982	1	US-S	0.0	93.0	360.0	477.0	68.0	0.0	651
	2	US-F	0.0	389.7	849.9	1137.8	293.2	2.9	2672
	2	MX-F	0.0	70.1	367.4	154.2	45.0	0.2	637
	3	MX-F	57.1	374.5	641.5	179.7	26.3	0.0	1279
	4	MX-F	317.3	146.9	164.2	29.6	1.9	0.0	660
1983	1	MX-F	0.0	399.1	223.1	54.8	3.1	0.0	680
	1	US-S	0.0	742.0	112.0	108.0	38.0	0.0	582
	2	MX-F	0.0	431.6	41.3	7.1	0.0	0.0	480
	3	MX-F	56.4	431.4	44.2	8.1	0.0	0.0	540
	4	MX-F	393.2	369.7	49.1	7.9	0.0	0.0	820
1984	1	US-S	0.0	348.0	585.0	53.0	13.0	0.0	518
	2	MX-F	30.7	510.1	269.5	23.0	5.7	0.0	839
	3	MX-F	93.0	217.0	29.0	1.0	0.0	0.0	340
	4	MX-F	1298.9	449.2	31.9	0.0	0.0	0.0	1780
1985	1	US-S	0.0	718.0	191.0	76.0	5.0	8.0	464
	2	MX-F	0.0	644.4	571.5	176.4	13.6	4.0	1410
	4	MX-F	755.6	168.1	113.0	32.9	6.4	0.0	1076
1986	1	US-S	0.0	170.0	598.0	203.0	24.0	5.0	790
	2	MX-F	0.0	476.9	130.0	57.2	13.2	2.6	680
	3	MX-F	90.5	828.6	67.3	9.3	3.2	1.1	1000
	4	MX-F	779.2	292.7	58.6	21.6	8.0	0.0	1160
1987	1	MX-F	0.0	468.0	33.0	7.0	4.0	0.0	512
	2	MX-F	0.0	1852.6	364.3	129.5	44.9	24.7	2416
	3	MX-F	885.0	960.5	169.5	83.1	13.4	25.5	2137
	4	MX-F	2191.8	721.9	1387.1	243.6	36.3	6.4	4587

Fishery age composition is in numbers of fish at age. Fractional fish are due to the weighting of raw monthly age compositions by the monthly landings. Survey age composition is expressed in thousandths and should be scaled by *N* aged.

the level of recruitment and number of age 0 fish. A temperature-dependent fraction of these recruits contributes to the coming winter's spawning biomass (Methot, in press).

Four periods were defined in each year, based on distinct changes in monthly landings, age composition, and weight at age (Methot and Lo 1987) (tables 2-5). Within each period, monthly age

composition and weight-at-age data were weighted by the total landings for that month before combining with other months in the period. The U.S. non-reduction fishery landings were similar to 1986, and weights at age were assumed to be equal to the historical mean (table 2) (Methot and Lo 1987). The four periods of the 1987 Mexican fishery are similar to 1986 except for month 4–5, when 1987 landings are higher than for the same period of 1986 (tables 3 and 4). The weight at age in the fourth period is significantly smaller than the long-term average for fish of age >2 (table 4). In particular, the mean weight of four-year-old anchovy was only 14.4 g, whereas the average from 1974–86 was 17.9 (SD = 1.96); these fish were born in the El Niño year of 1983. The fraction of age 0 fish in the Mexican fishery in the last period in 1987 was 0.48 as compared to 0.67 in 1986 (table 5).

#### **Modified Historical Egg Production Index**

Spawning biomass of northern anchovy is measured most accurately by the egg production method (EPM), which was used during the period 1980–85. This method measures the abundance of newly spawned eggs and the rate at which mature adults are producing eggs. Estimates of the abundance of newly spawned eggs before 1980 were made by Lo (1985), using data from CalCOFI surveys. This index of historic egg production (HEP) included samples from approximately San Francisco, California, to Punta Baja, Baja California (30°N) during January–April (figure 2). The egg production values and mortality rate were estimated by the solutions to two equations: the abundance of eggs as the integral of mortality curve, and newly hatched larvae as the eggs at hatching time.

Beginning in 1985 the CalCOFI survey pattern changed. The frequency of surveys was increased from almost monthly every three years to quarterly each year, and the geographic extent was restricted to CalCOFI lines 77.0 (rounding off from 76.7, Pt. Buchon, California, north of Pt. Conception) to 93.0 (rounding off from 93.3, Del Mar, California, north of San Diego; figure 2). This change required a recalibration of the HEP index because the mean egg density in this restricted area is not expected to be the same as the mean density in the larger area. Since 1980, only samples collected during February–March have been used for this revised index, because this is the period during which subsequent data are expected to be collected.

The modified historical egg production (MHEP) index was derived from the egg mortality curve:  $P_t = P_0 \exp(-zt)$ , where  $P_t$  is the abundance of some

life stage (or size category) corrected for the duration of that stage, and  $z$  is the mortality rate. By rearranging the terms in the equation, one obtains  $P_0 = P_t \exp(zt)$ , and an estimate of  $P_0$  can be computed if the egg mortality rate ( $z$ ) and at least one age-specific egg production are known. Because of the reduced sample size in the modified survey area, estimates of  $z$  were taken from Lo (1985) for years before 1986, and were computed from staged eggs sampled from the current CalCOFI survey area for years after 1985 (table 1).  $P_t$ 's can be computed from egg and larval data from the modified survey area. We have for the historical data set two  $P_t$ 's that are reasonably close in age to the age at spawning; one for the egg stage ( $P_{\text{egg}}$ ) and the other for the yolk-sac larvae ( $P_{\text{ys}}$ ). The historical anchovy data base provides only the standing stock of anchovy eggs, with no information on the distribution of egg stages. To obtain an average egg production rate, we divided the standing stock by the average temperature-specific incubation time to obtain the egg production rate ( $P_{\text{egg}}$ ) at the mid-age ( $t_{\text{egg}} = \text{incubation time} / 2$ ). From the mortality curve fit to sized larvae (Lo 1985), we estimated the larval production rate at the age of yolk absorption ( $P_{\text{ys}}$ ). Assuming that eggs and yolk-sac larvae suffer the same mortality, two initial egg production estimates were computed as follows:

$$P_{0\text{-egg}} = P_{\text{egg}} \exp(zt_{\text{egg}})$$

and

$$P_{0\text{-ys}} = P_{\text{ys}} \exp(zt_{\text{ys}}).$$

The MHEP egg production index is the average of the above two estimates:

$$\text{MHEP} = (P_{0\text{-egg}} + P_{0\text{-ys}}) / 2$$

The variance of MHEP was computed as

$$\text{var}(\text{MHEP}) = [\text{var}(P_{0\text{-egg}}) + \text{var}(P_{0\text{-ys}})] / 4.$$

To compute the MHEP index for 1988, we used a total of 58 plankton samples on the Jan. 19–Feb 2, 1988, CalCOFI cruise (Methot and Lo 1987). Anchovy eggs were collected with the CalCOFI vertical egg tow (CalVET) plankton net (Smith et al. 1985). The mouth area of the net is 0.05 m<sup>2</sup>. The mesh size of 0.15 mm is the maximum size to retain all anchovy eggs. The standard net tow is a vertical cast to 70 m in 1 minute, held at depth for 10 seconds, and retrieved in 1 minute. The larval data were obtained from bongo oblique net tows (figure 2). In the past 30 years, different gears were used to

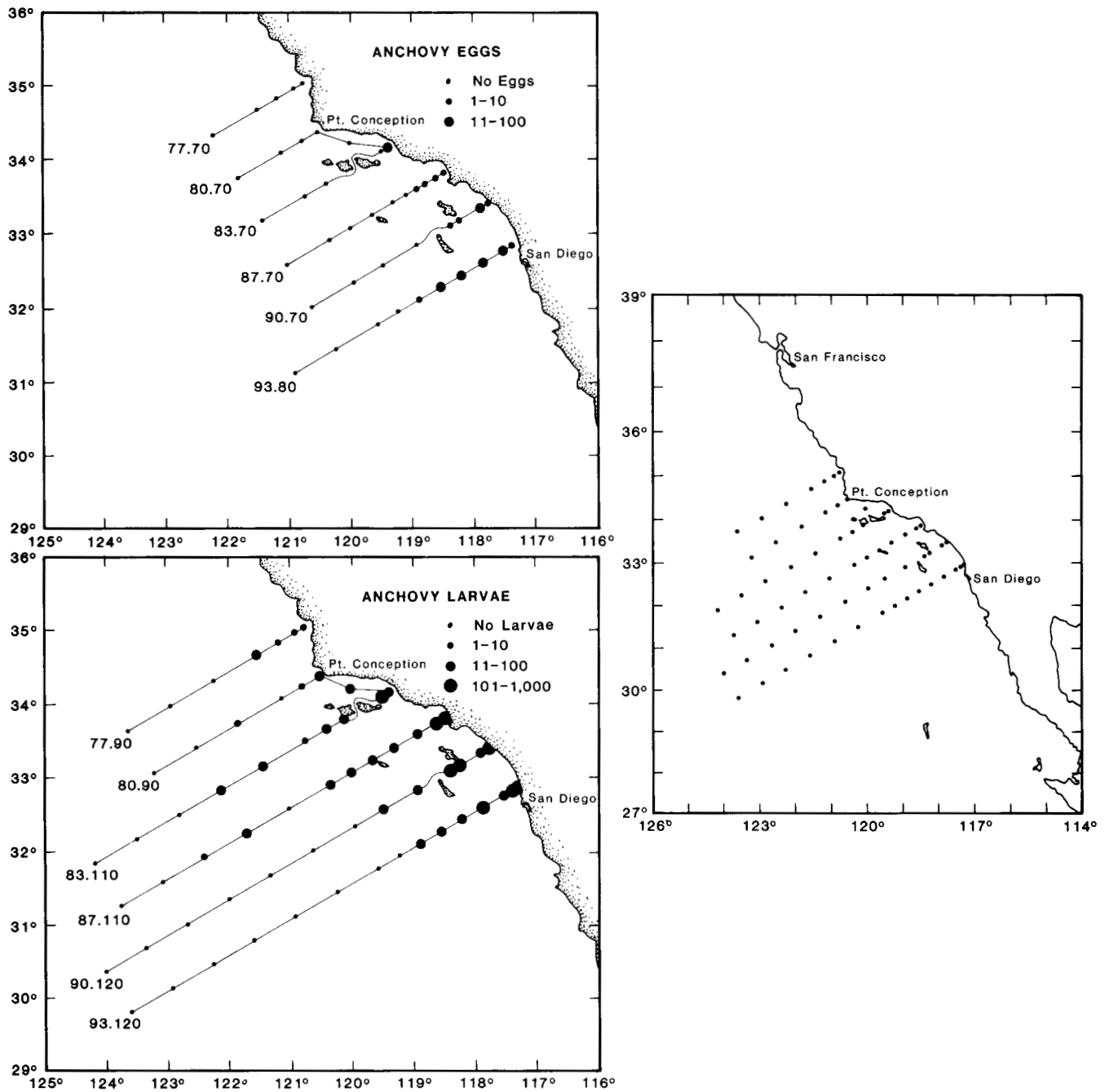


Figure 2. The map on the right shows the CalCOFI survey pattern since 1985 from Point Buchon, north of Point Conception, to Del Mar, north of San Diego, compared to the historical survey area from San Francisco to Punta Baja, Baja California. The maps on the left show the distribution of anchovy eggs and larvae from the 1988 CalCOFI survey. The number at the end of each line is the line and station number. The egg samples cover stations up to 70, except line 93.

collect anchovy eggs and larvae for CalCOFI surveys. Calibration factors were used to standardize egg and larval catch (Lo 1985).

As mentioned earlier, the MHEP takes the average of two daily egg production rates, one based on eggs and the other on yolk-sac larvae. Both egg production rates incorporate the daily egg mortality ( $z$ ), which was computed from staged eggs (table

1). Analysis of the number of eggs and yolk-sac larvae taken during the 1988 CalCOFI cruise indicated a daily egg mortality of  $-0.53$  per day in 1988.

The estimated egg production rate for 1988 was  $6.9/0.05 \text{ m}^2/\text{day}$  ( $SE = 3.42$ ), similar to  $7.2$  ( $SE = 2.57$ ) in 1986 and  $7.6$  ( $SE = 3.34$ ) in 1987. The biomass in 1988 appears to be higher than it was during the 1980–85 period, because in 1980–85 the average

TABLE 6  
 Time Series of Environmental Deviations and Weight-at-Age Deviations

Year	Qtr.	Temp.	WTDEV-US	WTDEV-MX	Year	Qtr.	Temp.	WTDEV-US	WTDEV-MX
1964	2	.900			1976	5	-.412	2.77	
	5	-.935				8	-.259	0.69	
	8	-.402				11	1.539	0.03	
	11	-.797				1977	2	2.144	—
1965	2	-1.122			5		-.282	0.28	
	5	.295			8		-.508	1.17	
	8	-1.351			11		.474	1.12	
	11	.020			1978	2	1.562	—	
1966	2	-.074				5	1.181	—	
	5	.274				8	-.422	0.91	1.13
	8	.532				11	.783	0.85	2.48
	11	-.065			1979	2	-.546	—	—
1967	2	-.178	0.34			5	-.301	0.95	0.44
	5	-.680	0.56			8	.157	—	0.33
	8	.021	—			11	.086	2.01	-0.11
	11	1.050	—		1980	2	.524	—	—
1968	2	-.005	—			5	.296	-0.18	0.37
	5	.142	—			8	-.999	—	0.70
	8	-.007	—			11	-.883	-1.26	1.26
	11	-.040	0.79		1981	2	.242	—	—
1969	2	-.141	1.01			5	1.061	-0.44	-0.43
	5	-.547	-0.29			8	1.472	—	-1.03
	8	-.563	—			11	.073	-0.74	0.19
	11	-.283	1.99		1982	2	-.093	—	—
1970	2	-.124	1.68			5	.282	0.51	1.30
	5	.059	0.18			8	-.131	—	-0.20
	8	-.403	2.37			11	.559	—	0.53
	11	-.107	1.95		1983	2	1.393	—	-2.29
1971	2	-.819	2.95			5	.808	—	-3.07
	5	-1.580	1.38			8	.200	—	-2.91
	8	.958	—			11	1.965	—	-3.90
	11	-1.022	-1.23		1984	2	.924	—	-2.99
1972	2	-1.716	-0.25			5	1.091	—	-1.72
	5	-.164	-1.31			8	2.184	—	-1.92
	8	.451	—			11	2.000	—	-2.22
	11	.156	-2.90		1985	2	-.427	—	—
1973	2	1.051	-4.67			5	.015	—	2.94
	5	-.354	-2.62			8	.614	—	4.59
	8	-.489	-2.37			11	.953	—	1.63
	11	-1.285	-0.45		1986	2	.602	—	—
1974	2	-1.114	-2.30			5	1.258	—	-1.07
	5	-.494	-1.20			8	.130	—	1.44
	8	-.425	—			11	.734	—	-0.45
	11	.185	-1.06		1987	2	1.230	—	0.00
1975	2	-1.041	1.34			5	1.355	—	-0.34
	5	-1.668	2.40			8	-.718	—	0.48
	8	-1.481	0.47			11	1.566	—	-0.01
	11	-1.494	0.69		1988	2	-.083	—	—
1976	2	-.646	2.12	5		1.198	—	—	

Deviations are calculated from monthly means, then averaged into quarters. Environmental deviations are lagged -1 month (e.g., quarter 1 contains average Dec.-Feb. deviation). Temp. is the surface temperature at the SIO pier. WTDEV-US and WTDEV-MX are average weight-at-age deviations for ages 2-4 based on data from the commercial reduction fishery at San Pedro in the United States and ages 1-3 at Ensenada in Mexico.

daily egg production rate was only 3.1 if one assumes that the adult reproductive output in 1988 is similar to the average of 1980-85 (table 1).

**Environmental Data**

Temperature anomalies at the SIO pier were used as an indicator of environmental changes (table 6). During Jan.-Feb. 1988, the mean temperature at the

SIO pier was 13.9°C, whereas it was 15°C in 1987 and 15.2°C in 1986 (figure 3). Monthly temperature deviations were averaged into trimonthly periods to be compatible with age-composition data. Two series of temperature indexes were derived from these temperature anomalies. The first series comprised short-term temperature indexes, which averaged the current and previous anomaly, with the

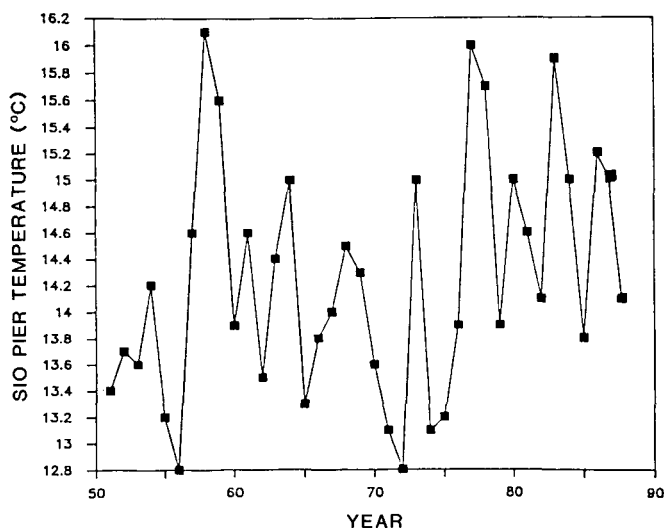


Figure 3. Time series of Jan.-Feb. water temperature (°C) at SIO, 1951-88.

current anomaly having twice the weight of the previous. The second series comprised long-term temperature indexes, which used the current and 15 previous quarters with a linear weighting scheme, with the current value having a weight of 16. The first, high-frequency series was detrended by subtracting the second series from it.

The 1987 SS model also includes time series of weight-at-age deviations, which are used to model the availability to the fishery. Methot and Lo (1987) note that the fraction of age 3+ fish in the Mexican fishery was never greater than 0.02 when the weight of the age 2 fish was less than 12 grams. Appearance of small fish is an indication that the stock has shifted northward, thus a clue that availability to the geographically fixed fisheries should be modified. The weight-at-age deviations for the United States were reproduced from Methot and Lo (1987). The weight-at-age deviations for the Mexican fishery were recomputed by adding 1987 weight at age to the data set (table 6). Availability parameters were modeled as linear functions of environmental and weight deviations.

Methot (1986, in press) presents a relation between percentage of mature fish and temperature at the SIO pier. In 1988, at 13.9°C, the temperature-maturity relation indicates that 63% of the age 1 fish are sexually mature, and 33% of them are actively spawning according to the relationships:

$$\text{Fraction mature at age 1} = \frac{\exp(-33.4 + 2.44 \text{ temp})}{[1 + \exp(-33.4 + 2.44 \text{ temp})]}$$

and hence contribute to spawning biomass.

$$\text{Fraction of age 1 spawning} = \frac{\exp(-17.51 + 1.21 \text{ temp})}{[1 + \exp(-17.51 + 1.21 \text{ temp})]}$$

and hence contribute to the MHEP index.

One of the major sources of natural mortality of northern anchovy is believed to be predation by Pacific mackerel (Methot 1986). Pacific mackerel biomass was estimated to be 500,000 MT on July 1, 1987 (Methot and Lo 1987), and projected to be 290,000 MT on July 1, 1988 (Patty Wolf, CDFG, pers. comm.). The decrease of biomass was possibly due to the changed estimation procedure. (The historical time series of Pacific mackerel biomass are being reexamined; the results are not available at the time of this writing.) At the level of 290,000 MT of mackerel biomass, the model specifies that natural mortality of anchovy increases from the nominal level of 0.6 to a level of 0.7 per year.

## RESULTS AND DISCUSSION

The spawning biomass in February 1988 is estimated to be 1,009,000 MT (table 7, figure 4). Although this value is a slight decrease from 1,212,000 MT in 1987 (Methot and Lo 1987), it is still higher than the 1985 spawning biomass of 521,000 MT, estimated by the EPM. The high level of spawning

TABLE 7  
 Time Series of Estimated Biomass and Recruitment

Year	Total biomass	Spawning biomass	Recruitment
1964	782	773	0.46
1965	705	607	0.20
1966	537	511	0.15
1967	369	354	0.52
1968	353	334	0.48
1969	374	348	0.55
1970	391	301	1.72
1971	723	309	1.63
1972	1040	605	2.35
1973	1440	1412	2.37
1974	1720	1148	0.80
1975	1432	1251	0.32
1976	1011	970	1.12
1977	826	825	0.25
1978	443	442	2.12
1979	813	536	1.72
1980	763	756	1.52
1981	806	768	0.57
1982	470	428	1.70
1983	556	538	0.71
1984	382	376	1.53
1985	675	529	1.01
1986	636	630	2.27
1987	900	878	3.00
1988	1297	1009	0.62

Biomass estimates are in units of thousand metric tons as of Feb. 15 of the indicated year. Recruitment estimates are in units of 50 billion age 0 fish as of July 1 of the indicated year.

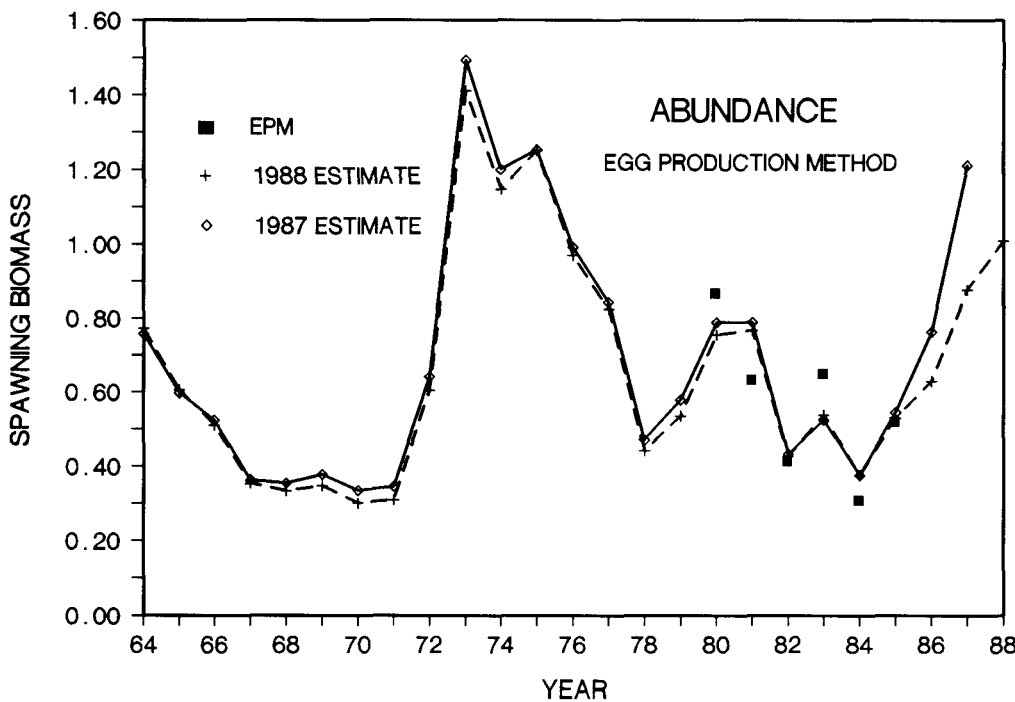


Figure 4. Estimated time series of spawning biomass, using data up to 1987, data up to 1988, and observations made by the egg production method.

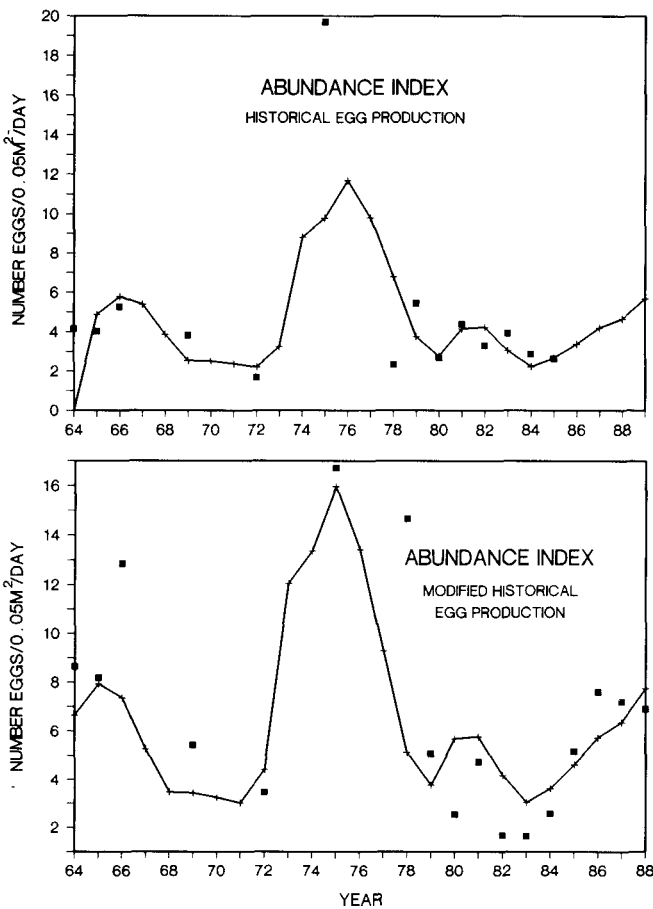


Figure 5. Estimated (squares) and observed (+) time series of historical egg production (Lo 1985) and modified HEP for the current CalCOFI survey area (see figure 2).

biomass was partially due to the high egg production rate estimated from MHEP (figure 5) and partially due to the strong incoming year class in 1987 (figure 6).

The SS model provided a time series of yearly biomass estimates (table 7). The computation of sample variance of the estimates, although it is technically feasible, has not been implemented in the model. Without variance estimates, it is impossible to judge the precision of the biomass estimate for a single year. However, a time series of biomass can indicate long-term change in the population, and it is useful for management.

The current estimate of the 1987 spawning biomass from the SS model using the 1964–88 time series is 880,000 MT; when the 1964–87 time series was used it was 1,212,000 MT (Methot and Lo 1987) (figure 4). Thus some uncertainties exist in estimating the magnitude of the 1986 and 1987 year classes. These year classes seem to be very abundant, because they dominate in the fourth-period Mexican fishery, even though their predicted availability to the fishery is one-third that of the 1984 and 1985 year classes (table 8). It is not surprising that the abundance of the second-year cohort differs from that of the first year, since the cohort in the second year is estimated from an additional year of age-composition data. For this reason, the first year's estimate of cohort biomass in the SS model will always be more uncertain than the subsequent year's estimate.

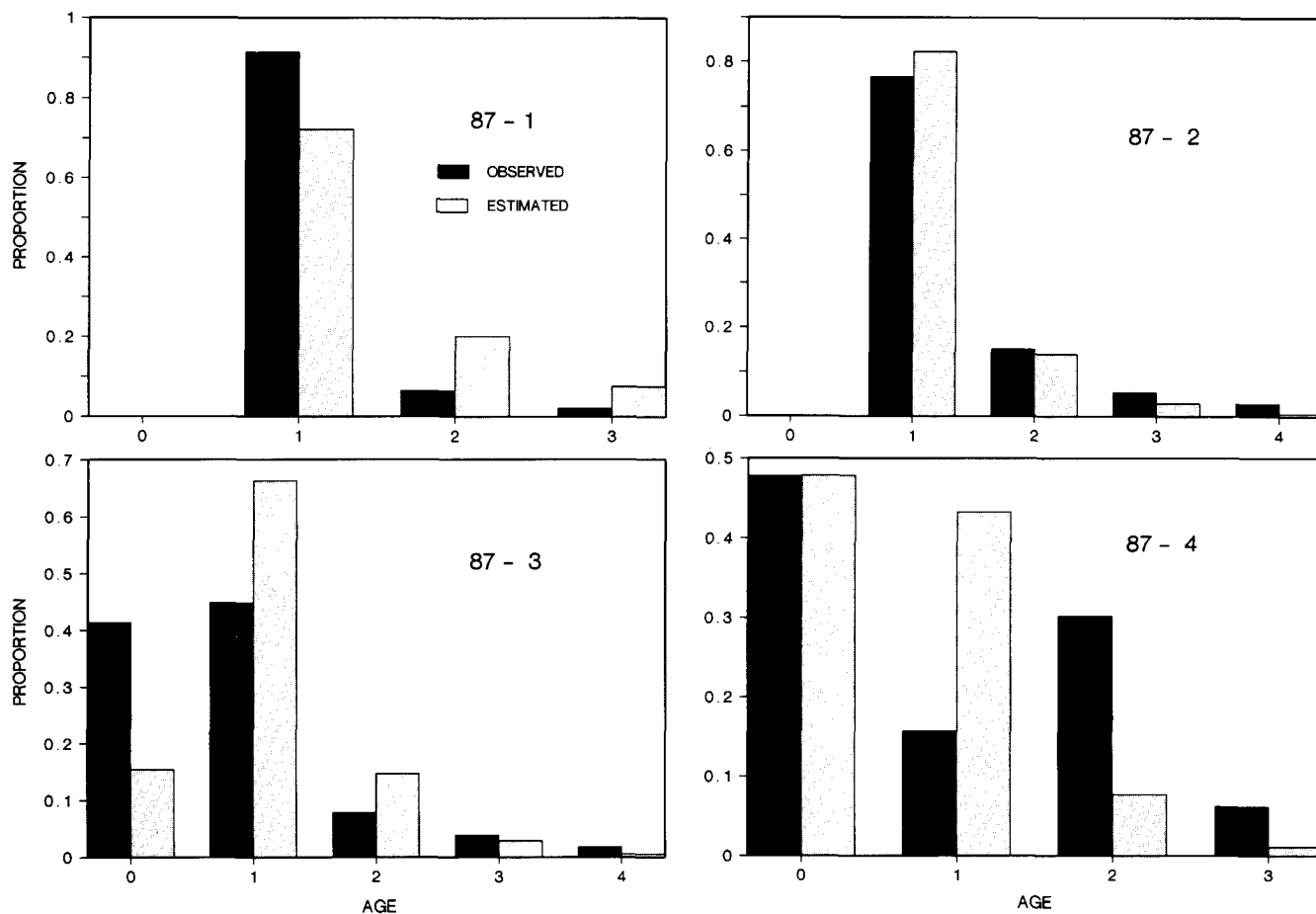


Figure 6. Observed and estimated age composition in 1987 for four periods: period 1, Jan.-Mar.; period 2, April and May; period 3, June and July; period 4, Aug.-Dec. (see table 3).

In the assessment conducted last year with data through the winter of 1987 (Methot and Lo 1987) the 1986 year class was fixed at a high value because when unconstrained, the model assigned an even higher value to the 1986 year class. The same situation occurred in the current assessment, which used data through winter 1988. In this case we fixed the abundance of the 1987 year class at a high value, and estimated the 1986 year class to be somewhat lower than the assumed large 1987 year class. Consequently, the revised estimate of the spawning biomass in 1987 declined when the additional year of data was included. This revised estimate of the 1987 spawning biomass, 880,000 MT, is nearly identical to the alternative estimate, 840,000 MT, made by Methot and Lo (1987) under the assumption that availability to the fourth-period Mexican fishery has been 1.0 since 1983.

The abundance of age 0 fish is difficult to assess because it is affected by two factors: the absolute abundance of age 0 fish in the population and the

availability of these fish to the Mexican fishery. The availability of juvenile anchovy to the Mexican fishery is a critical parameter in the SS model. The abundance of juveniles relative to older fish in this fishery fluctuates because of year-to-year changes in the true relative abundance of these new recruits, and because of changes in their availability to the fishery. In the model, temporal changes in age-specific availability were assumed to be a function of long-term temperature trends, deviations from this trend, and deviation in weight at age. Estimated availability of these young fish to the Mexican fishery was very high during, and immediately following, the 1982-83 El Niño (table 8). Consequently, high incidence of young fish during this period is partially explained by their increased availability to the fishery. In the fourth periods of 1985, 1986, and perhaps 1987, the model predicts somewhat lower availability, while the abundance of age 0 fish stayed high. Thus the model indicates that the recruits of these three year classes were very abundant. We



TABLE 8  
 Recruitment to the Fishery at Ensenada, Mexico

Year class	Age 0						Age 1					
	Period 3			Period 4			Period 1			Period 2		
	O	E	AV	O	E	Av	O	E	Av	O	E	Av
1975	.017	.011	.004	.122	.026	.032	—	—	—	.070	.256	1.00
1976	.233	.091	.053	.666	.451	.468	.313	.576	.633	.337	.368	.211
1977	.039	.041	.007	.194	.198	.205	—	—	—	—	—	—
1978	.100	.152	.017	.732	.690	.194	—	—	—	.652	.692	.235
1979	.046	.146	.013	.365	.420	.162	—	—	—	.502	.447	.269
1980	.008	.065	.008	.350	.204	.048	—	—	—	.576	.488	.349
1981	.060	.103	.039	.251	.231	.160	—	—	—	.110	.338	.260
1982	.045	.159	.015	.481	.632	.215	.587	.767	.384	.899	.873	1.00
1983	.104	.111	.015	.480	.362	.376	—	—	—	.631	.656	1.00
1984	.274	.213	.043	.730	.755	.714	—	—	—	.457	.592	.326
1985	—	—	—	.702	.530	.725	—	—	—	.701	.708	1.00
1986	.091	.171	.028	.672	.544	.230	.914	.722	.549	.767	.824	1.00
1987	.414	.153	.027	.478	.473	.234	—	—	—	—	—	—

Note: Age 0 anchovy are partially recruited to this fishery in the third period of the year. They typically are fully recruited in the second period of the following year. The symbols indicate the observed ratio of recruits to total numbers in the Mexican fishery (O), the ratio expected by the model (E), and the estimated, environmentally sensitive availability used by the model (Av).

intend to reexamine the submodel that predicts availability from environmental deviations, but it seems unlikely that the generally good fit apparent in table 8 can be substantially improved.

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Part II

## SYMPOSIUM OF THE CALCOFI CONFERENCE

Lake Arrowhead, California

November 8, 1988

### CAN MARINE FISHERIES BE ENHANCED? POINT/COUNTERPOINT

Fisheries managers have only a few choices. We can limit the area fished, the season, the size of the fishery, or the size or age of the fish taken. But finally, traditional fisheries management distills down to one concept: controlling the impact on the stock, which translates into a "Thou shalt not" approach to regulation. It is my view that such methods have often proven to be ineffective at best. This is particularly true for many nearshore marine species.

Pelagic fishery managers can point to their successes. In California, the anchovy and, more recently, the sardine, Pacific herring, and Pacific mackerel are offered as shining grails of hope and enlightened management regimes. But as a jaundiced observer, admittedly unschooled in the arcane nuances of pelagic fish, I would offer that anchovy fishery management in California might have been successful, but only coincidentally with greatly reduced demand. The sardine fishery was never really managed until after its collapse. After almost two decades of moratorium, and four years of quota management, we are still unsure about the recent optimism concerning the recovery of this resource. Some fishery. . . . Some management. And yet the Pacific herring and Pacific mackerel fisheries, managed by quota based upon annual assessments, which vary in their scientific sophistication, have produced sustained yields that rival those of years gone by. These species/fisheries have at least two things in common, other than being pelagic: a long history of exploitation and, more important, research.

For most nearshore species this is not true. We have consistently been asked to manage their populations, knowing nothing much more than that they do indeed swim, and presumably reproduce (given appropriately low levels of DDT, PCB, and

other pollutants). This form of management has been likened to a cattleman attempting to manage his herd with no knowledge of its numbers, the number of cows in calf, the size or carrying capacity of his range, or indeed the extent to which his herd stays on his range and doesn't wander off to be harvested elsewhere.

It appears that this is probably going to continue for some time, unless we can begin to understand the dynamics and early life requirements of nearshore species as well as, or better than, those of pelagic species. This assumes that our politico-economic system will suddenly allow us the money to do what is necessary. I, for one, would be interested in my own behavior, if suddenly asked to "put up or shut up" — if actually offered the funds to do the job.

Without these funds we are, and have been, left with the choices of forging ahead, hopefully making incremental gains, by regulating gear, area, and size. This is all in the face of almost geometrically increasing pressures on these nearshore resources from burgeoning population and increasingly impacted or degraded habitats. We can continue on this course, or we can change direction and experiment with something new.

This year's CalCOFI symposium is an attempt to generate discussion among resource managers — discussion of nontraditional methods for improving stocks, in particular those of nearshore species. I believe in the potential of some of these concepts, but — as you must also — I see potential pitfalls. Therefore, when asked to put together this panel, I attempted to structure it in a point-counterpoint format. I was successful in getting speakers on both sides of each issue except for marine harvest refugia. Even though I could find no one to present any argument against the concept, few seem to want to

give it a try. Perhaps Gary Davis of the National Park Service, who presents that paper, is correct when he quotes Machiavelli. But that would be giving it away. When you have read his paper you may agree, not just with his hypothesis, but with the assessment of the risks involved in any unusual, and therefore uncomfortable, solutions.

My own professional interest, man-made reefs, is well debated by Ray Buckley from the Washing-

ton State Department of Fisheries and Jeff Polovina, NMFS-Hawaii. Marine fish hatcheries are discussed by Bill Rutledge of Texas Parks and Wildlife, who tells us they can work, and by Alec MacCall, NMFS, who insists they cannot. I hope you find these papers as stimulating as I have found working with the authors.

*John Grant*

## ARTIFICIAL REEFS: NOTHING MORE THAN BENTHIC FISH AGGREGATORS

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### ABSTRACT

The potential for artificial reefs to substantially increase standing stock of marine resources is considered. Three sources — the Japanese artificial reef program; relationships between fishery production and the area of natural habitat for several fisheries; and population dynamics — offer evidence that artificial reefs do not substantially increase the standing stock of marine resources.

### RESUMEN

Se considera el potencial de los arrecifes artificiales para aumentar sustancialmente el stock disponible de los recursos marinos. Tres fuentes de evidencia: el programa de arrecifes artificiales japonés, la relación entre producción y área del hábitat natural de varias pesquerías, y la dinámica de poblaciones, indican que los sustratos artificiales no aumentan sustancialmente el stock disponible de los recursos marinos.

### DISCUSSION

Artificial reefs can be excellent fish aggregators, but they do not effectively increase standing stock. This position will be supported with three types of evidence: first, with observations from the Japanese artificial reef program; second, from the relationship between habitat and fishery production; and finally from considerations of population dynamics.

Between 1976 and 1987, the Japanese spent U.S. \$4.2 billion to construct and deploy 6,443 artificial reefs, covering 9.3% of the ocean bottom from shore to a depth of 200 m (Yamane, in press). But despite this enormous volume of artificial reefs deployed in coastal water, there has not been any measurable increase in coastal fishery landings (Japan: Statistics and Information Department 1984). Studies specifically investigating the impact of the artificial reefs have generally not documented any significant increases in fish production that can be attributed to the reefs (Kawasaki 1984; Kakimoto and Okubo 1985). After three visits to Japan and numerous discussions with people involved in all aspects of the Japanese artificial reef program, I be-

lieve the real benefit of the reefs is that they aggregate wide-ranging fishes close to shore so they can be harvested by fishermen with small vessels and thus keep the fleet of small vessels economically viable.

Outside of Japan, artificial reefs have not been deployed on a large enough scale to evaluate their effectiveness in increasing standing stocks. However, examining the relationship between habitat and fishery production can provide estimates of the level of fishery yield per area of habitat that might be expected from appropriately designed and sited artificial reefs. One example is penaeid shrimp: worldwide fishery yields range from 8 to 200 kg/hectare of intertidal nursery habitat (Turner 1977). In the case of artificial reefs, yields are measured in production per unit of reef volume. Thus if a square meter of intertidal habitat is assumed to also contain about a meter of vertical structure, grass, or mangrove, then these yield figures are equivalent to 0–0.02 kg/m<sup>2</sup>. Another example is the coral reef systems, from which fishery yields have been reported in the range of 5–20 t/km<sup>2</sup> (Marten and Polovina 1982). If one square meter of coral reef habitat is conservatively assumed to be equal to one cubic meter of reef volume, then production per volume of reef habitat is 0.005–0.02 kg/m<sup>3</sup>.

To put this production-per-unit-of-habitat volume in perspective, I will relate it to an example from California, where recent annual commercial landings for rockfishes are about 15,000 metric tons (MT) (California Department of Fish and Game 1987). I will assume that the average figure for fishery production per habitat volume from coral reef fisheries, 0.01 kg/m<sup>3</sup>, can be applied to rockfishes. I will further assume that artificial reefs can be ten times more effective than natural habitat that might include barren or unproductive areas. With a level of fishery production of 0.1 kg/m<sup>3</sup> of habitat volume, it would require 15 million m<sup>3</sup> of artificial reefs to increase the annual rockfish catches by 10%. At the extremely low cost of \$10/m<sup>3</sup> of reef for construction and deployment, this would cost \$150 million. To put 15 million m<sup>3</sup> of artificial reefs into perspective, consider a space 100 × 50 m, about the

size of a football field, covered with 1-m cubes. One such field would contain 5,000 m<sup>3</sup>; therefore, 3,000 such fields covered with 1-m cubes would equal 15 million m<sup>3</sup>. Of course the major flaw in this brute force approach to fishery enhancement is that even if this enormous volume of artificial reefs was built and deployed, any benefits would not be noticeable, because landings annually fluctuate by 10% to 20%. That is exactly one of the lessons the Japanese learned with their \$4.2 billion experiment.

There is also the question of which resources lose habitat when low-relief habitat is covered with artificial reefs. There is a perception that low-relief habitat is not used by important commercial species, whereas high-relief habitat is preferred by valuable species. This is often based on the observation that the adults are seen and caught in high-relief habitat. This has been commonly accepted in Hawaii, but recently, when correct sampling gear was used, the juvenile habitat of the very valuable deepwater snappers was found to be the low-relief, flat-bottomed, sandy habitat, which had been considered a biological desert. Large-scale deployment of artificial reefs on this flat, sandy-bottom habitat would have attracted shallow-water reef fishes at the cost of destroying juvenile habitat for the more commercially valuable deepwater snappers. In Japan, a study around an artificial reef site found that the artificial reef attracted some species and repelled others and that the effectiveness of the reef could be negative, depending on which species were attracted or repelled (Kawasaki 1984).

The wide ranges in the levels of fishery production per area of habitat suggest that, although habitat is necessary, it is not limiting to production. Current research suggests that for many species, population size is determined during the larval rather than benthic phase. For example, the adult population of the Caribbean coral reef fish, *Thalassoma bifasciatum*, is determined primarily by recruitment and not by the supply of space on the reef (Victor 1983). In another study, the survival of juvenile reef fishes was estimated for varying levels of recruitment, and survivorship appeared constant— independent of juvenile density on the reef (Sale and Ferrell 1988). These studies indicate that even for coral reef fishes that require reef habitat during juvenile and adult phases, more reef habitat would not increase standing stock.

Insight into whether a resource can be enhanced with artificial reefs can be obtained from the relationship between larval settlement density and fishery catches. If the relationship is linear, then the same percentage of the larval settlement is caught

by the fishery, independent of density. However, if the fraction of the settled larvae, which ultimately contribute to the fishery, declines as the density of settled larvae increases, then density dependence may be a factor, and artificial reefs, which provide additional habitat and reduce the density at some stage, may increase fishery production. A relationship between larval settlement and fishery catches is available for a spiny lobster (*Panulirus cygnus*) fishery in western Australia (Phillips 1986). This relationship is linear, indicating that the same fraction of the settled larvae are captured as adults by the fishery, independent of the level of larval settlement. Thus, even for a spiny lobster which requires shelter, larval settlement is the limiting factor to production, and even at high postlarval densities, habitat is not limiting to fishery production.

Artificial reefs are often suggested as a solution to overfishing. Yet they do not help if either growth or recruitment overfishing is occurring. In the case of growth overfishing, they may aggregate younger fish, making them more vulnerable to capture and actually increasing overfishing. In the case of recruitment overfishing, standing stock is a fraction of its unexploited level, and habitat is certainly not limiting. Aggregating adults further simply increases catchability, and hence fishing mortality, which further reduces the spawning stock biomass.

Reefs are popular as management options because they do not require reductions in fishing effort and they aggregate fish, resulting in higher catches in the initial stages. Thus artificial reefs may actually be detrimental to the fishery and the stock simply because they allow managers to delay making hard but necessary decisions, such as imposing size limits or reducing effort.

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## HABITAT ALTERATIONS AS A BASIS FOR ENHANCING MARINE FISHERIES

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### ABSTRACT

Artificial reefs and fish aggregating devices (FADs) can be used to alter marine habitats to increase fishery productivity. Artificial reefs enhance marine fisheries through both aggregation and production of marine resources. FADs can also enhance resource production. Most artificial reef designs do not completely replicate natural reef habitats. Considerable artificial reef construction has been in response to incentives for solid waste disposal. Recruitment and survival of juveniles is restricted because of the prevalent use of "materials of opportunity" for constructing artificial reefs. FADs are usually lost as a result of inadequate design and engineering. Funding has been haphazard and inadequate for developing artificial reef and FAD technologies. Most applications lack realistic, justified fishery enhancement objectives as the incentive for altering habitat. Solving these major constraints will make it possible to evaluate habitat-alteration technologies as a basis for enhancing marine fisheries.

### RESUMEN

Los arrecifes artificiales y los aparatos para agregar peces (AAPs) pueden ser usados para modificar hábitats marinos, con el fin de aumentar la productividad en peces. Los arrecifes artificiales acrecientan las pesquerías marinas a través tanto de la agregación como de la producción de los recursos marinos. Los AAPs también pueden mejorar la producción del recurso. La mayoría de los arrecifes artificiales no duplican completamente el hábitat de los arrecifes naturales. Muchos arrecifes artificiales se construyeron como respuesta a incentivos formulados para disponer de los desperdicios sólidos. El reclutamiento y la supervivencia de juveniles se ha visto restringida por el uso generalizado de "materiales de oportunidad" en la construcción de arrecifes artificiales. Se pierden AAPs como resultado de diseño e ingeniería inadecuados. La financiación para el desarrollo de tecnologías de arrecifes artificiales y de AAPs ha sido impredecible e inadecuada. Muchos de los usos no tienen objetivos prácticos y justificados de acrecentamiento de las pesquerías

como incentivo para alterar el hábitat. Si estas restricciones principales se solucionan será posible la evaluación de la tecnología de alteración de hábitats como fundamento para acrecentar las pesquerías marinas.

### INTRODUCTION

If we eliminate from consideration the obvious enhancement successes enjoyed in anadromous fishery resources, then it is a true statement that current technology provides few options for enhancing marine fisheries. The most historically viable technique is to use the spectrum of regulations to control harvests, but these restrictions are limited in power to increase the resources available for harvest, or to affect the temporal or spacial distribution of these resources.

The successful enhancement of anadromous fishes is linked to artificial production in hatcheries. This technique supplements natural levels of recruitment of juveniles, which can dramatically increase the resources available for harvest if the other factors necessary for survival are not restricted in the natural environment. Marine fish hatcheries may be a functional and productive enhancement technique for the few species that have accessible spawning aggregations, culturable embryonic and larval development, and adaptable juvenile rearing stages, if (and it is a big if) fishery demand for these species justifies continual large amounts of capital and operational funding. So far, all of these factors have been satisfied for only one species in the United States — red drum (*Sciaenops ocellatus*) (Rutledge 1989).

Preserving critical, productive natural marine habitats is rapidly being recognized as the key to preserving and enhancing marine resources and the dependent fisheries (the marine ecosystem is finally being realistically defined as critically finite). The National Marine Fisheries Service has requested that regional fisheries management councils consider adopting a marine habitat policy to "Conserve, restore and develop habitats upon which commercial and recreational fisheries depend, to increase their extent and to improve their productive

capacity. . . ." (Anon. 1988). The third of the three objectives supporting this policy is to "create and develop productive habitats where increased fishery productivity will benefit society."

Altering marine habitats to increase fishery productivity is well within current technological capabilities. The two most prominent forms of marine habitat alterations — artificial reefs and fish aggregating devices (FADs) — can be used to enhance marine fisheries by increasing the amount of marine resources available for harvest, and by controlling the temporal and spacial distribution of these resources (Buckley and Hueckel 1985; Wilson and Krenn 1986; Alevizon 1988; Buckley et al. 1989; Polovina and Sakai 1989; and many others; see Buckley et al. 1985). Evidence is mounting that biological development on artificial reefs can also supplement natural production and recruitment of reef-related species. The capital costs for artificial reefs and FADs *can be* low relative to other enhancement options, and operational costs *can be* in the range of miniscule to moderate. However, to be completely objective and honest, it is necessary to point out that the validity of these statements is directly related to the "can be" provisos. Attempts to apply these habitat alterations have been both effective and ineffective in enhancing marine fisheries. Further, the level of effectiveness appears to be directly correlated with the amount of science included in applying and evaluating these technologies.

This may seem to be so obvious a correlation that it is trivial; however, it is disturbingly common to find artificial reef and FAD projects that do not have enhancement of marine fisheries as the real objective. These projects are conceived and implemented with methods ranging from absolutely no science to sloppy science at best. It is even more disturbing when these "nonscientific applications" are cited in the attempts to assess the values of these technologies as fishery enhancement and management tools. This error is compounded when poorly conceived projects and inappropriate evaluations are recycled in new evaluations; it seems that the learning curve has had insignificant slope.

## ARTIFICIAL REEFS AND FISH AGGREGATING DEVICES

The real potential for using artificial reefs to enhance marine fisheries that target benthic and semi-pelagic resources has eluded most fishery managers, at least until recently. Little definitive research has been conducted on practical applications of artificial reefs since their rise to a certain level of prominence in the 1960s. As late as 1983 a comprehensive review

of the research indicated that the potential of artificial reefs for improving fishery resources would only be realized when emphasis was shifted from construction and qualitative studies to quantitative analyses of governing biological and ecological factors (Bohnsack and Sutherland 1985).

There has been a recent evolution, on a multiregional scale, toward designing and evaluating artificial reef projects that target on specific questions about resource enhancement, particularly recruitment and survival of juveniles<sup>1</sup>. Recent research has shown that, when applied correctly, this technology creates long-term, if not permanent, alterations of benthic habitats, which develop biologically into replicates of productive natural reefs (Buckley and Hueckel 1985; Wilson and Krenn 1986; Alevizon 1988; and others). These alterations enhance the aggregation and production of important resources at locations that are atypical of the natural system. Artificial reef technology gives fishery managers some degree of power to direct the marine ecosystem and selected biota toward desired responses, which can be immediate and far-reaching in both time and area. These changes can increase the accessibility and fishability of traditional or new resources, and alleviate problems of fishery interaction by redistributing competing fisheries.

The potential for FADs to enhance marine fisheries for pelagic species has not eluded fishery managers as completely as the potential of artificial reefs. But there has been even less definitive research on this technology. The enthusiasm for using anchored buoys to enhance catches seems to be based on the successful use of *payaos* (bamboo rafts) in the Philippine purse seine fishery for tuna in the early 1970s (Matsumoto et al. 1981). The widespread use of FADs has received considerable funding from various states and nations, even though there was little, if any, scientific evidence that FADs met the fishery enhancement objective.

The first multiyear, quantitative assessment comparing FADs, offshore banks, and open-water areas was completed in 1987 in the tropical South Pacific (Buckley et al. 1989). This study verified the potential for correctly sited and engineered FADs to enhance marine fisheries to a level comparable to large, productive, offshore banks. When applied correctly, this technology provides the only practical method for increasing the accessibility of pelagic marine fish resources by affecting the movements

<sup>1</sup>Compilation of this research is presented in the Proceedings of The Fourth International Conference on Artificial Habitats for Fisheries, Bulletin of Marine Science, University of Miami, volume 44(2), March 1989.

of wandering schools of fish. This development of new, productive fishing locations is a powerful management tool for increasing catches while decreasing searching time, and for affecting the distribution of the fisheries.

### WHAT IS THE PROBLEM?

An obvious question is, "Given the potential that artificial reefs and FADs have for meaningful enhancement of marine fisheries, why haven't these habitat alterations been integrated into comprehensive fishery management programs in the United States to a greater degree?" The answer seems to be centered on the perpetuation of our early decision that these technologies could be applied by amateurs, and at little cost! This resulted in a disregard for science and adequate funding, which created a preponderance of haphazard, unsuccessful applications to serve as the basis for evaluating the potential of these technologies. The facts are that until recently these habitat alterations have not been advanced as serious methods for enhancing marine fisheries.

The situation with artificial reefs has been superbly stated in the excellent editorial "The Rediscovery of the Free Lunch and Spontaneous Generation: Is Artificial Reef Construction Out of Control?" (Bohnsack 1987). Artificial reef programs in the United States are characterized as "poorly or haphazardly funded, and in the best of American traditions depend on voluntary community involvement with donated labor and surplus 'materials of opportunity.' Emphasis is on minimizing short-term expenses." The policy controlling artificial reef applications, as well as the need for evaluations, is established by individuals with little fisheries experience or training, and is "often based on meager anecdotal information or whim." The regulatory agencies involved give only incidental consideration to biological impact and fishery management issues, and there are no significant requirements for monitoring or evaluating artificial reefs.

The home base for the editorial, Florida, is probably the best example of the worst type of artificial reef program in the United States. Florida has almost 300 sites permitted for artificial reef construction, and claims to be the national leader based on the number of reefs. Unfortunately, Florida did not put forth concurrent effort to establish realistic fishery enhancement objectives for the projects, or to evaluate the resulting benefits or impacts. In fact, in Florida, "state funding of [artificial reef] projects is restricted to cleaning materials; use of funds for re-

search, monitoring, or buying materials is prohibited!" (Bohnsack 1987).

It must be added that Florida does not deserve total responsibility for establishing this approach to artificial reef projects in the United States. Virtually all other coastal states have contributed by actively importing this flawed technology, or inventing their own mistakes, factors that have perpetuated past errors and discouraged improvement and refinement of the technology. As late as 1987, Oregon was considering a permit request to construct a large artificial reef in the ocean using materials of opportunity, with one of the objectives being to determine if the materials were "being buried or moved by waves or currents" (Buckley 1989).

It should not be surprising to learn that the home base for this paper, the Pacific Coast, has probably the two best examples of the best type of artificial reef program in the United States. Washington has virtually eliminated past policy errors that allowed artificial reef construction by diverse state agencies and the private sector, with no specific, testable fishery enhancement objectives. This habitat alteration is now controlled by the Department of Fisheries as a resource enhancement and management tool with potential impacts and benefits. An agency policy for artificial reef construction establishes criteria for fishery enhancement objectives, baseline surveys, biota-index-based siting, reef-to-natural-substrate ratios, and long-term monitoring (Buckley 1982). There are 11 active artificial reef sites in Washington, all intended to enhance specific urban recreational fisheries.

California, the site of some of the original applications of science to artificial reef projects, has recently reestablished its prominence in this field. Under the leadership of the Department of Fish and Game, a comprehensive Reef Plan, requiring specific objectives, has been promulgated to all state agencies involved in applying artificial reef technology. Current artificial reef projects are well funded for both construction and research, and they are based on the findings from several years of evaluations. The designs of a recent major series of artificial reefs, sited in three locations, incorporate many of the factors critical for accurately assessing the potential of this technology for resource enhancement.

Although most of the artificial reefs in the United States have ostensibly been to improve fisheries, many are "little more than disguised solid waste disposal programs, tax write-offs, or public relation gimmicks" (Bohnsack 1987). This fact is emphasized by the variety of junk, waste material, and

garbage that has been used for construction, as well as the questionable objectives of maximizing the amount of material deposited or area covered. "Many of these reefs are of questionable value and in fact may have future detrimental impacts" (Bohnsack 1987). The best method for judging the fishery enhancement value of these artificial reefs is to determine which really came first, the excess solid waste, or the need for resource enhancement. It is clear that the solid waste disposal incentive has been and still is the reason that artificial reef projects fail to effectively enhance marine fisheries. For many, the terms *artificial reefs* and *solid waste disposal* are synonymous; visualize the 70-mile-long "artificial reef" being proposed in the Caribbean by Waste Central, Inc. of Philadelphia (Morrissey 1988). Is it any mystery why this technology lags so far behind its potential to enhance marine fisheries, and fails to receive adequate funding?

The history of how FADs got to where they are is less well documented; however, there are disturbing similarities with artificial reefs in the early use of "materials of opportunity," volunteer labor, and haphazard funding, all applied to projects with no testable objectives for enhancing fisheries. Perhaps the early applications of this technology followed the same pattern of thought. Clearly, the needed engineering and design, monitoring and research, and fishery management infrastructures are either not established or are not well funded in the majority of FAD programs in the United States. Hawaii has the most successful and largest FAD program, which seems to be correcting past errors in engineering and design to improve FAD durability; however, long-term, quantifiable assessment of the fishery enhancement objectives appears to be lacking (Matsumoto et al. 1981; Shomura and Matsumoto 1982; Brock 1985).

Comparisons of effective and ineffective FAD programs are not as easy, or as fair, as for artificial reefs; many of the "United States" FAD programs are in developing territories or possessions where technological capabilities vary, and usually cannot overcome the complexities of anchoring systems in hundreds of fathoms in the open ocean. Despite all of these problems, FAD programs are very popular with fishermen and fishery management agencies. They are exceedingly practical because they can dramatically increase catches, even over the short term, and they appear to serve as physical monuments to government responsiveness, monuments that fishermen can see in the void of the open ocean. However, it is the pressure of this popularity, combined with the lack of consideration for adequate

engineering, that are major factors in the failure of FADs to achieve their potential to enhance marine fisheries.

In summation, the problem is that the lineage we have established for artificial reefs and FADs, combined with the paucity of long-term, quantifiable research to evaluate both forms of habitat alteration, impairs the acceptability of these enhancement technologies. Unfortunately, this past record is firmly entrenched and is proving difficult to displace.

### CRITERIA FOR APPROPRIATE APPLICATIONS

Appropriate applications of artificial reef and FAD technologies can only occur if there is adequate funding for research, development, and evaluation of each project. This will enable the development of "good-quality" projects in a variety of regions, environments, and ecosystems, in response to a variety of fishery management situations. The subsequent evaluation of these projects over the long term will develop an accurate information base that can be used to correctly assess the fishery enhancement potential of these habitat alterations. Adequate funding is the key to advancing these technologies from their current, primarily amateur, status.

For responsible application of artificial reefs and FADs, the first criterion must be the careful evaluation of realistic and justified fishery enhancement objectives, which are the bases (incentives) for habitat alteration. These objectives have to be far beyond the overused, and self-serving, desire to "improve fishing"; they must address the species to be enhanced, the fisheries that will benefit, and the potential for adverse impact. This means that the technologies must be controlled by professional fishery managers and researchers. It is irresponsible to continue to allow marine habitat alterations that do not have high potential to produce the desired enhancement without causing offsetting impacts (Buckley 1989).

Appropriate siting and design criteria must be applied to both artificial reefs and FADs to ensure that there is high potential for each habitat alteration to produce the desired biological development. A biota index siting system, based on comparisons of biota at proposed artificial reef sites and on productive natural reefs, can be used to predict the occurrence of target species on artificial reefs (Hueckel and Buckley 1989). Areas of naturally occurring aggregations of target pelagic fishes can be analyzed to enhance the aggregating effectiveness of FADs. Physical and oceanographic parameters must also

be given careful consideration in applying both of these technologies. (It has been common practice for the sites chosen for habitat alteration to be based on accessibility from harbors, and not on the potential for biological development.) The physical and spacial designs of artificial reefs must consider habitat configurations that allow replication of natural reef systems, especially for the recruitment, survival, and growth factors that control biological production.

As projects for artificial reefs and FADs proliferate, they must be incorporated into comprehensive fishery management and enhancement programs that cover ecologically relevant areas. These technologies are applied to create fishing locations, but the related removals can impact stocks over broad ranges, especially for migratory species. Stock level can also be affected by disruptions of normal recruitment patterns of planktonic juveniles, which can lead to increased survival or increased predation. In addition to the biological factors, management concepts such as "orderly fisheries" can benefit or suffer from something as basic as the juxtaposition of enhancement sites. The bottom line is that both artificial reefs and FADs create significant perturbations in the ecosystem, as well as significant redistributions of fisheries; these factors must be controlled and balanced so that they do not overpower the natural processes or disrupt the fisheries.

#### THE "PRODUCTION OR AGGREGATION" QUESTION

The "production or aggregation" question is an old issue that was raised about the biological processes occurring on artificial reefs. This was not an issue for FADs, because they were intended to take advantage of the tendency of pelagic fishes to gather around floating objects. The controversy over whether artificial reefs simply redistribute existing resources, or add to the total has been generated partly by the implied lack of fishery enhancement potential of the aggregation response when it occurred on reefs. This contradiction—FAD aggregation is good, artificial reef aggregation is not—seems a little absurd. Reviews of the literature show a distinct lack of research projects designed to test these alternate hypotheses. However, it is highly probable that the original lack of a scientific approach to applications of artificial reefs not only created the "production or aggregation" question, but also kept it from being answered.

Fortunately, there have been enough good artificial reef projects in recent years to provide ample evidence that this habitat alteration has both pro-

duction and aggregation functions for the associated biota. The "either production or aggregation" constraint is not valid, and these two processes should be considered as two extremes on a continuum of biological development on artificial reefs (Bohnsack 1989). Production of new resources for fishery harvest is an easy management concept to understand, but the appreciation of benefits associated with aggregation of "new" resources for harvest seems to give some researchers and managers problems. The aggregation function of artificial reefs has fishery production benefits ranging from increased accessibility and harvestability of resources to increased deposition of feces-related nutrients on the reef habitat. The changing levels and interactions of both the production and aggregation functions, over species and over time, are important factors in determining the potential of this technology for fishery enhancement.

The fishery production benefits of FADs are obvious in the increased accessibility of pelagic fishes that exist naturally as wandering schools in a very large ocean. Aggregating these fishes in a particular area significantly reduces unproductive searching time, and increases catches. Although the "production or aggregation" question has not been applied to the biological processes occurring at FADs, there has been considerable speculation about how aggregation into situations for intense removal (and increased natural predation?) may affect the natural production of some species. There is concern about possible excessive harvests of juvenile yellowfin tuna (*Thunnus albacares*), which gather around FADs in nearshore areas that are accessible to intensive fisheries (Frusher 1986; Buckley et al. 1989; R. E. Brock, University of Hawaii, unpublished).

Recent research on yellowfin tuna feeding around FADs indicates that for some species the FAD may contribute to increased natural production by "causing resident fishes to change their feeding habits to take advantage of otherwise untapped resources" (Brock 1985). This has occurred when yellowfin tuna at FADs fed almost exclusively on deepwater oplophorid shrimp, whereas non-FAD yellowfin tuna did not eat this food (Brock 1985). Thus FADs may function as more than passive aggregators; they may create production, as well as aggregation, benefits to marine fisheries.

#### CONCLUSION

It is clear that altering marine habitats to increase their fishery productivity is technologically possible using artificial reefs and fish aggregating devices. Artificial reefs can enhance marine fisheries

through both aggregation and production processes. The FADs' aggregation capabilities can also result in production through optimizing the use of alternate, atypical food resources.

The present designs of most artificial reefs do not provide the total habitat configurations that replicate natural reef systems, especially for recruitment and survival of juveniles. This is primarily due to the prevalent use of materials of opportunity to construct artificial reefs, a methodology that has been driven by incentives for solid waste disposal. Some modern artificial reefs using specific designs and construction techniques and selected materials meet many of the habitat requirements for resource production; however, the technology is still evolving toward complete replication of natural reefs. Critics of "artificial reefs in general" must realize that they are comparing natural reefs with incomplete, poorly conceived substitutes. The artificial reef idea is good; most current applications and designs are flawed.

Most of the FADs that have been deployed to date are severely underdesigned and underengineered. They often successfully aggregate target resources, but usually they are lost in a relatively short time. The failure to develop and apply adequate design and engineering criteria seems related to the "materials of opportunity" philosophy borrowed from artificial reefs, combined with pressures for rapid, popular solutions to oceanic fishery management problems.

Technologies for artificial reefs and FADs have suffered from inadequate, haphazard funding, and lack of realistic, justified fishery enhancement objectives as the incentives for altering habitats. Solving these two major constraints will allow refinement of these technologies and accurate evaluation of these habitat alterations as a basis for enhancing marine fisheries.

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## AGAINST MARINE FISH HATCHERIES: IRONIES OF FISHERY POLITICS IN THE TECHNOLOGICAL ERA

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### ABSTRACT

Marine fish hatcheries have a long history of expensive operation with no demonstrable positive effect on the resource. It is exceedingly difficult to detect hatchery-produced fish. Although very expensive, full hatchery operation may be necessary to determine effectiveness. Modern techniques of genetic marking and fingerprinting provide new tools for determining hatchery success. Unfortunately, legislation to fund research on hatcheries is forestalling vitally needed legislation to stop further deterioration of fish stocks. Popular interest in marine fish hatcheries is having a deleterious rather than beneficial effect on the resources.

### RESUMEN

Las piscifactorías marinas poseen una larga historia de costosas operaciones que no han demostrado un efecto positivo sobre el recurso pesquero. Resulta excesivamente dificultoso detectar peces de criaderos. A pesar del alto costo, tal vez sea necesario mantener criaderos totalmente funcionales por un tiempo prolongado para determinar su eficacia. Las técnicas modernas de marcación genética e identificación individual (equivalente al uso de impresiones digitales) proveen nuevas herramientas para determinar el éxito de un determinado criadero. Nos urge la necesidad de una legislación que legisle la disponibilidad de fondos para la investigación de piscifactorías para evitar o frenar el deterioro de las poblaciones de peces.

### INTRODUCTION

Several of California's marine fish stocks have declined severely over the past 70 years. Recreational and commercial fishermen have become increasingly vocal about rights to the dwindling supply of fish. In California, the concept of marine fish hatcheries was successfully promoted in the state legislature as a painless answer to this problem. A well-meaning California politician explained that instead of fighting over smaller and smaller slices of the pie, we now have the opportunity to increase the size of the pie itself. A modern technological solution to a politically difficult problem is hard to argue against. Yet I doubt that marine hatcheries are

likely to solve the problem of declining fish stocks. Rather, consideration of artificial propagation is making fishery resource problems worse.

### HISTORICAL PERSPECTIVE

The "hatchery solution" has a long history of attempted marine application, and from that history we should be able to learn a few lessons. Cod (*Gadus morhua*) larvae were released into the Atlantic Ocean for nearly a hundred years, beginning in the late nineteenth century. In the United States, some 50 billion cod larvae were released between 1890 and 1950, but it wasn't until 1952 that the operation was terminated due to lack of evidence that any worthwhile benefits had been obtained (Duncan and Meehan 1954).

The history of the Norwegian cod hatchery initiated by Captain Dannevig at Flødevigen (reviewed by Solemdal et al. 1984) provides further evidence that wishful thinking can postpone rational decisions almost indefinitely. The Norwegian hatchery operation was not closed until 1971, despite decades of research that failed to demonstrate any effect on the fish population. In 1911, Johan Hjort and a minority faction of a government committee issued an opinion that the question concerning the benefit from the Flødevigen hatchery was unsolvable, and that the hatchery should be discontinued. The majority of the committee advised against the hatchery's termination, but did point out that current methods needed to be replaced by unspecified "more complete" methods (cited in Solemdal et al. 1984). Ironically, the result was conversion of the Flødevigen hatchery from a privately funded operation to a government operation, which was to continue in virtually the same mode of operation for 60 more years.

It is interesting to read portions of Solemdal et al. (1984) in view of currently renewed hatchery interest in Norway. Whereas the former practice was to release early larvae, the new approach is to raise the fish to somewhat larger size and release them as juveniles; this is similar to the California plan.

The seemingly obtuse custom of introducing a practice prior to investigating its effect, as was the convention in Flødevigen in the 1880's may in fact have been a necessity



during those pioneer days of small scientific staff and little experience. With our knowledge, experience and well established research institutions the scientific investigations should precede the practice. We are specially thinking of the mass production of cod 0-group and the possibilities of restocking depleted populations.

Though the consistency of fry production still has to be demonstrated it is obvious that mass production will be a reality within some years. The fry produced can be used either in intense farming or released into the sea as a method for population restocking. Many people have a strong belief in the latter concept, while others are more skeptical. In fact, the situation is about the same as when Captain Dannevig was applying for support in the early 1880's.

The primary difference is that today the development is mostly an official task and therefore should be both under scientific and economic control. But the American hatcheries which were also developed within the official system, show that this is not a guarantee for the proper, logical and sound development of a project. The most obvious pitfalls today are lack of knowledge by the administration, too optimistic statements by scientists quoted by mass media, the general tendency of "fashion thinking" among administrators and scientists, and probably also critical funding from outside sources, e.g. the oil industry.

These statements apply equally to the marine fish hatchery program in California. To the credit of the California program, there is an explicit research component that is supposed to examine the effectiveness of such a program. However, determining the survival rate of hatchery-produced fish requires such a large output of those fish that a hatchery program must be fully implemented in order to determine its effectiveness! Thus the ideal of investigation preceding practice may not be achievable. Yet, as history has shown, the momentum generated is very hard to stop, despite lack of evidence that the program is effective. In fact, our technology for demonstrating positive effect in the open ocean is little better than it was at the turn of the century when Hjort deemed the question unsolvable.

## SCIENCE AND HATCHERY EVALUATION

The fundamental requirements for evaluating stock enhancement by means of a hatchery operation are twofold: first, we must be able to identify hatchery-produced fish in subsequent catches, and second, we must be able to identify the genes of hatchery-produced fish in subsequent wild populations. The remaining information needed to evaluate a hatchery program is relatively trivial. If a sufficient fraction of hatchery fish live long enough to be harvested, it may be possible to justify a put-and-take operation, as is often done for inland rec-

reational species. But without the second kind of evidence, there is no way of knowing whether the resource itself is being enhanced, which is the usual stated goal of these operations. There is no reason to believe a priori that the hatchery-reared fish is capable of natural reproduction in the wild; the fact is that we just don't know, and have little chance of finding out.

As a scientific problem, the null hypothesis is not clear. We could choose either  $H_0$ : hatchery fish are not reproductively viable, or  $H_0$ : hatchery fish are reproductively viable. The extreme difficulty of testing either hypothesis suggests that the null hypothesis, whichever it is, will not be rejected. Therefore, I submit that this either is bad science or it is not science at all. Moreover, without a substantial technological breakthrough, it is fraudulent to claim that a marine hatchery program can be evaluated "scientifically."

Fortunately, such a breakthrough may have occurred. About the only conclusive way to answer these questions is to mark and count the fish that are released from the hatchery, and monitor their recapture. Physical tags or markings can pose a handicap to survival in the wild, and could bias the results; they also provide no information on reproductive success. Only through genetic marking, a technology that recently has become practically feasible, can effective reproduction be tested. A genetic strain, as well as its offspring, should be detectable by genetic fingerprinting methods. Again, development of a genetic strain requires a long time and a large investment in hatchery facilities, before the program's potential effectiveness can be determined. Although evaluating a marine hatchery program may now be feasible, it remains extremely difficult and expensive. And that very expense bodes ill for an objective accounting of cost-effectiveness.

The few cases where marine hatcheries seem to have produced recoverable fish have been associated with estuarine rather than open-ocean fisheries (e.g., Rutledge 1989). Application to a slow-growing, late-maturing, long-lived oceanic fish such as white seabass (*Atractoscion nobilis*), as is being considered in California, strains biological and economic credibility. These fish will not become vulnerable to the commercial fishery for nearly ten years, which entails a substantial discount in economic value as well as attrition by natural mortality. The recreational fishery may encounter these fish somewhat younger, and values are undoubtedly higher to this segment of the fishery, but relative fishing pressures indicate that the bulk of the catch will be taken by the commercial fishery.

Also, the main body of the white seabass resource lies south of the Mexican border. We must further discount our hatchery production by the presently unknown but potentially large fraction that migrates south to join the main body of the population where it will be unavailable to California fisheries. Ironically, the more fish that display normal behavior and migrate south, the better is our chance of enhancing the population reproductively, but the poorer is our chance of catching those fish. Only the monitoring of genetic tags can address these difficult problems.

The critical question of whether a marine hatchery will be effective is not answerable before the attempt, and is exceedingly difficult to answer even after the attempt. Meanwhile, the operation is very expensive. Moreover, the program is prone to justification by wishful thinking: history has shown that a hatchery program can generate a broad base of public and political support in the total absence of any objective evidence that it actually works.

#### FINAL IRONIES

Effective management of fisheries on declining natural stocks has always been difficult to obtain. In California, effective management often has been legislated only after a resource has declined to a level so low that politicians no longer fear criticism for restricting catches (e.g., sardines, Pacific mackerel, Pacific bonito). The California fisheries for white seabass have declined severely (Vojkovich and Reed 1983), and in the 1980s we seemed to be nearing the historically proven conditions for effective fishery legislation. Now the "hatchery option" has changed this pattern: discussion of legislation to manage the white seabass fishery suddenly ceased

with the creation of the marine hatchery program in California. Even though this program is only intended to be exploratory, the people responsible for enacting fishery management feel that they have effectively addressed the issue, and they appear to have little interest in taking action to conserve the remainder of the natural stock.

California's hatchery *research* program is now the main factor preventing rehabilitation of the white seabass resource. This is not the first time that a research program has forestalled effective fishery management in California: CalCOFI itself is a similar case, having contributed to the final collapse of the California sardine fishery (Radovich 1982). Of course, in the present case of white seabass hatchery research, the fishing industry is not intentionally forestalling management as it was in the sardine case cited by Radovich. Yet I believe that the late John Radovich, who was a strong proponent of research on marine fish hatcheries, would be dismayed to find that a legislated program of fishery research once again has postponed effective management, and is contributing actively to collapse of another fish resource.

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## THE TEXAS MARINE HATCHERY PROGRAM – IT WORKS!

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### ABSTRACT

Red drum (*Sciaenops ocellatus*) is an estuarine-dependent sciaenid that ranges from New York to Mexico and has historically supported sport and commercial fisheries throughout its range. Red drum populations in Texas began a dramatic decline in the 1970s, prompting regulatory measures such as size, bag, and possession limits; restrictions on gill nets and their operation; a commercial quota; and license restrictions. These measures proved ineffective, and finally in 1981 the commercial sale of red drum was banned. Presently the sport bag limit on red drum is three per day, and only fish that are 20–28 inches may be retained.

In 1982, the Texas Parks and Wildlife Department began operating a marine fish hatchery to enhance dwindling populations of red drum. To date, over 42 million red drum fingerlings (25 mm TL) have been raised and stocked into Texas bays. Recent expansions of the facility have boosted production capabilities to 20 million fingerlings annually. Impact evaluations begun in 1983 indicate that the enhancement of red drum populations in Texas bays by stocking is a successful and effective management tool.

### RESUMEN

La corvina roja (*Sciaenops ocellatus*) es un sciánido de estuario cuya distribución geográfica se extiende desde Nueva York hasta México, y que históricamente ha soportado la presión de pesca tanto deportiva como comercial. Durante la década del 70 las poblaciones de corvina roja en Texas experimentaron una caída dramática, lo cual llevó a poner en práctica ciertas medidas reguladoras limitando el tamaño y la cantidad de la captura, restringiendo el uso de redes de enmalle, limitando la cuota comercial e imponiendo restricciones a los permisos de pesca. Estas medidas no resultaron satisfactorias y finalmente en 1981 se prohibió la venta comercial de la corvina roja por completo. Actualmente, la pesca deportiva está restringida a 3 corvinas por día, de talla 20 a 28 pulgadas.

En 1982 el Departamento de Parques y Vida Silvestre de Texas ("Texas Park and Wildlife Department") comenzó a operar un criadero con el objeto de realzar la población de corvina roja mermada.

Hasta la fecha, más de 42 millones de alevinos (de talla total 25 mm) han sido criados y sembrados en las bahías de Texas. Gracias a una expansión en la infraestructura, la capacidad de producción de alevinos aumentó a 20 millones por año. En 1983 se comenzó a evaluar el impacto de criaderos; estas evaluaciones demostraron que la siembra de crías en las bahías de Texas para realzar las poblaciones de corvina roja es una herramienta exitosa y efectiva en el manejo pesquero.

### INTRODUCTION

Red drum (*Sciaenops ocellatus*) is an estuarine-dependent sciaenid that ranges from New York to Mexico, and historically supported sport and commercial fisheries throughout its range. Unfortunately, this species has become another poignant example of the pervasive attitude that fishing (both sport and commercial) can have no significant impact on marine fisheries (Rutledge and Matlock 1986). Red drum populations that had experienced dramatic declines over a ten-year period were dealt a severe blow in 1983 when the blackened redfish craze created strong consumer demand for the fish (NMFS 1986). This demand increased commercial fishing for the spawning stock in the Exclusive Economic Zone (EEZ), accelerating the move toward the extreme regulatory measures that are now in effect to protect this species.

Today, red drum caught in South Carolina, Alabama, Texas, Louisiana, and the Gulf of Mexico EEZ cannot be sold. Greater restrictions on harvest have also been placed on all fishermen in every Gulf state. In Texas, commercial harvest of red drum has been prohibited; bag limits have been reduced from five to three; and a size limit of 20–28 inches has been imposed. In 1988, netting of any type was prohibited in Texas waters to reduce the by-catch and illegal netting of this species.

Managers in Texas have also been fortunate to have the opportunity to use hatchery-produced red drum to evaluate stock enhancement. Based on the preliminary successful results from Texas, Florida and Alabama are also going to use red drum from saltwater hatcheries for stock enhancement, and California is presently considering the feasibility of saltwater hatcheries.

In the fall, Texas red drum spawn in the surf. Their larvae migrate through passes into estuarine nursery grounds. Matlock (1987) postulated that larval recruitment into the bays could be a limiting factor of annual year class abundance. He presented results showing that in the bay hardest hit by Hurricane Beulah in 1967, the recruitment of red drum was larger than during any of the eight previous years. Further, this bay was the only one to show an increase in recruitment. Increased larval transport into estuarine nursery areas caused by high tides was listed as one explanation for this phenomenon.

## RESULTS AND DISCUSSION

### *St. Charles Bay Study, 1979–1981*

Matlock's limited recruitment theory and the possible use of hatchery-produced fish for stocking purposes was tested in St. Charles Bay from 1979 through 1981 (Matlock et al. 1986). This 3,400-hectare bay was stocked with 978,829 fingerlings in 1979, 276,540 in 1980, and 577,500 in 1981. Fish were stocked in the summer of 1979, fall of 1980, and spring of 1981. Because red drum spawn in the fall, fish stocked the following spring and summer were smaller and were tracked by length frequency for up to 9 months in both bag seine and gill net samples. Fish released in August 1980 apparently did not survive, possibly because of a hurricane later that month that caused salinities to drop from 25 to 9 ppt almost overnight.

Matlock found a significantly higher mean catch of red drum in bag seines for 1979 and 1981 in St. Charles Bay compared to an adjacent bay that was not stocked. However, the 1980 summer catch was similar in both areas when only native fish were present. He also concluded that "poststocking surveys indicated that fish stocked in 1979 and 1981 enhanced the native population to different degrees, undoubtedly because almost twice as many fish were stocked in 1979 as in 1981. Therefore, future evaluations should concentrate on repeated stockings into limited areas to determine the relationship between stocking rate and enhancement."

### *GCCA/CPL Marine Development Center*

The St. Charles Bay pilot study, and other evidence that had been accumulated from previous years, sparked the interest of the Gulf Coast Conservation Association (GCCA). This group of conservationists enlisted the support of the Central Power and Light Company (CPL), a public utility company, and a unique tripartite project was devel-

oped. The GCCA provided money to construct a 20-acre fish hatchery on land provided by CPL. The Texas Parks and Wildlife Department provided personnel and annual operating expenses for the project. The hatchery produced its first fingerlings in 1983. The success of the hatchery in the past six years has resulted in additional support from the corporate sponsors, and a major \$4.3 million expansion of the facility is nearing completion. To date, the facility has produced over 42 million red drum fingerlings; the annual production from the expanded facility can reach 20 million fingerlings.

### *Evaluations of Stocking Success*

The success of enhancing red drum populations using hatchery-reared fingerlings has been evaluated since 1983. One of the first evaluations involved the initial survival of stocked fishes. Hammerschmidt and Saul (1984) reported that average survival of stocked fish that were held for 24 hours in cages was  $89.4\% \pm 2.7\%$ . Similar tests were conducted in 1984 and 1985; overall 24-hour survival of pond-reared red drum held in cages was  $86.2\% \pm 2.2\%$  (Hammerschmidt 1986). Mortality associated with harvest and hauling stress usually occurs within 24 hours; therefore the 24-hour survival experiments have been discontinued.

Biweekly bag seine samples in the vicinity of the stocking site were used to determine longer-term survival. Dailey and McEachron (1986) captured stocked red drum fingerlings in San Antonio Bay up to 1.5 months after stocking. After that period of time, fingerlings were not vulnerable to capture gear.

An intensive study to determine long-term effects of stocking red drum was begun in 1983 in the San Antonio and Corpus Christi bay systems. The preliminary results of this work were presented by Matlock (1986b), and a detailed analysis is currently being prepared. About 14 million fish were released in 1983, late 1984, and early 1985 into these two bay systems. In the two stocked bays and one unstocked bay sport-boat anglers were surveyed, and fishery-independent monitoring was done with gill nets (7.6, 10.2, 12.7, and 15.2-cm stretched meshes). Results indicated that mean catch rates in gill nets in the Corpus Christi Bay system were much higher in the two years after stocking than in the years before stocking. Matlock also noted that the increased catches after stocking were primarily in the 7.6-cm stretched mesh. This pattern was not apparent in the unstocked bay, reflecting recruitment of the stocked fishes one year after each stocking. Stocked fish also were evident in each subsequent

season in the larger-mesh portions of gill nets. Stocking apparently increased the fishing success of sport-boat anglers for red drum. The mean landing rate by these fishermen increased 150% over the mean historic rate in the stocked bay system. Harvest rate in the unstocked bay also increased, but only by 50%.

### **Results of Tagging Efforts**

Precise determination of the contribution of hatchery-reared fish to the sport creel requires a reliable method of marking. In the case of red drum in Texas, this is the single hurdle left to overcome in evaluation efforts. Initial efforts to tag red drum using magnetic coded wire tags inserted in the snout were unsuccessful. Gibbard and Colura (1980) reported tag loss rates ranging from 59% within 3 months to 73% at 12 months. Matlock et al. (1986) reported that only 3 of the 38,000 fish that were tagged in this manner were recovered in the St. Charles Bay study. More recent studies using the same type of tag implanted in the cheek musculature revealed that the minimum size fish that could be tagged was 70 mm TL, which is larger than fish that are currently being introduced (Bumguardner et al. 1988). Current research efforts center around the use of oxytetracycline, optical pattern recognition using scales and otoliths, and genetic marking. Genetic marking would provide the most valuable tag because it can label very small fish (even fry); it will last the lifetime of the fish; and it will pass to future generations.

### **Cost-Benefit Analysis**

The question of cost versus benefits is constantly raised in analyses of the effectiveness of hatchery stocking programs. Fisheries managers question whether stocking hatchery-reared fish constitutes the best use of resource dollars, especially when stocking programs require capital investment to build hatcheries. The cost benefit of a stocking program can be calculated with the formula

$$\text{Cost benefit} = \frac{\text{number harvested} \times \text{value of fish}}{\text{operating costs}}$$

where number harvested is the number of hatchery fish that enter the anglers' creels; value of fish is the value to the state of an angler catching a single fish (usually calculated as direct expenditures multiplied by a factor of 3 to account for indirect and induced costs); and operating costs include annual salaries, operating expenditures, equipment, and depreciation on capital expenditures. For the Texas situation, number harvested has not yet been

determined. Value of fish, however, was calculated by Matlock (1986a). He estimated the direct market value of the angling experience for red drum at \$29.7 million in 1976. This amounts to \$89.1 million in direct, indirect, and induced impacts. This value adjusted with the Consumer Price Index to 1987 dollars would be \$178 million. Sport harvest in 1976 was approximately 400,000 red drum, making each fish worth \$445 in 1987 dollars. Operating costs for 1989 are estimated at \$362,000 for salaries, operating expenses, and equipment. An additional \$285,500 was added for depreciation of capital construction costs (straight-line depreciation of \$5.71 million over 20 years), making total operating costs \$647,500 each year.

Having two factors in the equation permits the calculation of the break-even point (number of fish that must enter the creel to produce a 1:1 cost-benefit ratio). Based on these figures, 1,455 red drum would have to survive and be harvested each year for the state to receive \$1 of benefit for every \$1 of cost to operate the hatchery. Based on a conservative anticipated production of 15 million fingerlings per year, cost benefits of 1% survival would be 1:103; 5% survival would be 1:515; and 10% survival would be 1:1031. Seneca and Taussig (1974) indicate that opportunity costs must be included in evaluations of cost benefits using public expenditures. Opportunity costs account for the rationale that money invested in fish hatchery construction, for example, could be invested in an interest-bearing account. The interest that could be earned on this money becomes an opportunity cost that must be added to the operational costs of the hatchery. Addition of opportunity costs (construction costs  $\times$  10%) would increase operating costs to \$1.2 million per year; but still only 2,738 fish would have to survive to break even. These very positive cost-benefit projections demonstrate the economic viability of a saltwater hatchery even at low survival rates.

### **CONCLUSIONS AND RECOMMENDATIONS**

Evaluation of the 6-year red drum stocking program in Texas highlights the success of enhancing red drum populations using hatchery-reared fish. Stocked fish do survive for the first 24–48 hours (>84%). Bag seine samples in the stocking areas have documented but not quantified survival up to 60 mm (at which size the fish escape the capture gear). But most important, the number of fish harvested in bays that have been stocked has nearly doubled over historic mean harvest rates in those systems.

The Texas experience has shown several things that are generically applicable to the evaluation of other marine stocking programs:

1. The effectiveness of marine fisheries stock enhancement programs cannot be evaluated on an a priori basis. To measure the impact, fish must be stocked. Once they have been stocked successfully, the system will be forever changed.

2. Substantive impact on a large, dynamic fishery may require massive stockings. Experimental designs using small numbers of fish may not show up against annual variation in population abundance.

3. Although managers may strive for statistical accuracy measured with a micrometer, benefits may only be measurable with a yardstick. Long-term trends may be the only indicator of success.

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## DESIGNATED HARVEST REFUGIA: THE NEXT STAGE OF MARINE FISHERY MANAGEMENT IN CALIFORNIA

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### ABSTRACT

Marine fishery management has traditionally been based on the biology and population dynamics of individual target species. Management controls are generally exercised through limits on individual fish sizes, seasons of harvest, catch limits, and restrictions on gear efficiency designed to protect reproductive stocks. Distance from port and depth provided de facto refugia from harvest during the first century of modern exploitation, but recently few California nearshore demersal fisheries have been able to sustain high yields using traditional species-specific management strategies.

Designated harvest refugia, or fisheries reserves, should now be evaluated as management tools to enhance or sustain these coastal fisheries. In other parts of the world, designated harvest refugia provide recruits to adjacent harvest zones, protect the genetic diversity of wild stocks, and serve as experimental controls for determinations of potential yield. This concept could be adapted to California's coastal ecosystems by applying accepted theories from ecology and conservation biology. Hypotheses regarding the optimum number, size, and distribution of fishery reserves in relation to harvested zones should be empirically tested in existing marine parks and reserves and in additional protected areas set aside especially for this purpose.

### RESUMEN

La explotación racional de los recursos pesqueros se basó tradicionalmente en el conocimiento de la biología y la dinámica poblacional de ciertas especies. En general, el control de la explotación se realiza imponiendo limitaciones en el tamaño de los individuos, restringiendo la pesca a ciertas estaciones del año, limitando el tamaño de la captura, y limitando la eficiencia del equipo de pesca con el objeto de proteger el stock reproductor.

Durante el primer siglo de la explotación pesquera moderna, la distancia desde el puerto y la profundidad ofrecían refugios seguros, pero recientemente una pequeña parte de la pesquería de-

mersal costera en California ha podido mantener un alto rendimiento usando estrategias de explotación tradicionales.

Actualmente, se debe evaluar el uso de refugios de pesca o reservaciones perqueras como herramientas de trabajo alternativas si queremos aumentar o mantener estas pequerías costeras. En otras partes del mundo, los refugios de pesca proveen reclutas a las zonas de pesca adyacentes, protegen la diversidad genética de la población salvaje y sirven como control experimental para determinar el rendimiento potencial. Este concepto podría ser adaptado al ecosistema costero de California, empleando teorías ecológicas y de conservación biológica. Las hipótesis que consideren el número óptimo, el tamaño y la distribución de las reservaciones protegidas de la pesca en relación a las áreas de pesca deberán probarse empíricamente en los parques marinos y reservaciones existentes y en áreas de protección adicionales especialmente diseñadas para este propósito.

### INTRODUCTION

For more than a century, California's nearshore demersal fisheries were sustained by de facto harvest refugia. Zones beyond the economic reach of vessels and gear went largely unharvested and served as sources of replenishment for harvested areas closer to port or in shallower waters. These refugia have been lost to technological advances in the last 30 to 40 years. Conservation of fishery resources in the future may require designation of management zones to recreate these harvest refugia. This paper describes large-scale, long-term ecological research to test hypotheses regarding the optimum sizes and distributions of harvest refugia required to maximize sustained yields from California's nearshore fisheries.

For more than two decades, fatal flaws in single-species and population-based maximum sustainable yield (MSY) approaches to fisheries management have been seriously discussed in the scientific literature (Roedel 1975; Larkin 1977; Barber 1988).

Despite this discussion, little has changed in management approaches to coastal marine fisheries during the past 40 years or so. In California, fisheries are still managed by species-specific limits on seasons, individual fish sizes, types and sizes of gear, and daily take (bag limits) designed to achieve some approximation of MSY, or a socioeconomic derivative of it called optimum sustainable yield (OSY). I do not wish to enter the debate on the efficacy of traditional single-species, population-based management, but rather to acknowledge that its persistence identifies a significant doubt regarding this approach to fisheries management. I will discuss possible alternatives whose efficacy can be scientifically tested and evaluated.

Larkin (1977) identified two extreme alternatives to single-species MSY, and a wide spectrum of middle-of-the-road management philosophies between them. One extreme may be described as technocentric, resource-information-dependent and -driven, providing rigid control and order, and sociologically simple. A good example of this approach is the Western Australian rock lobster fishery, where harvest rates are based on extensive biological knowledge of the target species, *Panulirus cygnus*, and the number of fishermen and their fishing power are closely regulated (Bowen 1980). The alternative extreme path is to intervene as little as possible in relation to social and economic market forces, imposing only enough regulation to prevent complete stock collapse. Most nearshore California fisheries seem to be managed somewhere between these extremes, but clearly nearer the latter philosophy. Commercial and recreational landings of sea urchin, rockfish, abalone, rock crab, angel shark, California halibut, and spiny lobster have shown greatly reduced yields in recent years in southern California (CDFG unpub.), which not only suggests reduced stocks, but, more important, also indicates a potential for increased production with a different management regimen.

The management strategy I will discuss here may be nontraditional for California marine fisheries, but it is neither unique nor a new idea. It is, nonetheless, an approach that I believe represents the next logical step in the management of California's coastal marine fisheries. It is time to investigate the possibility of setting aside and protecting ecologically discrete zones that are naturally buffered from environmental perturbations and that can produce larval and juvenile recruits for sustainable harvests in adjacent zones. Implementation of such a strategy will require significant social and economic change, and no small amount of courage. It will also

suffer from all of the inherent uncertainty and distrust new endeavors always face.

In *The Prince*, a classic treatise on exercising political power, Machiavelli warned 400 years ago:

It must be considered that there is nothing more difficult to carry out, nor more doubtful of success, nor more dangerous to handle, than to initiate a new order of things. For the reformer has enemies in all those who profit by the old order, and only lukewarm defenders in all those who would profit by the new order, this lukewarmness arising partly from fear of their adversaries, who have the laws in their favor; and partly from the incredulity of mankind, who do not truly believe in anything new until they have had actual experience of it. Thus it arises that on every opportunity for attacking the reformer, his opponents do so with the zeal of partisans, the others only defend him half-heartedly, so that between them he runs great danger.

If a new order of fisheries management is to succeed, it must be based on sound research to reduce the inherent uncertainty of environmental systems and to develop confidence from actual experience in the new approach. This research will take years to conduct and should begin now. As coastal ecosystems become more and more stressed by coastal development, pollution, and fishery harvests, and as landings continue to decline, the case for a new order of fishery management will become easier and easier to make. But at some point it may be too late, as the plight of the Mediterranean Sea reminds us today. We need bold decisions now to apply what is known of ecosystems and ecological processes to fishery management in order to develop a new order of things for the future.

After a century of European investigations and experience, limnologists and oceanographers long ago adopted holistic approaches to aquatic ecosystems that led to the development of several bodies of modern ecological theory on system structure and function and on the roles of predation and competition in ecosystem dynamics. Conservation biologists are currently debating issues of genetic diversity, minimum viable populations, and island biogeographical theory in order to determine optimum reserve boundaries (Lewin 1983; Schonewald-Cox et al. 1983; Quinn and Harrison 1988). This body of theory and knowledge should now be applied to coastal marine fisheries in order to provide a testable ecological basis for management that could increase fishery productivity and stability. What is required is nothing less than a long-term, large-scale experimental ecological study in which socially managed fishery harvest is the major experimental variable.



## THE SOUTHERN CALIFORNIA ABALONE FISHERY

The California abalone fishery serves as an example of a mature coastal fishery that could benefit from a new approach to management. The modern fishery was developed intertidally for black abalone, *Haliotis cracherodii*, in the 1850s by Chinese immigrants, and grew to an annual harvest of nearly 2,000 MT by 1879 (Cicin-Sain et al. 1977). Regulations prohibiting sale of abalone collected in the littoral zone shifted the fishery to Japanese hard-hat divers and four subtidal species—red abalone (*H. rufescens*), pink abalone (*H. corrugata*), green abalone (*H. fulgens*), and white abalone (*H. sorenseni*)—until World War II. For 20 years following the war, approximately 2,000 MT were harvested commercially each year until those stocks were depleted and black abalone replaced them as the major harvested species in 1973 (Burge et al. 1975). By the early 1980s, total annual harvest was down to about 500 MT (Ault 1985) and had fallen to 276 MT by 1986 (CDFG unpub.). In the late 1950s, development of scuba diving provided access to subtidal resources for a new segment of the burgeoning human population of southern California. No reliable data on total recreational harvest are available for the abalone fishery, but for two years (1982–83) in Channel Islands National Park the reported recreational harvest from commercial passenger fishing vessels alone was 8% of the reported commercial harvest in the park, which was 273 MT in 1982 and 150 MT in 1983 (Forcucci and Davis 1989).

In apparent response to economic pressure, California fishing statutes were changed in 1984 to permit commercial harvest of previously protected black abalone stocks in the ecological reserves around San Miguel, Anacapa, and Santa Barbara islands. Populations of intertidal black abalone around the northern Channel Islands, particularly Anacapa, Santa Cruz, and Santa Rosa, suffered 90% mortality between 1984 and 1988 (Davis 1988). The apparent source of mortality was not harvest, but some natural agent, such as protozoan parasites in environmentally stressed segments of the population. Fur hunting and fishery harvest have reduced predator populations, thereby reducing the influence of natural predation as an ecological process buffering southern California coastal ecosystems against extreme changes (Paine 1974; Tegner 1980; Tegner and Levin 1983). Competition for food and space among the prey species, such as sea urchins and abalone, correspondingly increased, and losses of some species under extreme conditions would be expected (Paine 1974). Perturbations in algal pro-

duction, such as those due to the recent (1982–83) El Niño, would thus be expected to precipitate dramatic, competitively driven population fluctuations in abalone and also urchin populations, exactly like the fluctuations observed at the Channel Islands. Recovery from these losses by such long-lived, slow-growing animals will be slow and economically disruptive. We are thus seeing signs that California coastal ecosystems are losing their “buffering capacity,” and we may expect to witness more frequent and extreme fluctuations in these resources in the future.

The abalone fishery has evolved from a laissez-faire management approach in the mid-nineteenth century to a highly regulated, limited-entry fishery in the late twentieth century, and yet stocks and landings are still falling precipitously. Because it is further along in its socioeconomic evolution, the California abalone fishery provides a useful early warning for more recently developed fisheries, such as the sea urchin fishery. The abalone fishery also provides a useful model for developing new management approaches, such as that suggested above, because it is not unique; many other long-lived, slow-growing, late-maturing, resident species such as rockfish and spiny lobster could also benefit from this geographic and ecologic approach to management.

## ECOLOGICALLY BASED MANAGEMENT UNITS

The concept of ecologically based management units is not new, but it has not yet been broadly applied to coastal marine fisheries. Most ecological units can be described as geographical zones, and zoning human use on such a geographic basis is broadly applied in natural resource management, especially in terrestrial environments. Wildlife and waterfowl refuges are essentially zones where harvest is restricted or prohibited for the purpose of producing and perpetuating stocks for human use elsewhere. Montane national parks regularly produce “overflows” of ungulates and predators, such as elk, deer, wolves, and grizzly bears, which are harvested in neighboring areas. In Australia, the Great Barrier Reef Marine Park Authority uses six kinds of zones within this 348,700-km<sup>2</sup> marine park to regulate human uses and conserve natural resources (GBRMPA 1981). Zoning is also a cornerstone of marine park management in Canada (Parks Canada 1986) and in the policies of the International Union for the Conservation of Nature and Natural Resources (Kelleher and Kenchington 1987).

In marine fisheries, single-species sanctuaries for

spiny lobster have proven to be effective and popular ecologically based management tools. In both New Zealand and Florida, closing moderately large areas (100 to 1,000 km<sup>2</sup>) of juvenile lobster habitat to harvest increased adjacent adult populations, and thereby overall yields to the fisheries (Booth 1979; Davis and Dodrill 1980). A 190-km<sup>2</sup> marine park at Dry Tortugas, Florida, also serves as an adult lobster (*Panulirus argus*) harvest refugium as part of the Gulf of Mexico Fishery Management Council's and State of Florida's lobster fishery management plans. In this regard it provides larval and juvenile recruitment to adjacent and distant zones, protects genetic diversity of stocks, and serves as a site for research on natural mortality rates and environmental carrying capacity (Davis 1977).

The effectiveness of multispecies harvest refugia in marine fisheries has not yet been well tested (Johannes 1978), but evidence from coral reefs in the Philippines (Alcala 1981, 1988) and from a temperate ecosystem off the North Island of New Zealand (Jeff 1988) provides encouragement that such refugia may be extremely effective fishery enhancement tools. In the Philippines, eight small areas, ranging in size from 8 ha to 10,000 ha, were excluded from fishery harvest for varying periods of time (3 to 10 years). The area with the longest period of protective management, a 750-m-long segment of reef on the west side of Sumilon Island, was closed to all forms of fishing in 1974. Mean harvest rate for local fishermen was 0.8 kg man-day<sup>-1</sup> before the closure. Within two years, the mean harvest rate from areas adjacent to the closed zone had tripled, and over a 5-year period the sustained yield of fish per unit area from the adjacent zones was one of the highest reported for any coral reef in the world, 16.5–24 MT km<sup>-2</sup>yr<sup>-1</sup> (Alcala 1981; Russ 1987). After 10 years without harvest in this reserve area, fishermen began violating the reserve boundaries; within 2 years, fishery yields in entire area had declined more than 50% (Alcala 1988).

Harvest has been prohibited in the 547-ha Leigh Marine Reserve in New Zealand for 11 years. Not only have lobster and fish populations in the reserve increased to 2.5 to 20 times the densities in similar adjacent habitat, but both recreational and commercial fishers believe the reserve has increased their catches in adjacent areas. The reserve is also immensely popular with tourists (Jeff 1988). In spite of these successes, the small size of the closed area at Sumilon Island, the short duration of protective management at the other Philippine reefs, and the lack of conclusive fishery yield data from areas adjacent to the Leigh Marine Reserve require caution

in interpreting these results as a definitive test of the efficacy of multispecies harvest refugia.

Of the more than one hundred national, state, and city marine parks and reserves in California, only four prohibit all fishery harvest and may thus have the potential to increase fishery production in adjacent areas. They are the Point Lobos Ecological Reserve in Monterey County, the landing cove portion of the Anacapa Ecological Reserve in Ventura County, Heisler Park Ecological Reserve in Orange County, and the San Diego-La Jolla Ecological Reserve in San Diego County. Most of these are so small that any positive effect on adjacent fisheries would be virtually undetectable, even if harvest or population data were available for evaluation (Davis and Pillsbury 1983). The largest of these harvest-free areas at Point Lobos is the subject of a preliminary study focusing on a management strategy for rockfish, *Sebastes* spp., and appears promising as a fish-producing and fish-exporting zone (VenTresca and Lea 1987; J. Hardwick, pers. comm.). With appropriate harvest constraints, existing marine parks and ecological reserves in California could provide established management units suitable for evaluating optimum size and distribution of harvest refugia to maximize long-term sustained yields of nearshore fisheries. Additional areas could also be especially set aside for this purpose.

## DESIGN CONSIDERATIONS FOR HARVEST REFUGIA

Enough is known to design experiments to test the efficacy of harvest refugia. These experiments must incorporate both ecological and sociopolitical factors in their design. Perhaps the most critical factors affecting the efficacy and social acceptance of harvest refugia are size and location. The refugia must be large enough to be productive, assure perpetuation of target species populations, and be easily patrolled. They must be small enough to optimize the boundary-to-volume ratio and assure maximum export of harvestable products (eggs, larvae, juveniles, and maybe also adults). They must be located at sites that contain suitable juvenile and adult habitat, while taking advantage of natural processes that will promote dispersal and recruitment to convenient harvest areas.

Initial experiments should focus on a few species, say 10–12, whose life histories and environmental requirements are relatively well known. Good candidates would be giant kelp, *Macrocystis pyrifera*; abalone, *Haliotis* spp.; California spiny lobster, *Panulirus interruptus*; sea urchin, *Stongylocentrotus franciscanus*; kelp bass, *Paralabrax clathratus*; Califor-

nia sheephead, *Semicossyphus pulcher*; Pacific angel shark, *Squatina californica*; California halibut, *Paralichthys californicus*; and several rockfish such as copper, *Sebastes caurinus*, gopher, *S. carnatus*, vermilion, *S. miniatus*, blue, *S. mystinus*, and olive, *S. serranoides*. These species also have high potential for recreational and commercial fisheries.

Experimental design should deal with factors such as daily and seasonal migration patterns, the lengths and mobilities of larval stages, and the effects of natural processes such as currents, upwelling, storms, and El Niño events. Optimum refuge design will probably require compromises among the ecological requirements of several species, and empirical evidence should be gathered and applied to assure that the most valuable resources are not threatened by such compromises. Experimental controls for such large-scale social and ecological research units are difficult to design in space, and are best evaluated over time, but not simply as before-and-after studies (Green 1979). Definitive answers to the design questions will probably require many years of observation, but the actual time will depend on the various life-history characteristics of the target species, including annual variations in reproduction, recruitment, and mortality, and natural environmental cycles like El Niño events.

It is clear that, to be successful, this research must be transdisciplinary and socially acceptable to a broad constituency, including conservationists and recreational fishermen as well as fisheries scientists and commercial fishermen. The fishing community must be involved in the experimental design from the beginning to allow for selection of acceptable harvest zones and adjacent refugia. The boundaries between zones must be recognizable and enforceable. Existing marine parks and reserves represent most regions of the coast, and they already have established boundaries and law enforcement staffs to augment patrol activities. Zoning use, as opposed to seasons and size restrictions, would require a new approach to law enforcement (remember Machiavelli's warning). The prevailing philosophy is thus to "put all your eggs in one basket, and watch the basket." Watching the basket becomes even more important than it was under the traditional approach.

Zoning of uses is a viable approach to marine fisheries management that deserves serious evaluation in California in the late twentieth century. It has the potential of increasing consistent sustained harvests. It may allow reduced regulations and thus simplify enforcement and compliance. It may also allow dynamic market forces to optimize harvest

sizes and seasons, and may permit those same forces to drive development of more efficient nondestructive fishing gear.

## CONCLUSIONS

Historical records and the present condition of many nearshore California fisheries suggest that many of these stocks could sustain higher yields. Harvest refugia offer a promising new management strategy for many of these fisheries. Large-scale, long-term ecological research is needed to determine the optimum design of a harvest refugia system that will assure long-term maximum resource productivity. Existing marine parks and reserves meet many of the design criteria for conducting this research, and could be used effectively in initially developing a productive new approach to managing California's coastal fisheries.

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**Part III**

**SCIENTIFIC CONTRIBUTIONS**



## FECUNDITY AND OTHER ASPECTS OF THE REPRODUCTION OF SABLEFISH, *ANOPOLOPOMA FIMBRIA*, IN CENTRAL CALIFORNIA WATERS

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### ABSTRACT

Along the central California coast from Point Conception to Monterey Bay, sablefish specimens were taken in research trawls, in traps, and from the fishery. Sablefish in spawning condition occurred in October through early February. Fifty percent of the females 60 cm long were sexually mature. Most of the females with active ovaries were taken in the oxygen minimum zone; 96% of the reproductively active females occurred at depths of 800 m or deeper. The mean length of males and females taken in trawls increased with depth.

Five lines of evidence indicated that the standing stock of advanced yolked oocytes was equivalent to the total potential annual fecundity; in other words, fecundity is determinate in sablefish. The potential annual fecundity of a 2.5-kg sablefish was 107 oocytes per gram female weight; the batch fecundity averaged 24 hydrated oocytes per gram female weight for the last spawn, and 41 for earlier spawnings. Thus sablefish would have to spawn about three times to fully use their potential annual fecundity.

### RESUMEN

Varios especímenes de pez sable fueron capturados en arrastres de investigación, con trampas y por la pesquería a lo largo de la costa de California, desde Punta Concepción hasta la bahía de Monterey. Desde el mes de octubre hasta los comienzos de febrero se observaron especímenes en condiciones de desove. El 50% de las hembras de 60 cm de longitud se encontraban sexualmente maduras. La mayoría de las hembras con ovarios activos provinieron de la zona de mínimo oxígeno; el 96% de las hembras reproductoras ocurrió a profundidades iguales o mayores a los 800 metros. La longitud promedio de los machos y las hembras recolectados en los arrastres aumentó proporcionalmente con la profundidad de captura.

La evidencia demostró que el stock de ovocitos vitelinos en estadios avanzados fue equivalente a la fecundidad total potencial anual; en otras palabras,

la fecundidad en el pez sable está determinada. La fecundidad potencial anual de un pez de 2.5 kg de peso fue de 107 ovocitos por gramo de hembra. La fecundidad parcial promedió 24 ovocitos hidratados por gramo de hembra para el último desove y 41 ovocitos para los desoves anteriores. De esta manera, el pez sable debiera desovar 3 veces por año para hacer uso completo de su fecundidad potencial.

### INTRODUCTION

The objective of this study was to estimate fecundity, length at first maturity, bathymetric distribution, and frequency of spawning for sablefish, *Anoplopoma fimbria*, from central California, and to identify the spawning period. Sablefish occur along the northern rim of the Pacific Ocean from the southern tip of Baja California to the north-central Bering Sea and from there to central Honshu, Japan. Most of the U.S. catch is taken between southeastern Alaska and central California (MBC 1987).

We use our analysis of sablefish fecundity to evaluate the assumption of determinate fecundity. In fishes with determinate fecundity, the standing stock of advanced oocytes before spawning is equivalent to the total potential fecundity for the year. In many fishes (anchovy, sardine, mackerel, and others) fecundity is indeterminate (Hunter and Macewicz 1985a; Hunter et al. 1985); the standing stock of advanced oocytes is not equivalent to the total potential fecundity because unyolked oocytes are continuously matured and spawned during the reproductive season. Validation of the assumption of determinate fecundity is important because if determinate fecundity is wrongly assumed, total fecundity estimates are meaningless.

Some reports on sablefish reproduction exist: Mason et al. (1983) thoroughly studied fecundity (standing stock of advanced oocytes), identified the peak spawning period, and determined age and size at maturity of Canadian sablefish; Phillips and Imamura (1954) give some incidental values of standing stock of advanced oocytes for a few fish from California; Cailliet et al. (1988) estimated seasonality of reproduction, and report on the relation between bathymetry, size, and sexual maturity for

fish from Monterey Bay, California; Fujiwara and Hankin (1988) report similar information for northern California; and Norris et al. (1987) estimated the seasonality of reproduction for fish from the Oregon and Washington coasts. No sablefish study has considered the frequency of spawning or evaluated the assumption of determinate fecundity.

## METHODS

### *Collections and Shipboard Measurements*

Sablefish were collected along the central California coast (Point Conception to San Francisco Bay) during two research trawl surveys (January–February 1987; February–April 1988), during a trap survey conducted by the NWAFC (October 1986), and from the fishery by the California Department of Fish and Game (October 1986–February 1987). Research trawls were about one hour long in 1987, and were taken at fixed and repeated stations at seven depths (100–700 fath., 183–1280 m) in 1987. In 1988, random trawl samples were taken within three depth strata (30–249 fath., 55–455 m; 250–549 fath., 457–1004 m; 550–699 fath., 1006–1278 m) with tow durations of 0.5 hr in the first stratum and 1.0 hr in the middle and the deep strata. The trawl used was a 400-mesh Eastern with a mouth width of about 15 m, and height about 1.5 m (Wathne 1977).

In the 1986 trap survey, the females collected for fecundity were weighed and measured (FL, fork length) at the time of capture. In both trawl surveys (1987 and 1988) the total catch of sablefish was weighed; each fish was sexed and measured (FL); and a wet weight of most of the females was taken. The data were used to describe the bathymetric distribution of sablefish. We used the trawl catch of sablefish (kg/hr) to relate abundance to depth, but because the trawl extended only 1.5 m from the bottom, biomass is probably greatly underestimated by the catch; the average catch altitude for sablefish caught on setlines by Sullivan (1982) was 12 m off the bottom. In the 1987 survey, bottom temperatures and oxygen concentration were measured over the depth range of the survey (100–700 fath., 183–1280 m).

Reproductive measurements were made only during the 1986 and 1987 surveys. Data from the 1988 survey were used only to define the bathymetric distribution of sablefish. In 1988, ovaries were classed on shipboard into three types: hydrated (ovaries containing translucent hydrated yolkeed oocytes); active (ovaries containing yolkeed oocytes); and inactive (ovaries containing neither hydrated

nor other yolkeed oocytes). The inactive class includes stages designated in other classification schemes as “spent,” “immature,” and various “developing” stages. In 1986–87 a five-class table was used, but we believe no useful purpose was served by attempting to make such distinctions, which in some cases are highly subjective. Although “spent” ovaries can be identified with reasonable accuracy immediately after a spawning, we did not use this stage because it is an ephemeral stage of unknown duration. An ovary classified as “spent” transforms into an inactive or active state depending on whether the female has completed all spawnings or will spawn again. Ovaries from females used in fecundity estimates were frozen or preserved in 10% neutral buffered Formalin and then weighed in the laboratory.

The length at first maturity was estimated by calculating the fraction of the ovaries that were active per length class for fish taken early in the spawning season (October 1986).

The fraction of females with hydrated ovaries taken in research trawls (1987 and 1988) was used to estimate the time of day that sablefish spawn.

### *Total Fecundity*

We measured the total fecundity of 45 females captured in sablefish traps (October 20–27, 1986), and of 41 females taken in research trawls (January 17–February 14, 1987). Total fecundity ( $F_T$ ) is defined as the total number of advanced yolkeed oocytes in the ovary, including all hydrated oocytes.

We estimated total fecundity gravimetrically. Using this method, fecundity ( $F_T$ ) is the product of the gonad weight ( $G$ ) and oocyte density ( $C$ ). Oocyte density is the number of oocytes, within a specified diameter range, per gram of ovarian tissue, and is determined by counting the number of advanced oocytes in a weighed sample of ovarian tissue. We looked for differences in oocyte density between the right and left ovary and found none. We then removed two tissue samples from the right ovary, and counted all the advanced yolkeed oocytes in both samples. In one of the samples we also measured the diameters of 30 randomly selected advanced yolkeed oocytes. Advanced oocytes were identified, counted, and measured using a digitizer linked by a video camera system to a dissection microscope.

Measuring the diameter of the advanced oocytes served several functions. It provided a criterion for selecting ovaries that had matured enough to accurately estimate the density of advanced oocytes (see next section). Diameter was also used to determine seasonal changes in maturity of the advanced group



of oocytes. Finally, diameter provided an alternate method for estimating oocyte density. Oocyte density ( $C$ ) can be roughly estimated from the mean diameter ( $D$ ) of oocytes, because the weight of the advanced oocytes is proportional to their volume (assuming a spherical form and a specific gravity of 1). Hence,

$$C = K \frac{1}{\frac{1}{6} \pi D^3}$$

where  $\frac{1}{6} \pi D^3$  is the volume of a sphere, and  $D$  is mm/10.

The coefficient of proportionality  $K$  was estimated for the October and January–February collections to determine if the density of advanced oocytes in the ovarian tissue changed over the spawning season. We did not measure the diameter of hydrated oocytes, nor did we use data from hydrated ovaries to estimate  $K$ .

#### Identification of the Advanced Stock of Oocytes

As a sablefish ovary matures, the standing stock of advanced yolked oocytes, believed to constitute the total fecundity for the season, gradually separates from the stock of smaller immature oocytes. When sufficiently mature, the standing stock is easily identified because it is separated from the immature oocytes by a gap in the oocyte size-frequency distribution where no or few oocytes occur (figures 1C and 1D; and illustrations of Mason 1984). Estimates of the standing stock can be biased in ovaries in which complete separation has not occurred (figures 1A and 1B). Thus for our fecundity estimates we wished to select ovaries in which the advanced oocytes were well separated from the less-advanced oocytes.

The apparent density of yolk within oocytes viewed on the video screen was used to discriminate between developmental stages of yolked oocytes. Four developmental stages were defined: stage 0, no yolk granules present (primary oocytes), oocyte diameter greater than about 0.1 mm; stage 1, initial layer of yolk along the periphery of the oocyte, appearing as a narrow band not extending over 20% of the distance between the nucleus and the zona pellucida; stage 2, layer of yolk extending from periphery to the nucleus, but nucleus is clearly visible; stage 3, yolk sufficiently dense that the nucleus is indistinct or occluded (advanced oocytes).

Examination of six ovaries indicated that when the mean size of the oocytes in stage 3 (advanced yolked oocytes) was greater than 0.7 mm, the separation of the advanced mode of oocytes from those

#### DISTRIBUTION OF THE DIAMETERS OF OOCYTES WITHIN FOUR DEVELOPMENTAL STAGES

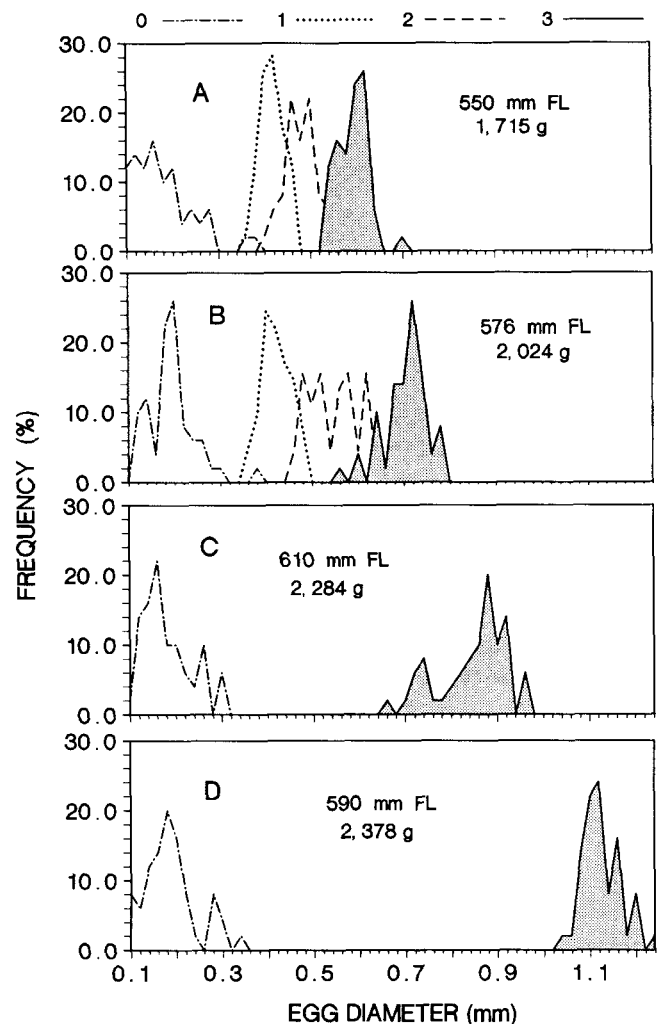


Figure 1. The frequency distribution of the diameter of oocytes within four maturity stages based on apparent yolk concentration. Each panel presents data for one female. Stages range from 0 (no yolk) to stage 3, the most advanced stage (used to estimate fecundity). A and B, sablefish ovaries in which separation of advanced standing stock (stage 3) is incomplete; C and D, ovaries where advanced oocytes are completely separated from other yolked oocytes.

in stages 1 and 2 was nearly complete. Thus, in our routine fecundity measurements we counted and measured only advanced yolked oocytes as defined above. If the mean of such oocytes was greater than 0.7 mm we included the data, but if the mean diameter  $\leq 0.7$  mm, the ovary was rejected because it was not sufficiently mature for an accurate estimate of the standing stock of advanced yolked oocytes.

#### Batch Fecundity

The number of hydrated oocytes in an ovary is equivalent to the batch fecundity ( $F_B$ ) — the number of oocytes released during one spawning. Owing to

their large diameter (about 2 mm) and translucent appearance, hydrated oocytes are easily identified. Batch fecundity was estimated for 17 females taken in the 1987 research trawl survey by counting the number of hydrated oocytes in two tissue samples per ovary. We also estimated the number of non-hydrated advanced oocytes present in the same ovary using the procedure described for estimating total fecundity. A sample of 17 ovaries was too small to determine the relation between fish weight ( $W$ , always calculated as ovary-free female weight) and batch fecundity; thus batch fecundity was expressed as relative batch fecundity ( $F_B/W$ ) [batch fecundity/ovary free female weight]. Total fecundity ( $F_T$ ) for females with hydrated ovaries was the sum of the hydrated and advanced yolked oocytes.

### Histological Analysis

Fresh ovaries from the 1987 research trawl survey were preserved in 10% neutral buffered Formalin and embedded in Paraplast. Histological sections were cut at 5–6  $\mu\text{m}$  and stained with Harris hematoxylin followed by eosin counterstain (H&E). We did not histologically examine ovaries from the October 1986 survey because most of the fish had been frozen before being preserved in Formalin. Consequently, they were unsuitable for detailed histological analysis. Ovaries of sablefish taken in 1988 were not preserved.

Each ovary was classified histologically in the manner developed for northern anchovy (*Engraulis mordax*) by Hunter and Goldberg (1980), and Hunter and Macewicz (1980, 1985a,b), with a few modifications appropriate for sablefish ovarian structure. In the ovary we identified the presence or absence of oocytes in the first vitellogenic stages; advanced yolked oocytes; migratory nucleus stage oocytes (precursor to hydration); hydrated oocytes; postovulatory follicles; and three stages of atretic oocytes. The rate at which postovulatory follicles are resorbed in sablefish is unknown. Thus no ages were assigned to postovulatory follicles. Spent ovaries usually contained two groups of postovulatory follicles of differing deterioration, indicating two past spawnings. The oldest group of postovulatory follicles had to be at least 48 hr old; we suspect they were older because of their small size and extent of resorption.

## RESULTS

### Seasonal and Daily Timing of Spawning

The percentage of all females with reproductively active ovaries declined between October and Feb-

ruary (figure 2). Similarly, ovary weight of Monterey sablefish declined markedly between November–December and January–February (Cailliet et al. 1988). These data indicate that the peak spawning period for sablefish in central California probably occurs sometime between October and February.

On a daily basis, peak spawning may occur between 1300 and 1600 hours. The proportion of females with hydrated ovaries was highest (24%) between 0900 and 1200 hrs and was low (2%) during the rest of the day, indicating that most females may have spawned by 1300 (table 1). No females with hydrated oocytes were taken at night (1700–0400), indicating that the hydrated oocyte stage may be shorter than 24 hours and that, collectively,

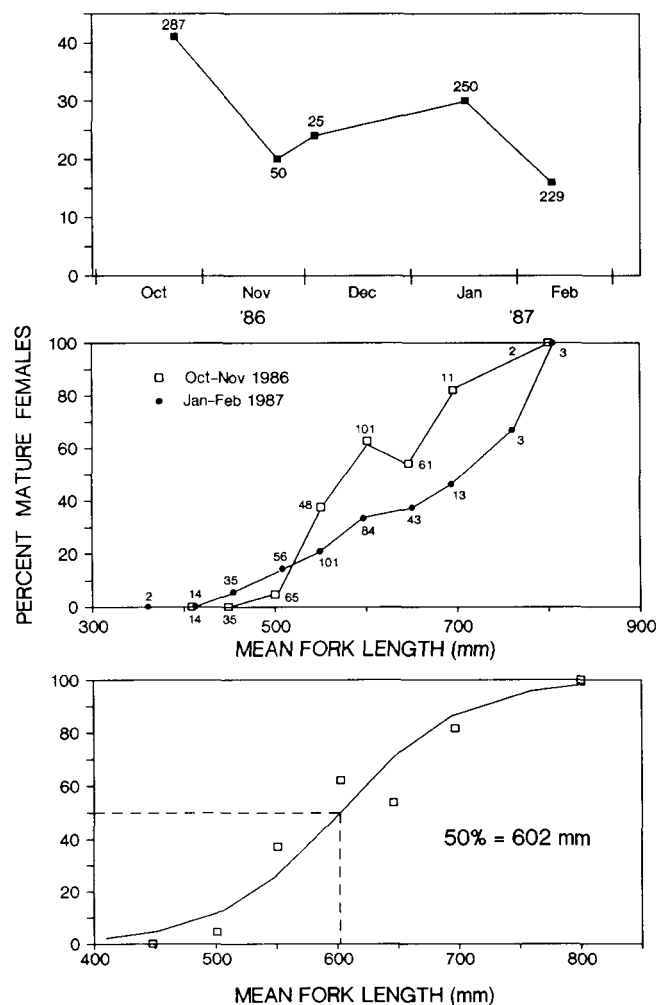


Figure 2. Fraction of sablefish ovaries that were active (yolked oocytes present) during 1986–87 spawning season as a function of collection date (upper panel) and fork length (middle panel), where squares are sablefish taken in October–November 1986 trap survey, and circles are January–February 1987 trawl survey; fraction active was calculated by 50-mm length classes; numbers are the number of fish per length class. Lower panel, fraction of females mature within each 50-mm length class; estimated length at 50% maturity = 602 mm.

TABLE 1  
 Percentage of Female Sablefish with Ovaries  
 Containing Hydrated Oocytes

Time of capture	Total N	Percent hydrated
0030–0429	20	0
0430–0829	50	2.0
0830–1229	67	23.9
1230–1629	111	1.8
1630–2029	30	0
2030–0029	75	0
Entire day	353	5.4

Data from January–February 1987 survey.

the processes of hydration, ovulation, and spawning may require less than 24 hours to complete.

### Length, Maturity, and Bathymetry

The percent maturity of sablefish females ( $P$ ) as a function of fork length was estimated using the logistic regression

$$P = \frac{e^{a+bx}}{1 + e^{a+bx}}$$

where  $x$  = forklength in mm;  $a = -11.978$ ,  $SE(a) = 1.439$ ,  $t(a) = -8.322$ ;  $b = 0.020$ ,  $SE(b) = 0.00244$ ,  $t(b) = 8.177$ ; and  $DF = 335$ . In October the percentage of females with active ovaries increased with length; about 50% of females were reproductively active at 60 cm FL (figure 2). Misclassification of mature females as immature was unlikely because October was early in the spawning season. Our estimate of female length at first maturity (60 cm FL) was similar to that for females from British Columbia, where values ranged from 58 to 62 cm FL (Mason et al. 1983), and to that for females from northern California (56 cm; Fujiwara and Hankin 1988).

The mean length of males and females taken in trawls increased with depth, and the rate of change of length with depth was about the same in the two surveys (figure 3). At most depths, the average female and male sablefish taken in traps were longer than those taken in trawls. The mean length of fish taken in traps increased more slowly with depth than it did for those taken in the trawl. The lengths of fish taken by the two gears were about the same at depths of 500 fath. (914 m) or more, presumably because small sablefish do not occur at such depths.

Of the 87 female sablefish with active ovaries taken in January–February 1987, 96% were taken at depths of 450 fath. (823 m) or greater; most of the active females (75%) were taken between 550 and

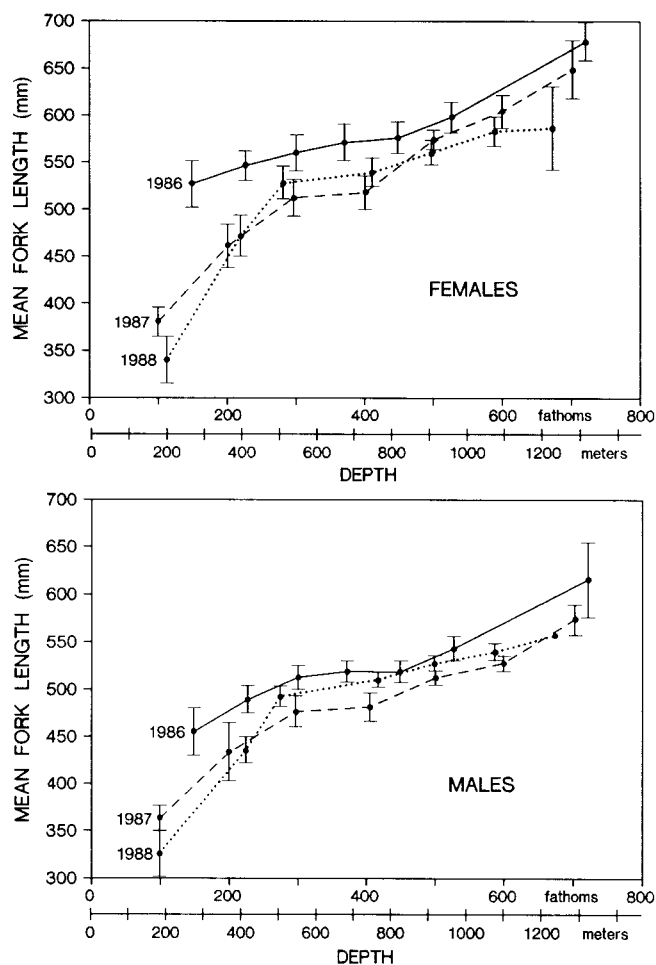


Figure 3. Upper panel, mean fork length ( $\pm 2 \times$  standard error of mean) of female sablefish for 100-fath. (183-m) depth classes: solid line, 1986 October–November trap survey; dashed line, 1987 January–February trawl survey; dotted line, 1988 February–April trawl survey. Lower panel, mean fork length of males for the same surveys.

650 fath. (1006 and 1189 m). Thus in central California, the principal spawning habitat of sablefish seems to be the continental slope at depths of 450 fath. (823 m) or greater. How far down the slope reproductively active sablefish occur is unknown. The mean length of sablefish increased with trawling depth up to the maximum depth of our trawl collections (700 fath., 1280 m), and nearly all of the females taken at 700 fath. (1280 m) were reproductively active. Although reproductively active sablefish probably occur at depths greater than 700 fath. (1280 m), their abundance may be low. The catch rates of sablefish in 1987 and 1988 reached a maximum at 500 fath. (914 m) and declined at greater depths (figure 4). The spawning habitat of sablefish in central California is characterized by low oxygen concentrations as well as low temperature (figure 5).

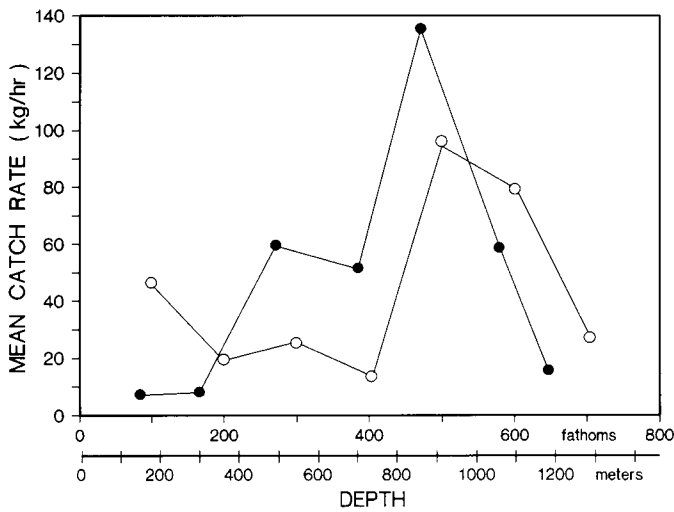


Figure 4. Catch rate of sablefish taken in 400-mesh Eastern trawl at 100-fath. (183-m) depth classes: open circles, 1987 survey; solid circles, 1988 survey.

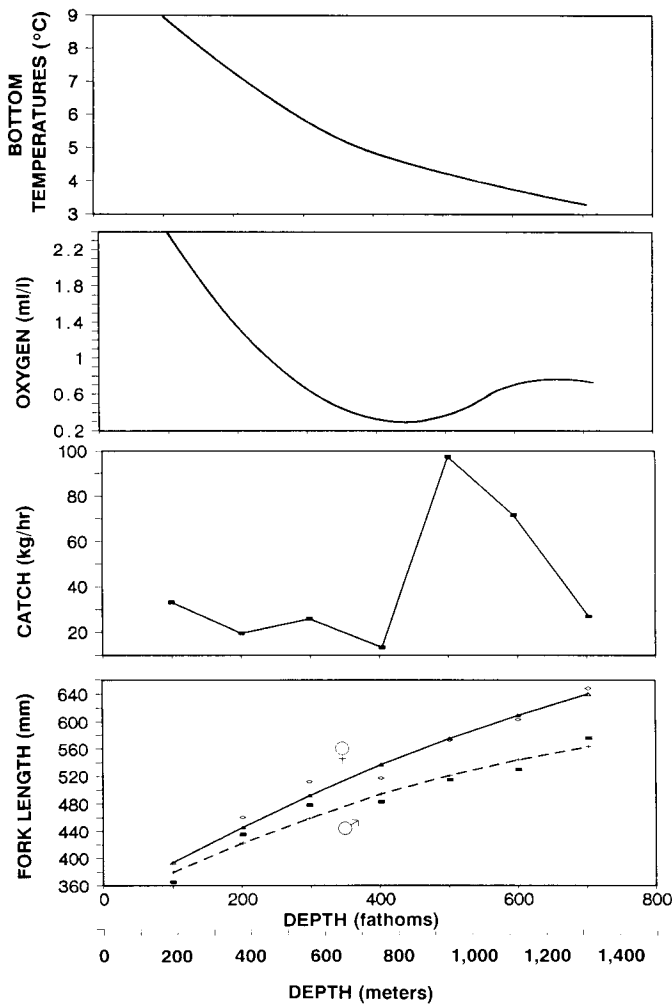


Figure 5. Relation between depth and bottom temperature, bottom oxygen concentration, sablefish catch, and fork length for 1987 survey.

### Total Fecundity

The total number of advanced oocytes in the ovaries ( $F_T$ ) of sablefish captured in October 1986 increased linearly with female weight ( $W$  in grams),

$$F_T = -45,223 + 125.1 W,$$

where  $r^2 = 0.50$ ; figure 6, upper, and table 2. According to this equation the total potential relative fecundity ( $F_T/W$ ) of the sablefish taken in October ranged from 100 oocytes/g female weight for a 1.8-kg female, to 107 for a 2.5-kg fish. The relation between female fork length ( $L$ ) and fecundity ( $F_T$ ) was

$$F_T = 2.145 \times 10^{-5} L^{3.616}$$

where  $r^2 = 0.40$ .

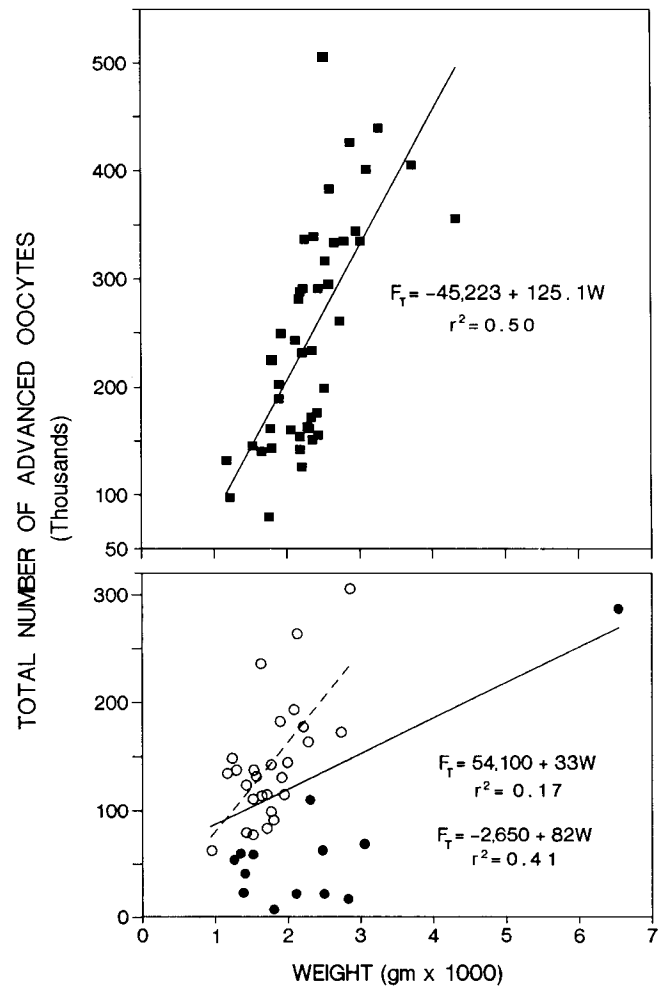


Figure 6. Upper panel, number of advanced oocytes in sablefish ovaries in October 1986 as a function of ovary-free female weight ( $N = 45$ ). Lower panel, standing stock of advanced oocytes in January-February 1987 as a function of ovary-free female weight: open circles, no postovulatory follicles present in ovary; solid circles, postovulatory follicles present in ovary. Solid line, regression for all data ( $N = 41$ ); dashed line, regression where ovaries with postovulatory follicles are omitted ( $N = 28$ ).

TABLE 2

Standing Stock of Oocytes in Sablefish Ovaries in Order of Female Weight (Ovary-Free) Within a Survey Period

October 20 to 28, 1986				January 16 to February 13, 1987						
Female			Standing stock of advanced oocytes (thousands)	Female			Thousands of advanced oocytes			Post-ovulatory follicles + = present - = absent
Wet weight (g)	Fork length (mm)	Ovary weight (g)		Wet weight (g)	Fork length (mm)	Ovary weight (g)	Non-hydrated	Hydrated	Total	
1165	500	110	132	944	474	86	62	0	62	-
1218	510	49	97	1173	528	133	136	0	136	-
1535	560	125	146	1228	500	172	149	0	149	-
1654	540	72	140	1262	515	235	0	54	54	+
1686	550	29	51	1300	520	136	139	0	139	-
1752	560	93	80	1355	502	281	1	59	60	+
1766	560	80	161	1394	538	130	0	23	23	+
1797	550	63	143	1418	552	194	0	41	41	+
1797	580	184	224	1434	522	148	124	0	124	-
1891	570	122	189	1441	530	104	80	0	80	-
1922	570	128	249	1515	540	109	78	0	78	-
1988	630	202	505	1525	557	125	112	0	112	-
2062	570	99	160	1529	548	237	6	53	59	+
2118	590	122	243	1543	550	169	138	0	138	-
2164	590	141	281	1568	540	194	132	0	132	-
2182	590	112	154	1645	632	791	103	134	237	-
2183	620	97	141	1656	540	169	114	0	114	-
2184	610	100	288	1698	547	171	126	0	126	-
2206	590	123	126	1722	572	147	21	63	84	-
2207	600	178	232	1729	545	355	64	51	115	-
2221	610	129	291	1760	524	245	143	0	143	-
2241	580	149	336	1779	545	291	14	86	100	-
2290	610	126	163	1799	577	109	91	0	91	-
2312	620	159	161	1807	595	77	6	0	6	+
2330	600	126	171	1892	550	238	182	0	182	-
2345	590	145	232	1920	560	215	131	0	131	-
2351	590	164	151	1958	595	134	116	0	116	-
2362	600	65	270	2003	605	423	74	71	145	-
2375	600	111	339	2094	590	268	194	0	194	-
2414	620	171	176	2107	610	153	0	22	22	+
2434	630	156	155	2143	597	351	264	0	264	-
2440	610	121	291	2215	590	163	178	0	178	-
2465	620	58	234	2291	594	239	164	0	164	-
2472	610	65	388	2309	620	391	28	82	110	+
2519	650	96	199	2470	630	315	2	62	63	+
2534	620	107	316	2501	636	44	22	0	22	+
2579	630	91	295	2744	582	296	173	0	173	-
2595	610	251	382	2838	625	122	0	17	17	+
2660	620	106	333	2866	660	564	207	99	306	-
2728	620	242	261	3058	665	326	0	69	69	+
2793	640	264	335	6543	818	938	31	255	286	+
2878	640	124	426							
2888	560	132	201							
2953	640	127	344							
3015	670	224	334							
3096	670	189	401							
3275	650	145	439							
3394	680	136	556							
3730	690	370	405							
4328	720	409	356							

By January–February 1987, the standing stock of advanced oocytes had declined to about 60% of oocyte stock observed in October 1986, and was only weakly correlated with female weight:

$$F_T = 54077 + 32.8 W,$$

$r^2 = 0.17$ , (figure 6, lower). Statistical documentation for this seasonal decline in oocyte standing stock is provided by multiple regression of fecundity on elapsed time and female weight:

$$F_T = 95,202 - 1150 T + 5.71 W,$$

where  $T$  is elapsed time from October 20, and  $R^2 = 0.50$ . Relative fecundity ( $F_T/W$ ) declined from 105 oocytes/g (SD = 36.0,  $N = 45$ ) in October to 64 oocytes/g (SD = 33.9,  $N = 41$ ) in January–February. A  $t$  test showed that the means were significantly different ( $p < 0.05$ ,  $t = 5.41$ ,  $DF = 83$ ). This seasonal decline in the standing stock of advanced oocytes indicates that some of the females had spawned part of their advanced stock of oocytes, and these oocytes were not replaced. Therefore determinate fecundity is indicated.

The weak relation between fecundity and fish weight in January–February ( $r^2 = 0.17$ ) was probably caused by variation in the number of spawnings completed by each female. That females with postovulatory follicles (solid circles, figure 6, lower) had the lowest fecundity for a given weight supports this conclusion. The relative fecundity of females without postovulatory follicles was 81 oocytes/g (SD = 24,  $N = 28$ ), whereas that for fish with postovulatory follicles was only 26 oocytes/g (SD = 15,  $N = 13$ ). Thus, spawning has reduced the standing stock of advanced oocytes and consequently supports the assumption of determinate fecundity. The relation between fecundity and female weight for January–February is much stronger if females with postovulatory follicles are excluded:

$$F_T = 82.5 W - 2652,$$

$r^2 = 0.41$  (figure 6, dashed line). This indicates that the high variability in the January–February 1987 data was caused by spawning. The slope of the regression of fecundity on weight for January–February 1987 is lower than the one for October 1986 even when fish with postovulatory follicles are excluded. Thus spawning probably occurred in females in which no postovulatory follicles were detected. Presumably, enough time had elapsed before capture for the postovulatory follicles to be resorbed in these fish.

#### Batch Fecundity and Spawning Frequency

The mean relative batch fecundity (based on counts of hydrated oocytes) was higher when many advanced yolked oocytes occurred with the hydrated batch than when few or none occurred. Thus the size of the last spawning batch was lower than that of earlier batches, and the number of oocytes in the last spawn averaged 24 oocytes/g, whereas the other spawnings averaged 41 oocytes/g (table 3). A  $t$  test showed significant difference in the means ( $p < 0.05$ ,  $t = 2.348$ ,  $DF = 15$ ).

The mean weight of the 17 females with hydrated

TABLE 3  
**Relative Fecundity (Number of Advanced Yolked Oocytes per Gram Ovary-Free Female Weight) of 17 Sablefish Females with Hydrated Oocytes**

Potential spawnings $\geq 2$			Potential spawnings = 1		
Not hydrated <sup>a</sup>	Hydrated	Total	Not hydrated <sup>b</sup>	Hydrated	Total
72	34	106	0.64	44	45
62	81	143	0.64	25	26
37	35	72	0.09	9.8	10
37	29	66	0.07	43	43
12	36	48	0	29	29
12	36	48	0	22	22
7.6	48	56	0	16	16
4.8	39	44	0	6.0	6
3.9	34	38			
Mean batch fecundity <sup>c</sup>	41.3			24.3	
SD	15.7			14.0	

<sup>a</sup>Mean diameter = 1.44, SD = 0.059, and range 1.31–1.52.

<sup>b</sup>Mean diameter = 1.46, SD = 0.015, and range 1.45–1.48.

<sup>c</sup>Calculated from the number of hydrated oocytes

Females separated into two classes: those likely to spawn two or more batches because, in addition to the hydrated batch, substantial numbers of advanced oocytes exist in the ovary; and those in which the hydrated oocytes may be the last spawning batch because, other than the hydrated batch, few or no advanced oocytes exist in the ovary.

oocytes was 2237 g, (SD = 1245). According to our fecundity equation for fish taken early in the season (October), a fish of this weight would have a standing stock of 234,836 advanced oocytes or about 105 oocytes/g female weight. This female would have to spawn three times to use this standing stock of oocytes, assuming that the number of advanced oocytes in the last batch is 24 and the other spawnings are 41 oocytes/g female weight. In other words, division of our estimates of relative batch size into what we believe to be the initial standing stock of oocytes indicates that the average female sablefish spawns about three times per season. We assumed that if the remaining advanced oocytes were fewer than one oocyte/g, the oocytes would not be spawned and would be resorbed. The smallest hydrated batch we observed was 6 oocytes/g.

#### Oocyte Diameter

The mean diameter of the advanced oocytes (excluding hydrated oocytes) increased from 1.0 mm (SD = 0.17,  $N = 50$ ) in October 1986 to 1.34 mm (SD = 0.15,  $N = 37$ ) in January–February. A  $t$  test showed that the means differed significantly ( $p < 0.05$ ,  $t = -10.04$ ,  $DF = 81$ ). This observation supports the assumption of determinate fecundity, because an increase in average diameter of the advanced oocytes would not be likely if new, smaller oocytes were recruited into the advanced

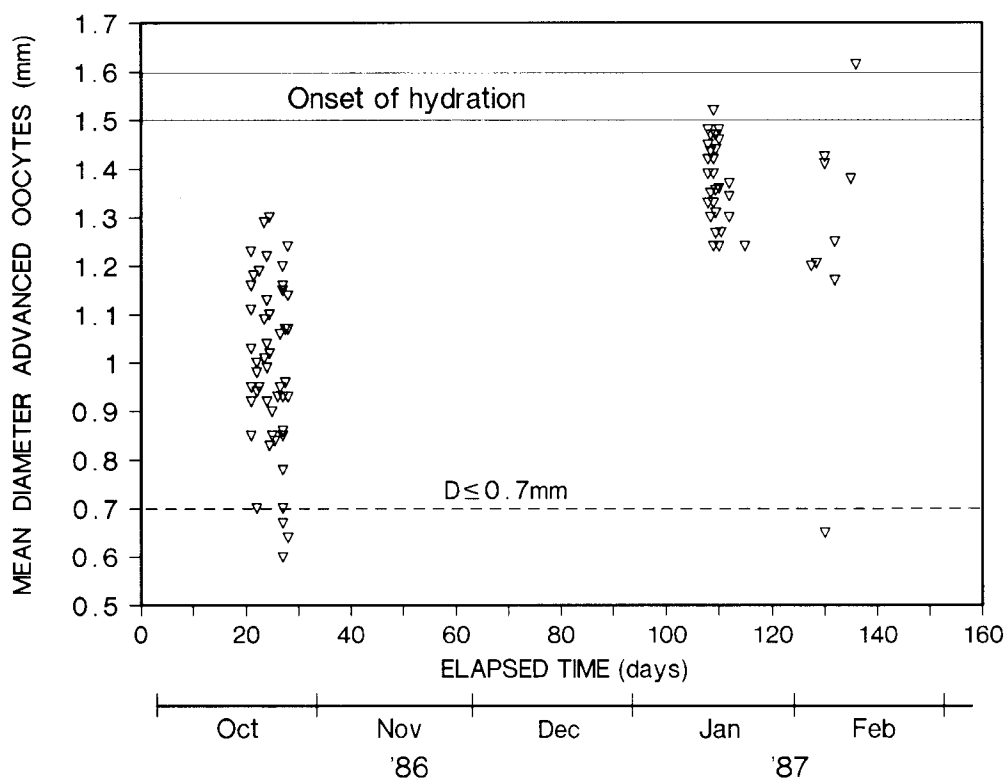


Figure 7. Mean diameter ( $D$ ) of advanced oocytes in sablefish ovaries as a function of elapsed time ( $T$ ) in days from October 6, 1986, to February 13, 1987. Shaded area indicates oocyte diameters at which the onset of hydration occurs; total fecundity was not estimated for ovaries in which the mean diameter was  $\leq 0.7$  mm (dashed line).

standing stock during the spawning season. By the middle of January the mean diameter of the advanced oocytes was 1.34 mm, which is close to the diameter at which hydration begins (1.5–1.6 mm) (figure 7). Thus by January, little maturation would be required to hydrate and spawn most of the advanced oocytes remaining in the ovary.

We compared the mean oocyte density (mean count of advanced oocytes in two tissue samples) to one calculated from the mean diameter by regressing mean oocyte density on the computed density  $(\frac{1}{6} \pi D^3)^{-1}$  for fish taken in October and in January–February. In both sampling periods the intercept was very small and did not differ from zero. Assuming a zero intercept, the slope ( $K$ ) was 0.94 for October and 0.88 for January–February. We tested the equality of the slopes by analysis of covariance (Zar 1974), and the results indicated that the slopes were not statistically different ( $t = 0.253$ ,  $DF = 65$ ). We combined the data from the two cruises to obtain a common slope of 0.94 (figure 8).  $K$  was less than one because samples of ovarian tissue contain material other than advanced oocytes (tissue fragments, postovulatory follicles, immature oocytes, etc.).

That  $K$  was nearly the same for fish taken in January–February as for those taken in October indicates that the fraction by weight of materials

other than advanced oocytes in the tissue samples remained constant over the season, even though many of the females taken in January–February had spawned some of their oocytes. This indicates that postovulatory follicles are resorbed relatively rapidly after each spawning, and no major proliferation of vitellogenic oocytes had occurred. The relationship between observed oocyte density and the one computed from oocyte diameter was more variable for fish taken in January–February than in October:  $r^2 = 0.55$  for January–February and 0.91 for October. Ovaries containing postovulatory follicles were substantially below the 0.94 line (figure 8, insert), indicating that the higher variability in January–February was probably caused by the occurrence of ovaries in which postovulatory follicles had not been resorbed.

The mean diameter of the advanced stock of oocytes was inversely correlated with total fecundity. A stepwise multiple regression of total fecundity ( $F_T$ , all data, October–February) on female weight ( $W$ ), oocyte diameter ( $D$ ), and elapsed time ( $T$ , during the spawning season) indicated that the diameter explained more of the variation in fecundity over the spawning season than did elapsed time (table 4). The final equation was

$$F_T = 351,992 + 71.4 W - 263,462 D,$$

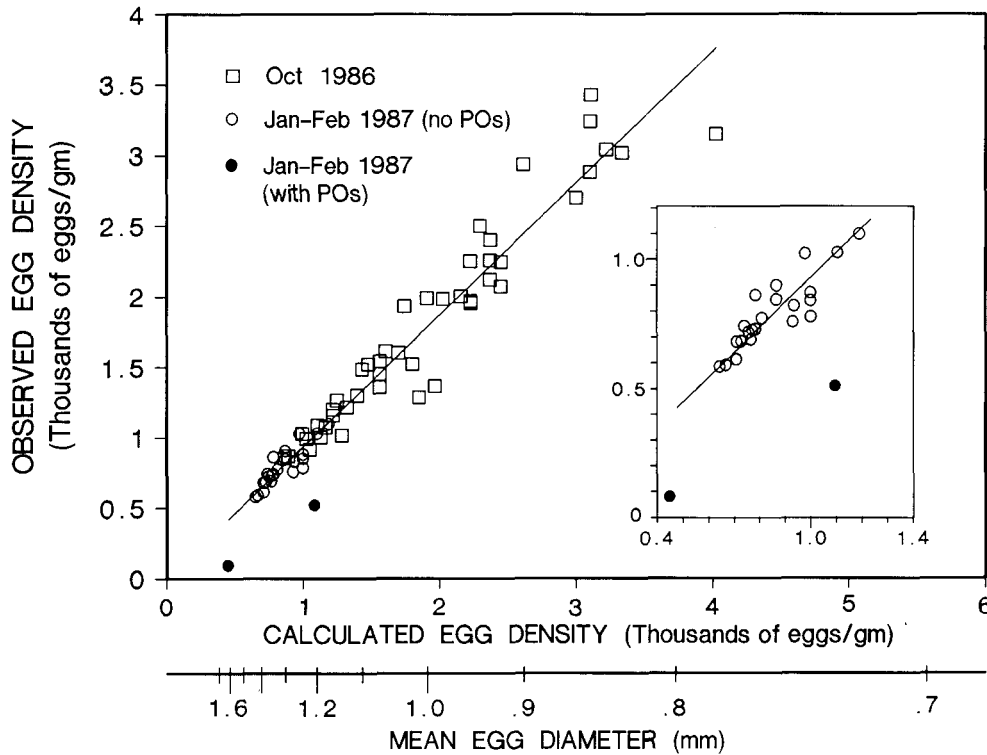


Figure 8. Relation between mean density of advanced oocytes in the ovary (Y axis) and density of oocytes calculated from the average diameter (X axis). The average diameter is calculated using the volume of a sphere and assuming oocyte specific gravity of 1.0:

$$C = K \frac{1}{\frac{1}{6} \pi D^3}$$

For October 1986 data (squares),  $K = 0.91$ ; for February 1987 data (open circles),  $K = 0.89$ ; and  $K = 0.94$  for all data combined (line). Inset shows 1987 data in greater detail; solid circles represent ovaries with postovulatory follicles.

where  $R^2 = 0.61$  ( $T$  was deleted as a variable because its contribution to  $R^2$  was negligible when diameter was included in the equation). Thus the mean diameter of the remaining advanced stock of oocytes appeared to be a better index of losses of oocytes due to spawning than was elapsed time. Diameter was also a significant variable in the fecundity equation when only the specimens taken in October were considered. The inclusion of diameter as a variable increased  $R^2$  from 0.49 for female weight alone to 0.66, yielding the equation

$$F_T = 278,114 + 127 W - 317,198 D.$$

We assumed that the ovaries of females taken in October for fecundity estimation were in a pre-spawning state. That the mean diameter of the advanced oocytes was inversely correlated with fecundity may indicate that some losses due to spawning may have occurred in some of our October specimens.

## DISCUSSION

### *Sablefish Reproduction*

Unlike many pelagic fishes such as anchovy, sardine, tunas, and mackerels, the standing stock of advanced yolked oocytes in sablefish is equivalent

to the total potential fecundity; in other words, fecundity is determinate. Five lines of evidence support this view. (1) In mature ovaries (mean diameter of advanced oocytes  $>0.7$  mm) a hiatus exists between the advanced stock of mature oocytes and smaller immature oocytes (this hiatus is obvious in our figure 1, and Mason [1984] provides many more illustrations). (2) The standing stock of advanced oocytes declined over the spawning season. (3) The standing stock of advanced oocytes was lower in females having postovulatory follicles. (4) The mean diameter of the oocytes in the standing stock increased over the spawning season. (5) Our estimates of batch fecundity, total fecundity, and numbers of advanced yolked oocytes in hydrated ovaries were consistent with the assumption of determinate fecundity.

Two uncertainties exist. Our analysis does not rule out the possibility that more than one stock of advanced oocytes might be developed and spawned in succession during the year. The extent to which the potential total fecundity is realized is also uncertain. However, the low incidence of atretic oocytes in our specimens indicated that the realized and potential fecundity may have been similar in 1987.

The total potential fecundity of sablefish from central California was about twice that of fish from Canadian waters (Mason 1984; Mason et al. 1983),



TABLE 4

Summary of Stepwise Regression of Total Fecundity on Ovary-Free Female Weight (*W*), Mean Oocyte Diameter (*D*), and Elapsed Time (*T*) and Analysis of Variance Table for Second Step with Independent Variables *W* and *D*

Stepwise regression Step	1	2	3			
Constant	13785	351992	340087			
<i>W</i>	84.2	71.4	70.7			
t-ratio	6.76	7.18	6.90			
<i>D</i>		-263462	-248948			
t-ratio		-7.08	-4.10			
<i>T</i>			-85			
t-ratio			-0.30			
<i>S</i>	85664	67260	67655			
<i>R</i> <sup>2</sup>	36.67	61.45	61.50			

Analysis of variance					
Source	DF	SS	MS	<i>F</i>	<i>P</i>
Regression	2	5.62 × 10 <sup>11</sup>	2.81 × 10 <sup>11</sup>	62.18	<0.0005
Error	78	3.53 × 10 <sup>11</sup>	4.52 × 10 <sup>9</sup>		
Total	80	9.15 × 10 <sup>11</sup>			

Source	DF	SEQ SS
<i>W</i>	1	3.36 × 10 <sup>11</sup>
<i>D</i>	1	2.27 × 10 <sup>11</sup>

but the length of females at maturity was about the same. This difference in fecundity could be due to differences between the regions. It is also possible that spawning may have been well underway when the Canadian fish were sampled, thus biasing Mason's estimates downward.

Sablefish from central California require about three spawnings to exhaust their standing stock of advanced oocytes; the last spawning batch is smaller than the first two. We are currently preparing a manuscript on reproduction of Dover sole (*Microstomus pacificus*), a species that lives and spawns in the same habitat as sablefish. The fecundity of Dover sole is determinate; relative to their weight, Dover sole have about the same fecundity as sablefish, but they spawn more frequently (9 or more times per year) and have a lower batch fecundity for their body weight. Thus spawning rate is an important life-history variable even in fishes with determinate fecundity.

Perhaps one of the more interesting unanswered questions concerning reproductive biology of sablefish is how a species that lives and spawns far below the penetration of significant sunlight is able to synchronize its spawning with season and possibly time of day. The reproductive energetics of such fishes as sablefish and Dover sole that live and reproduce in the cold and poorly oxygenated water of

the oxygen minimum zone also seem of particular interest.

### Fecundity Methodology in General

In this section we make a few comments on the analysis of fishes with determinate fecundity. The time of sampling is of key importance in estimating the total potential annual fecundity in sablefish, and probably in most fishes with determinate fecundity. Estimates will be biased if one samples either too early in the spawning season or too late. If one samples too early, the advanced stock may not have matured enough to be completely separate from the smaller immature oocytes, and consequently estimates may be imprecise or biased. We avoided this problem in sablefish by excluding ovaries in which the mean diameter of the advanced oocytes was 0.7 mm or less.

If one samples too late, spawning will have begun, the stock of advanced oocytes will have been reduced, and the total potential fecundity will be underestimated. In sablefish this bias could be large, since a single spawning batch may be a third or more of the standing stock. The possibility that such a bias may exist is usually not mentioned. Some authors may assume that in fishes with determinate fecundity all oocytes are spawned in one batch, or spawning is so frequent that capture of fishes with a partially expended stock of oocytes would be rare. This is not true for sablefish, because females with partially depleted stocks of oocytes were common during the spawning season. In fact, we do not know if our October estimate for sablefish was underestimated because of spawning. One female with hydrated oocytes was taken during the October cruise, indicating that spawning had begun by October. In addition, the inverse correlation of oocyte diameter and fecundity may indicate that some of the October females had spawned.

Accurate measurement of the diameter of advanced oocytes, counts of hydrated oocytes, and occurrence of postovulatory follicles were useful in validating and interpreting sablefish fecundity estimates. Using these measurements to estimate spawning rates for anchovy and other fishes with indeterminate spawning has become routine (Hunter et al. 1985), but their application to determinate spawners is new. Computation of the mean diameter of the oocytes constituting the advanced stock is usually not included in most fecundity studies. This procedure not only provided a quantitative method for selecting fish for fecundity estimates but was also useful in interpreting and validating our fecundity estimates. The mean diameter of the ad-

vanced oocytes increased during the spawning season, was inversely correlated with fecundity, and the reciprocal of the oocyte diameter was proportional to the density of oocytes in the ovary. These relationships helped substantiate the assumption of determinate fecundity. In addition, diameter measurement under certain circumstances may be a rapid method for estimating oocyte density and hence fecundity for determinate spawners.

The mean diameter of the advanced stock of oocytes is also the most accurate measure of ovarian maturity. Our histological analysis of sablefish ovaries indicated that hydration begins when the diameter of the yolked oocyte is 1.5–1.6 mm; investment of yolk ceases at this point, and the remaining increase in oocyte volume is due primarily to water uptake. Thus the ovary can be considered to have a full energy content when all advanced yolked oocytes have a diameter of about 1.5 mm and no oocytes have been spawned. This is a condition we rarely, if ever, encountered. Ovaries in which the mean diameter of the advanced oocytes was close to 1.5 mm were taken late in the season, and some batches may have been spawned. The advanced stock of oocytes in ovaries collected early in the season, when spawning was unlikely, had a smaller average diameter (about 1.0 mm). If one were to use the weight of such early ovaries (dia. = 1.0 mm) as a measure of reproductive effort, it would be necessary to about triple the ovary weight to account for future investment of yolk during the spawning season. Thus even in a determinate spawner such as sablefish, gonad weight is an inaccurate measure of reproductive effort unless values are adjusted for maturity (oocyte diameter) and spawning losses.

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## EFFECTS OF THE 1982–83 EL NIÑO EVENT ON THE EUPHAUSIID POPULATIONS OF THE GULF OF CALIFORNIA

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### ABSTRACT

Euphausiid species distributions and abundances in the central and southern Gulf of California were compared during successive springs: March 12–22, 1983 (peak of 1982–83 El Niño) and March 23–April 7, 1984 (relaxation period). Estimates of overall abundance of individual species did not differ significantly between the two years ( $p > .05$ ). Distributions of abundance suggested between-year differences of a much lower order than seasonal changes previously described. Certain of the marginally tropical or tropical species (*Euphausia eximia*, *E. distinguenda*, and *E. tenera*) were found more consistently to the north in March 1983 than in 1984, accompanying surface salinities  $<35\text{‰}$  and surface temperatures  $>21^{\circ}\text{C}$ , which characterized the influence of tropical water in the gulf in spring 1983. Surface warming during El Niño is suggested as the environmental agent most likely to have had biological effects; however, March temperatures of 1983 were only  $1^{\circ}$  to  $2^{\circ}\text{C}$  over those of 1984.

Youngest observed larvae (calyptopes) of the dominant species, warm-temperate *Nyctiphanes simplex*, exceeded 100,000 individuals/1000  $\text{m}^3$  at 30% of the sampling stations in the gulf during 1984; in 1983, 94% of the stations registered  $<7,000$  ind/1000  $\text{m}^3$ . However, due to high variances around means for each year, such observations are interpreted with caution. In 1983, 60% of *N. simplex* postlarvae were at the northernmost stations, near Tiburón Island, where the lowest temperatures were recorded.

### RESUMEN

Se compararon las distribuciones y abundancias de las especies de eupáusidos en el Golfo de California central y sur durante dos primaveras sucesivas: del 12 al 22 de marzo de 1983 (período de máxima intensidad de El Niño 1982–83) y del 23 de marzo al 7 de abril de 1984 (fase de relajamiento). Las estimaciones de abundancia total por especie no mostraron diferencias significativas entre años ( $p >$

0.05). Las distribuciones de abundancia sugieren que las diferencias entre años fueron de menor orden que la variación estacional previamente descrita. Ciertas especies marginalmente tropicales o tropicales (*Euphausia eximia*, *E. distinguenda*, y *E. tenera*) se encontraron presentes consistentemente más al norte en marzo de 1983 que en 1984, coincidiendo con salinidades en superficie  $<35\text{‰}$  y temperaturas en superficie  $>21^{\circ}\text{C}$ , valores característicos de la masa de agua tropical que invadió el golfo en la primavera de 1983. Se sugiere que el calentamiento superficial del agua durante el evento del Niño pudo haber sido el agente ambiental con mayores efectos biológicos; a pesar que los valores de temperatura registrados en 1983 fueron tan sólo de  $1$  a  $2^{\circ}\text{C}$  más altos que aquéllos en 1984.

Las larvas más tempranas (caliátopis) de la especie dominante, *Nyctiphanes simplex*, indicadora de aguas templado-cálidas, excedieron los 100,000 ind/1000  $\text{m}^3$  en 30% de las estaciones muestreadas en el golfo durante 1984; en 1983, el 94% de las mismas registraron  $<7,000$  ind/1000  $\text{m}^3$ . Sin embargo, estas observaciones deben tomarse con precaución debido a las altas varianzas asociadas a las medias de cada año. En 1983, 60% de las poslarvas de *N. simplex* se encontraron en las estaciones situadas más al norte, cerca de la isla Tiburón, donde se registraron las temperaturas más bajas.

### INTRODUCTION

The Gulf of California (figure 1) comprises a series of basins, deepening to the south, which are produced by transform faults (van Andel 1964). It averages approximately 1000 km long and 150 km wide. The benthic and pelagic inhabitants of the gulf have diverse biogeographical affinities. The benthic fauna is probably best regarded as subtropical, with its closest faunal affinity with the tropical "Panamic" region. Northeast Pacific temperate species form a smaller component that increases in abundance northward in the gulf, and also increases during the winter months (Brusca and Wallerstein 1979). Similarly, the pelagic fauna includes tropical, subtropical, and warm-temperate elements (Walker

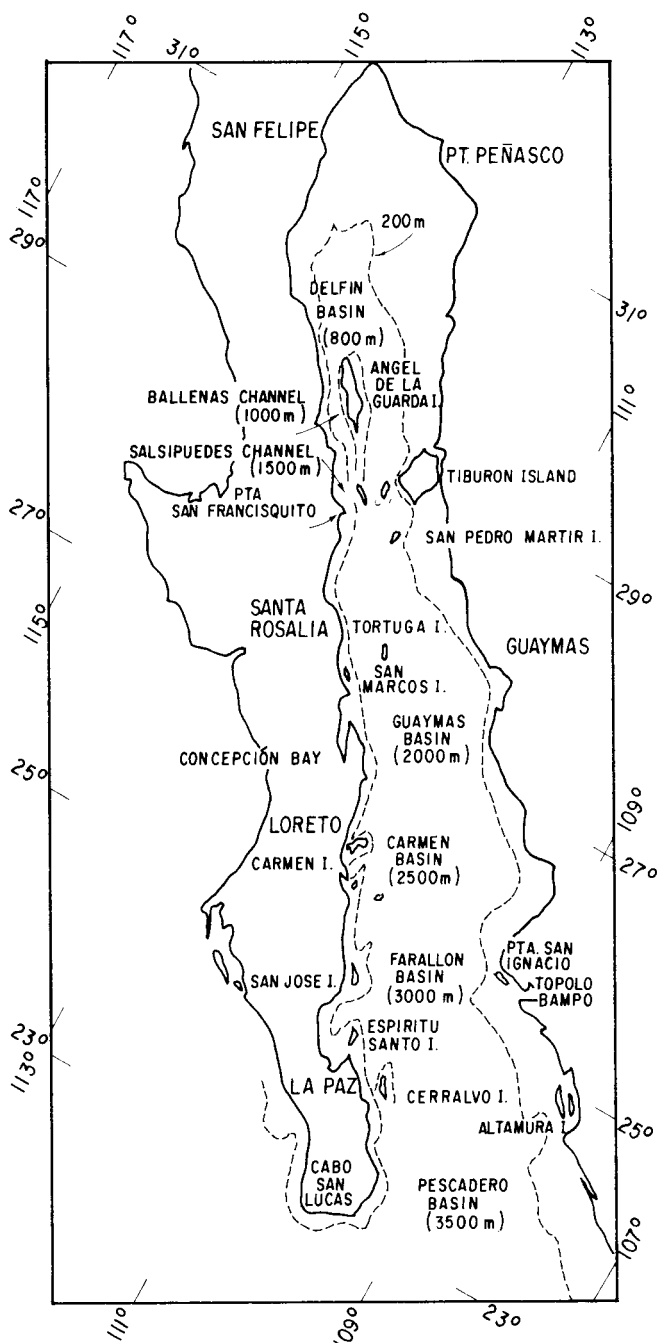


Figure 1. The Gulf of California. Dashed line is 200-m isobath.

1960; Brinton et al. 1986), but interannual changes in distribution or abundance of species have not been described.

Many of the gulf species also occur off the west coast of Baja California, where the California Current meets the equatorial circulation system. The equatorial and the subtropical systems alternately influence the gulf in response to shifts in wind stress (Wyrtki 1966; Baumgartner and Christensen 1985).

The gulf is an evaporation basin, with surface

salinity commonly  $>35\%$ . However, studies of interannual variability of abiotic conditions in the gulf have confirmed the existence of climatic anomalies resulting from strengthening of the equatorial circulation system as a response to El Niño/Southern Oscillation events (Baumgartner and Christensen 1985; Robles-Pacheco and Marinone 1987).

Analysis of preserved siliceous phytoplankton contained in laminated sediments in a 20-year time series from the central gulf has revealed strong abundance increments of tropical and subtropical diatoms in response to El Niño periods (Baumgartner et al. 1985). Periods of enhancement of phytoplankton microfossils in the deep anoxic basins of the central gulf probably correspond to periods of increased primary productivity and chlorophyll *a* content such as was measured during the 1982–83 El Niño event (Valdez-Holguin and Lara-Lara 1987). Zooplankton volumes were also reported to be high during that event (Jiménez-Pérez and Lara-Lara 1988). This contrasts with the diminished volumes observed in other eastern Pacific systems in 1982–83 (Barber and Chávez 1983, 1986; McGowan 1983, 1984, 1985).

In order to interpret effects of El Niño 1982–83 on euphausiid populations of the Gulf of California, we compared euphausiid species distributions and abundances in March 1983, when the event was intense, with those of March–April 1984, when the system was in transition to what is believed to have been more typical conditions. In an earlier study of seasonal changes in populations of euphausiids in the gulf, based on bimonthly cruises during 1957, Brinton and Townsend (1980) determined that February–April was a peak period of reproduction and abundance of most species. They found a close association of distribution and abundance of species with climatic conditions, particularly temperature.

## METHODS

Zooplankton samples were collected from R/V *El Puma* during two cruises extending from Tiburón Island (29°N) southward to the gulf entrance (23°–24°N) during March 12–22, 1983, and March 23–April 7, 1984 (figure 2). Oblique net tows were made from about 200-m depth to the surface, using a 60-cm-mouth-diameter bongo net with 0.333-mm mesh. Volumes of water strained by the nets were determined from flowmeter readings, and abundances of euphausiids were standardized as numbers of individuals per 1000 m<sup>3</sup> of water. Samples were preserved in 4% formaldehyde buffered with sodium borate. Stations were sampled at 12-hour intervals, near to noon and midnight.

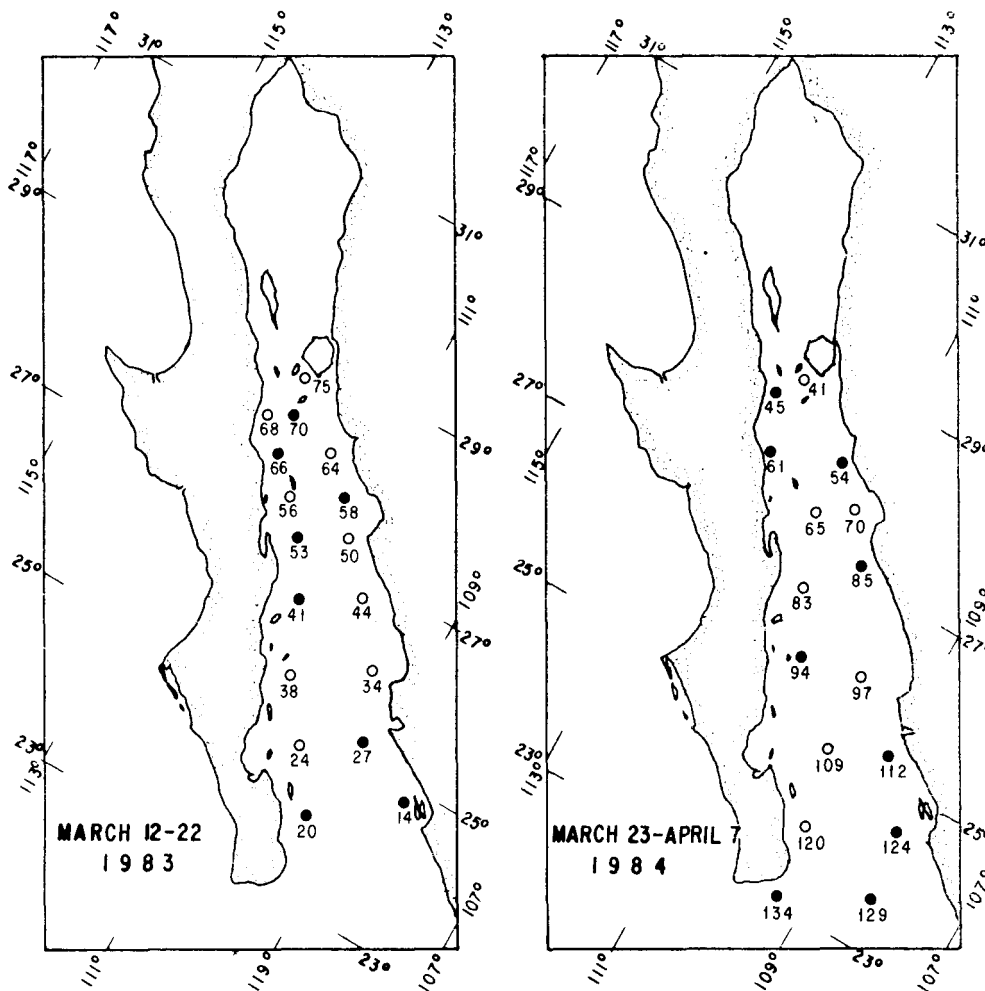


Figure 2. Location of zooplankton tows during CICESE cruises 8303 and 8403/04 (○ = day samples; ● = night samples).

Species were identified and counted in  $\frac{1}{32}$  aliquots, fractionated by means of a Folsom splitter. Three life-history stages — calyptopis and furcilia larvae, and postlarvae (juveniles and adults) — were sorted. When a life stage of a species was represented by fewer than three specimens, additional  $\frac{1}{32}$  aliquots were used, up to a total of  $\frac{1}{8}$  of the original sample. In order to estimate possible combined effects of vertical migration and net avoidance, day abundances of the stages of each species were compared with night abundances by means of Mann-Whitney's U test (Siegel 1980).

Temperature and salinity were measured with a Bissett-Berman CTD at 75 hydrographic stations in March 1983, and at 80 stations in March–April 1984. Dissolved oxygen determinations were done by the Micro-Winkler method at 39 of the 1983 stations. There are no available data for oxygen in 1984.

Frequency distributions of euphausiid abundances were consistently skewed; consequently,

abundances were  $\log_{10}(x \pm 1)$  transformed before calculation of means and 95% confidence limits. These values were then antilogged, 1 was subtracted, then reported in the original measurement unit.

## RESULTS

### *The Physical Environment*

During March 1983, highest surface salinities (34.9‰–35.2‰) were to the north, near Tiburon Island and along the eastern side of the central gulf (figure 3). Values decreased somewhat toward the south, reaching 34.5‰ in the gulf entrance. In March–April 1984, surface salinities were above 35‰ along the length of the investigated area, except at the mouth of the gulf.

In both years, the surface water temperature showed a gradient of increase from north to south (figure 4). In March 1983 it ranged from 18° to 25.5°C, and in 1984 from 15.8° to 23.8°C. In 1983,

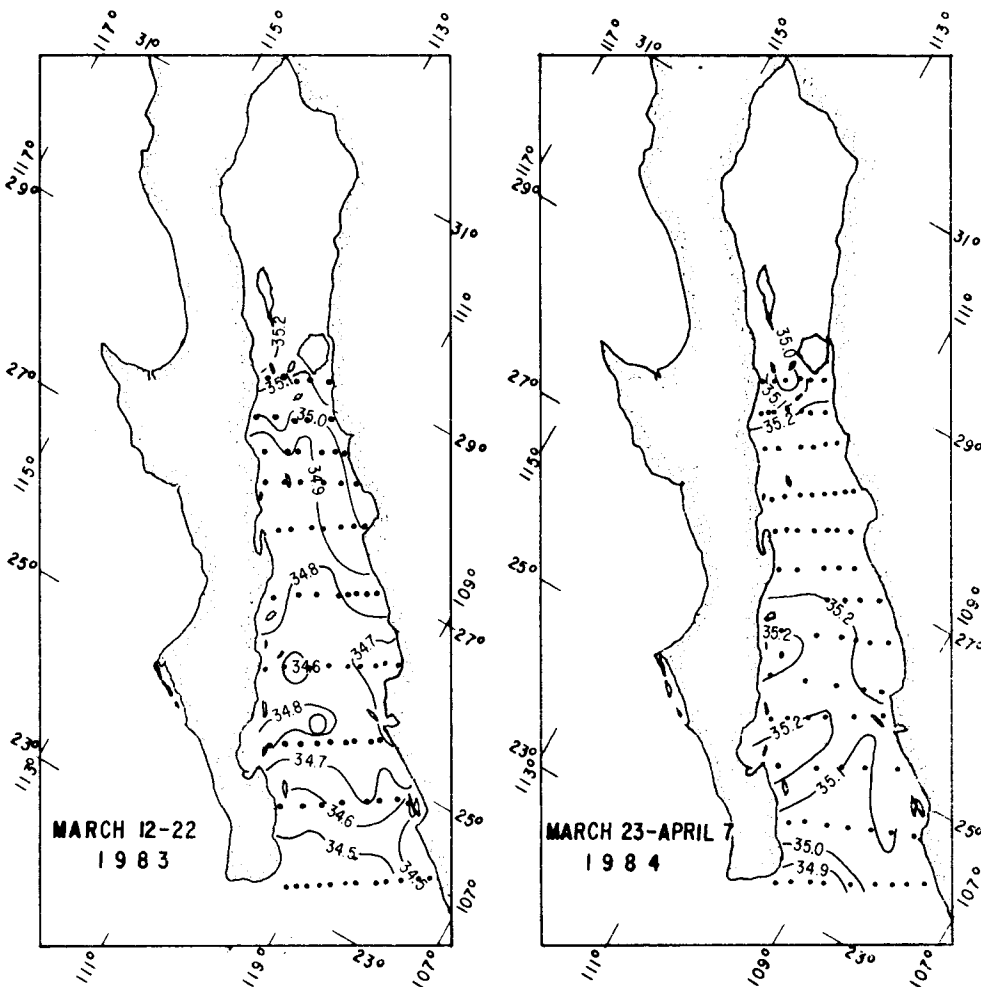


Figure 3. Surface salinity distributions (‰) in the Gulf of California.

tongues of cool water extended along the eastern coast, and in 1984, on both sides of the gulf.

The 1983 temperatures at 30-m depth were 1°C lower than at the surface, but the horizontal gradients were similar at the two levels (figure 5). In contrast, 1984 presented more isotherm distortion at 30-m depth in relation to surface distribution, with temperature differences between coasts as high as 4°C in the southern gulf. The interannual temperature difference persisted at 100-m depth (figure 6), with values about 2°C warmer in 1983 than in 1984.

The depth of the 1.5 ml/l dissolved oxygen isopleth in March 1983 (figure 7) increased northward from the mouth (120 m) to the central gulf (>200 m). There are no available data for 1984.

### Distribution

**Species populations.** Euphausiid mean abundance was 6,869 ind/1000 m<sup>3</sup> in March 1983, with eleven species present (table 1). In spring 1984, in the same

geographic area (24° to 29°N), euphausiid mean abundance was 29,921 ind/1000 m<sup>3</sup>. However, for each species, 95% confidence limits for the abundance estimates significantly overlapped between years (table 1). Two species not found inside the gulf (north of 24°N) in 1984 (*Nematoscelis gracilis* and *Stylocheiron carinatum*) were nevertheless present just outside the mouth, 23°–24°N, in that year.

Significant differences between day and night abundances were found only in postlarval *Nyctiphanes simplex* ( $p = 0.042$ ) and *Euphausia eximia* ( $p = 0.002$ ), with nighttime abundances being greater and, therefore, used to determine abundances of those species. Larvae did not show significant day-night differences in abundance ( $p > 0.05$ ). Therefore, both day and night samples were used to determine abundances of larvae of all species (table 2).

The greater average euphausiid abundance in 1984 was mainly due to the generally coastal species *Nyctiphanes simplex*, since it constituted 60% of the euphausiids sampled in 1983, and 96% in 1984. Five

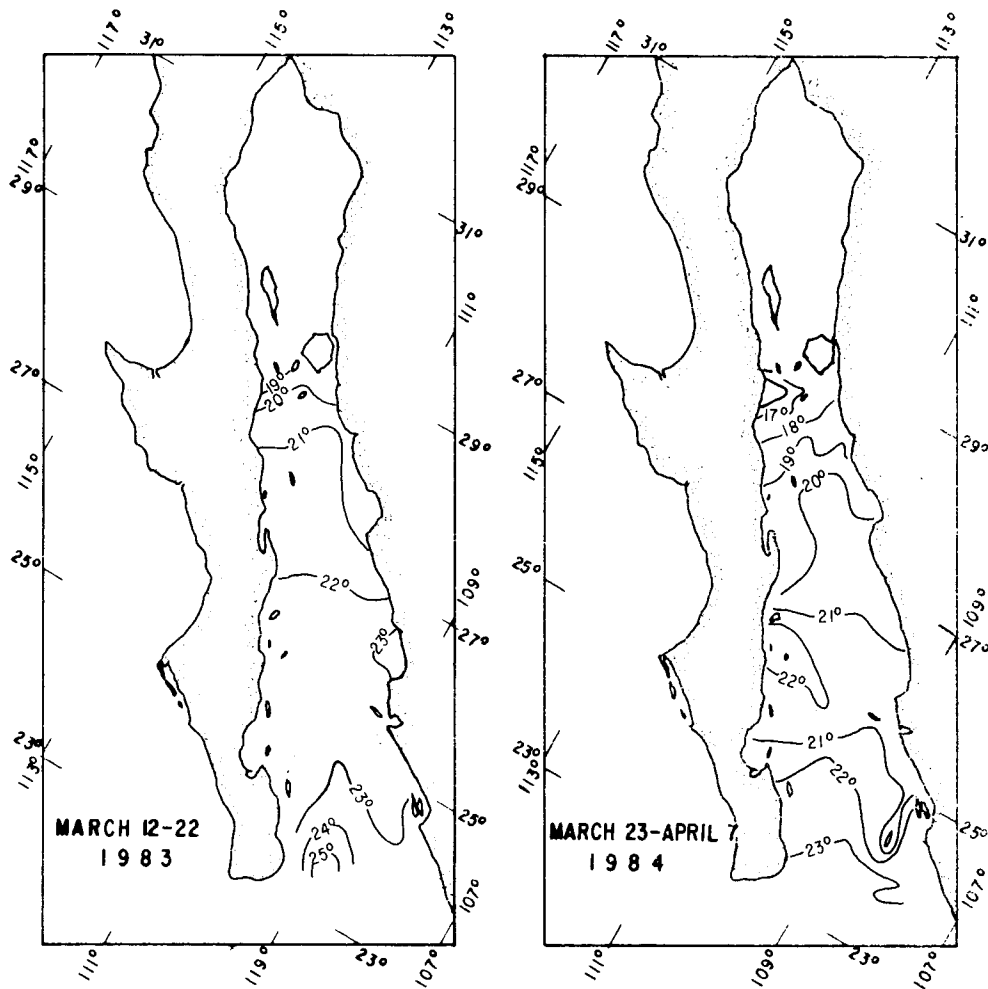


Figure 4. Surface temperature distributions (°C) in the Gulf of California.

TABLE 1  
 1983 and 1984 Mean Abundances (Antilogged), Also Showing Lower (LL) and Upper (UL) 95% Confidence Limits

Geographical range <sup>a</sup>	Species	1983 (N = 17)		1984 (N = 14) <sup>b</sup>	
		$\bar{x}$ (LL <sub>95%</sub> -UL <sub>95%</sub> )	%	$\bar{x}$ (LL <sub>95%</sub> -UL <sub>95%</sub> )	%
Warm-temperate North Pacific	<i>Nematoscelis difficilis</i>	2,555 (1,432-4,560)	37.2	1,120 (243-5,150)	3.7
Marginal to eastern tropical Pacific	<i>Nyctiphanes simplex</i> <sup>c</sup>	4,133 (995-17,146)	60.2	28,770 (3,108-266,267)	96.1
	<i>Euphausia eximia</i> <sup>c</sup>	110 (16-718)	1.6	9 (0-180)	<0.1
Equatorial Pacific endemics (adapted to regions with subsurface oxygen deficiency)	<i>Nematoscelis gracilis</i>	0 (0-2)	0.1	0 (0-0)	<0.1
	<i>Euphausia diomedea</i>	2 (0-9)	0.1	2 (0-9)	<0.1
	<i>Euphausia distinguenda</i>	56 (12-258)	0.8	9 (1-54)	<0.1
	<i>Euphausia lamelligera</i>	1 (0-2)	<0.1	1 (0-3)	
Cosmopolitan in tropical and subtropical waters	<i>Euphausia tenera</i>	7 (1-31)	<0.1	4 (0-21)	<0.1
	<i>Nematobrachion flexipes</i>	1 (0-3)	<0.1	1 (0-3)	<0.1
	<i>Stylocheiron affine</i>	2 (0-8)	<0.1	5 (0-28)	<0.1
	<i>Stylocheiron carinatum</i>	1 (0-2)	<0.1	0 (0-0)	0
	Total	6,869	100.0	29,921	100.0

<sup>a</sup>Defined in Brinton (1962, 1979).

<sup>b</sup>Excluding stations at mouth of gulf (23°-24°N).

<sup>c</sup>Means are from night samples only (1983 n = 8; 1984 n = 7), because night and day  $\bar{x}$ 's differed significantly.

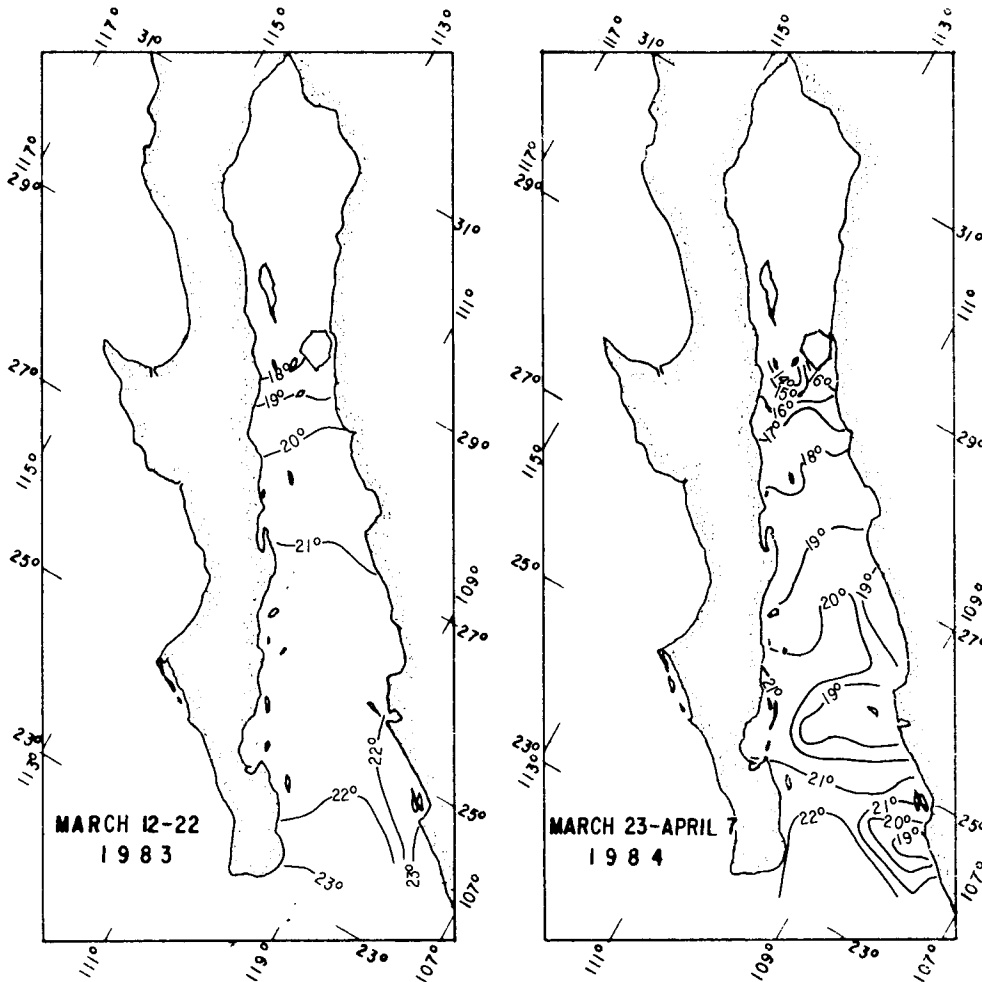


Figure 5. Temperature distributions (°C) at the 30-m depth.

TABLE 2  
 1983 and 1984 Mean Abundances (Antilogged), with Lower and Upper 95% Confidence Limits

Species		Calypt.	1983 Furc.	Postlar.	Calypt.	1984 <sup>a</sup> Furc.	Postlar.
<i>Nematoscelis difficilis</i>	$\bar{x}$	1,240 (726-2,118)	575 (207-1,595)	279 (115-676)	124 (12-1,188)	216 (43-1,063)	90 (14-560)
<i>Nyctiphanes simplex</i>	$\bar{x}$	835 (189-3,685)	2,046 (874-4,787)	396 <sup>b</sup> (145-1,079)	1,940 (143-26,091)	1,499 (189-11,821)	1,277 <sup>b</sup> (31-50,757)
<i>Euphausia eximia</i>	$\bar{x}$	3 (0-14)	7 (1-26)	62 <sup>b</sup> (13-294)	1 (0-6)	6 (1-30)	4 <sup>b</sup> (1-60)
<i>E. diomedea</i>	$\bar{x}$	1 (0-4)	0	1 (0-9)	0	1 (0-4)	1 (0-4)
<i>E. distinguenda</i>	$\bar{x}$	19 (3-90)	18 (4-75)	4 (0-18)	3 (0-13)	2 (0-8)	5 (0-29)
<i>E. lamelligera</i>	$\bar{x}$	0	0	1 (0-2)	0	1 (0-1)	1 (0-1)
<i>E. tenera</i>	$\bar{x}$	2 (0-8)	3 (0-9)	1 (0-5)	1 (0-7)	1 (0-6)	1 (0-3)
<i>Nematoscelis gracilis</i>	$\bar{x}$	0	1 (0-1)	0 (0-1)	0	0	0
<i>Nematobrachion flexipes</i>	$\bar{x}$	0	1 (0-3)	0	0	1 (0-3)	0
<i>Stylocheiron affine</i>	$\bar{x}$	1 (0-4)	1 (0-3)	1 (0-5)	1 (0-6)	4 (0-15)	3 (0-11)
<i>S. carinatum</i>	$\bar{x}$	0	0	1 (0-2)	0	0	0

<sup>a</sup>Excluding stations at mouth of gulf (23°-24°N).

<sup>b</sup> $\bar{x}$ 's are from night stations only (1983 n = 8; 1984 n = 7), because night and day  $\bar{x}$ 's differed significantly.

Total abundance for each species within a year differs from table 1 because of the properties of the log-normal distribution and, in the cases of *Nyctiphanes simplex* and *Euphausia eximia*, the inclusion of daytime abundance estimates for larval stages in the present table.



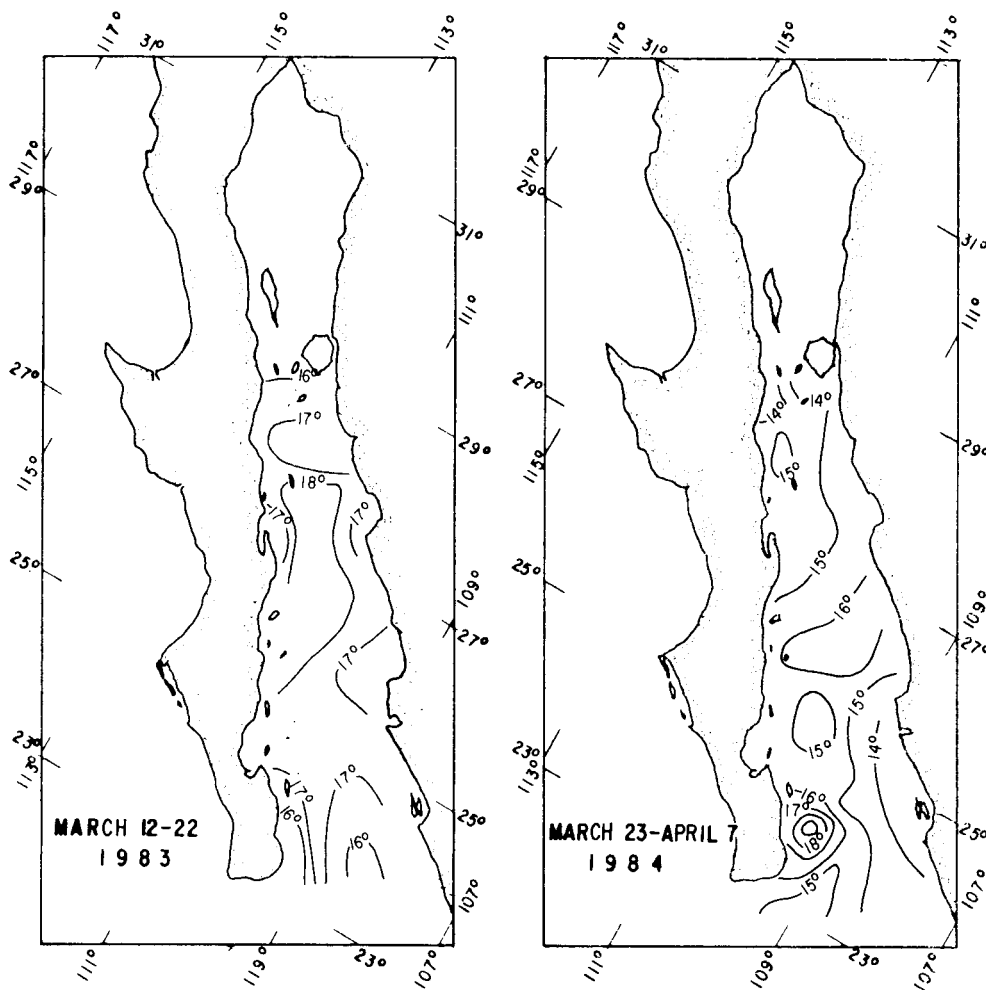


Figure 6. Temperature distributions (°C) at the 100-m depth.

of the six 1983 high abundances of *N. simplex*, >5,000 ind/1000 m<sup>3</sup>, were to the north, at stations where temperature was less than 21°C (figure 8). In 1984, abundances of >5,000 ind/1000 m<sup>3</sup> were more common, with the highest interval, >50,000 ind/1000 m<sup>3</sup>, extending along much of the eastern coast of the gulf. *Nematoscelis difficilis* was the species second in abundance at 37% of the total euphausiids in 1983, and 4% in 1984 (table 1). Highest abundances in 1984, >5,000 ind/1000 m<sup>3</sup>, appeared shifted somewhat toward the north in the central gulf with respect to 1983 (figure 9).

The remaining nine species contributed <5% of the total euphausiids in both years (table 1). Their individual mean densities were <200 ind/1000 m<sup>3</sup>. *E. distinguenda* (figure 10), *E. eximia* (figure 11), *E. tenera* (figure 12), and *E. diomedea* (appendix 1, 2) were more consistently found in the central part of the gulf during 1983, when warm temperatures (e.g., >21°C, surface) and low salinity (<34.9‰, surface) were farther to the north (figures 3, 4). No

specimens of these species were found at the northernmost group of stations, 28°–29°N. *Stylocheiron affine* showed no difference in distribution between the two years (figure 13).

**Life-history stages.** With the exception of *Stylocheiron carinatum*, of which only postlarvae were present, larvae of all species were present in the gulf. The youngest observed life-history stage, the calyptopis larvae (nauplii not sampled), was found for only seven of the eleven species (table 2). Calyptopes of *Nyctiphanes simplex* and the warm-temperate species *Nematoscelis difficilis* were abundant across the area sampled (appendix 1, 2); maximum densities were associated with surface temperatures of <22°C (figure 14). Recruitment of calyptopes of *N. simplex* was uneven across the sampling grids of both years, as seen in the high variances associated with mean abundance (table 2). However, in spring 1984, densities >100,000 ind/1000 m<sup>3</sup> were found at four of the stations (appendix 2), all of which were along the eastern coast, whereas in spring 1983, all

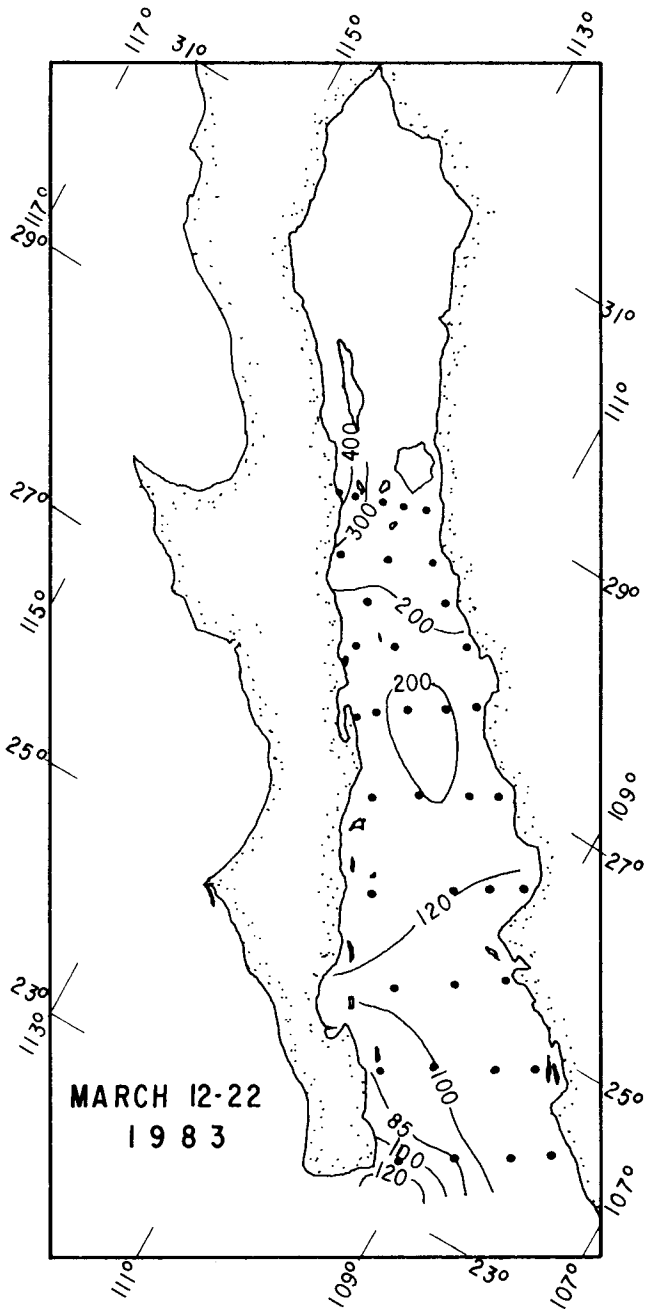


Figure 7. Depth of the 1.5 ml/l oxygen concentration.

but one of the stations yielded <7,000 calyptopes/1000 m<sup>3</sup> (appendix 1). Postlarvae of *N. simplex* included more ovigerous females in spring 1984 than in 1983.

In 1983 the northward extensions of the ranges of the two most abundant species from the eastern tropical Pacific, *E. distinguenda* and *E. tenera* (figures 10, 11) were entirely due to larvae (appendix 1), with postlarvae remaining restricted to the gulf entrance, in the zone characterized by the lowest subsurface oxygen levels (figure 7).

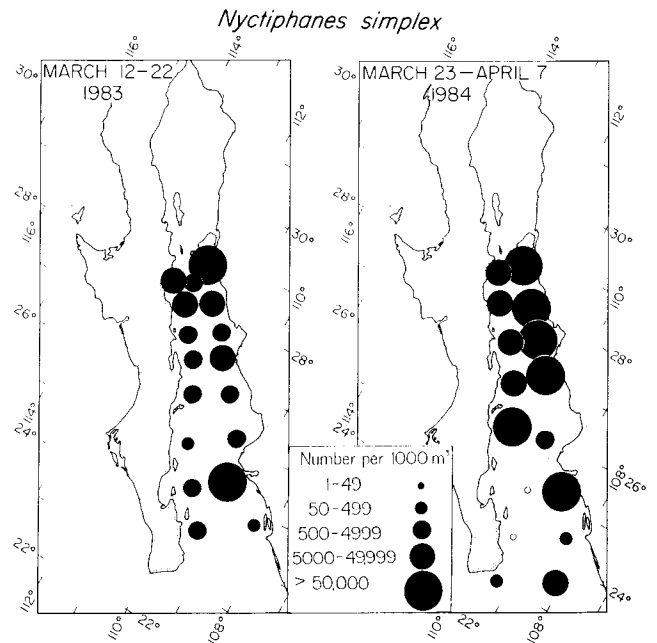


Figure 8. Distribution of *Nyctiphanes simplex*.

## DISCUSSION

Environmental conditions in the Gulf of California during March 1983 showed climatic anomalies that can be explained as a response to the El Niño event that affected the eastern Pacific Ocean beginning in fall 1982 (Cane 1983; Rasmusson and Wallace 1983; Simpson 1983; Barber and Chavez 1986). Those anomalies consisted mainly of sea-level rise and surface-water warming, both reaching record values for the last 30 years (Robles-Pacheco and

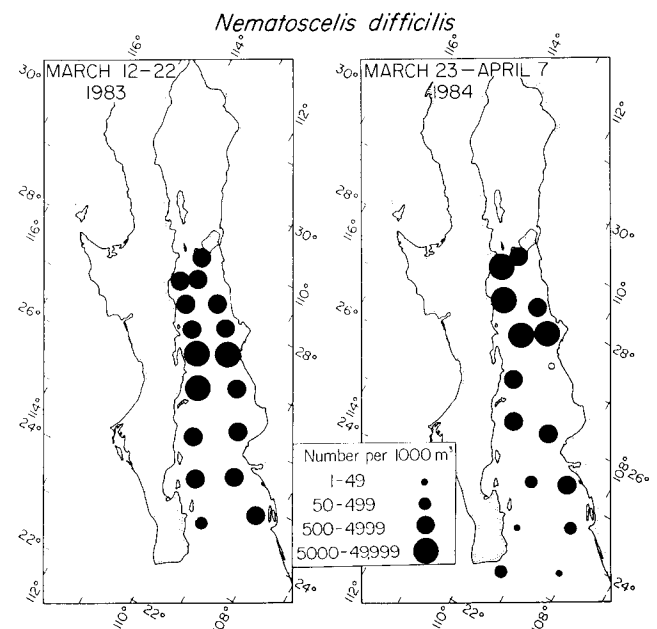


Figure 9. Distribution of *Nematoscelis difficilis*.

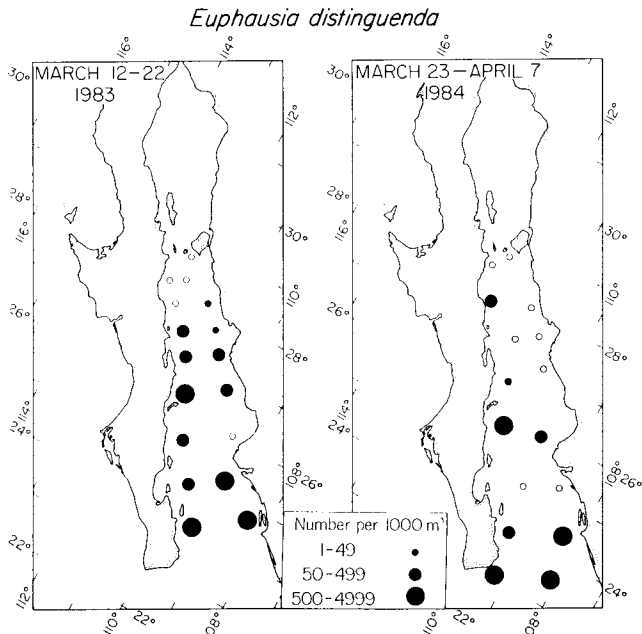


Figure 10. Distribution of *Euphausia distinguenda*.

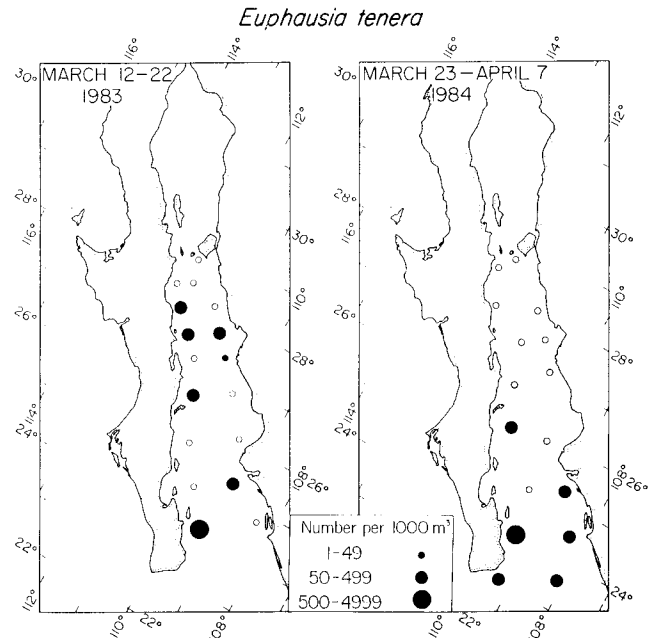


Figure 12. Distribution of *Euphausia tenera*.

Christensen 1984; Robles-Pacheco and Marinone 1987). The observed relatively low surface salinity of 1983 (<35‰) indicated that tropical surface water had invaded the gulf from the south (Robles-Pacheco and Marinone 1987). Subsequently, during spring 1984, surface salinity was reverting toward the more usual values reported by Roden and Groves (1959), Roden (1964), and Alvarez-Borrego and Schwartzlose (1979). Surface temperatures

were 1° to 2°C lower during spring 1984, showing that El Niño had weakened.

Surface temperatures and euphausiid species distributions observed in the gulf in April 1984 were similar to the conditions described for April 1957 (Brinton and Townsend 1980). April 1957 may have been the beginning of El Niño 1957-59, because water temperatures were reported to be 1°C warmer than in April 1956 (Anonymous 1963).

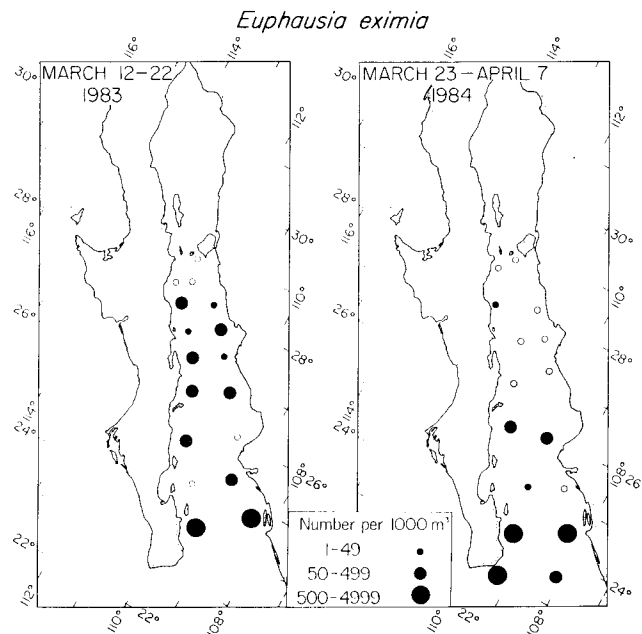


Figure 11. Distribution of *Euphausia eximia*.

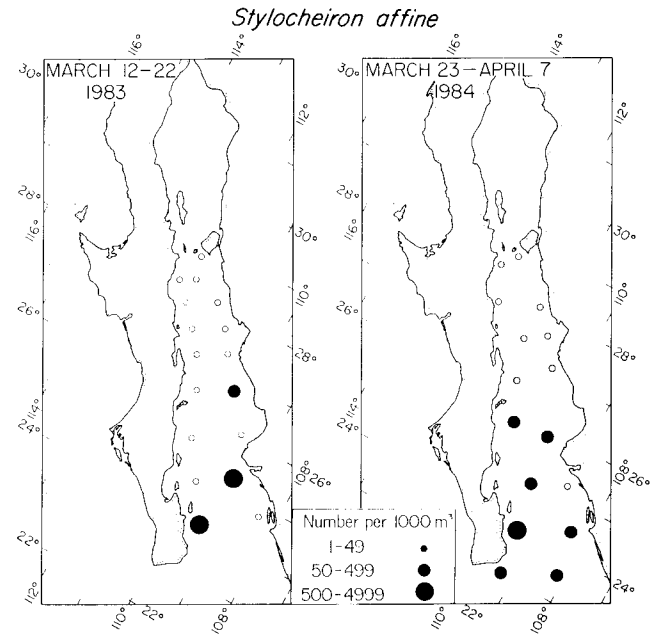


Figure 13. Distribution of *Stylocheiron affine*.

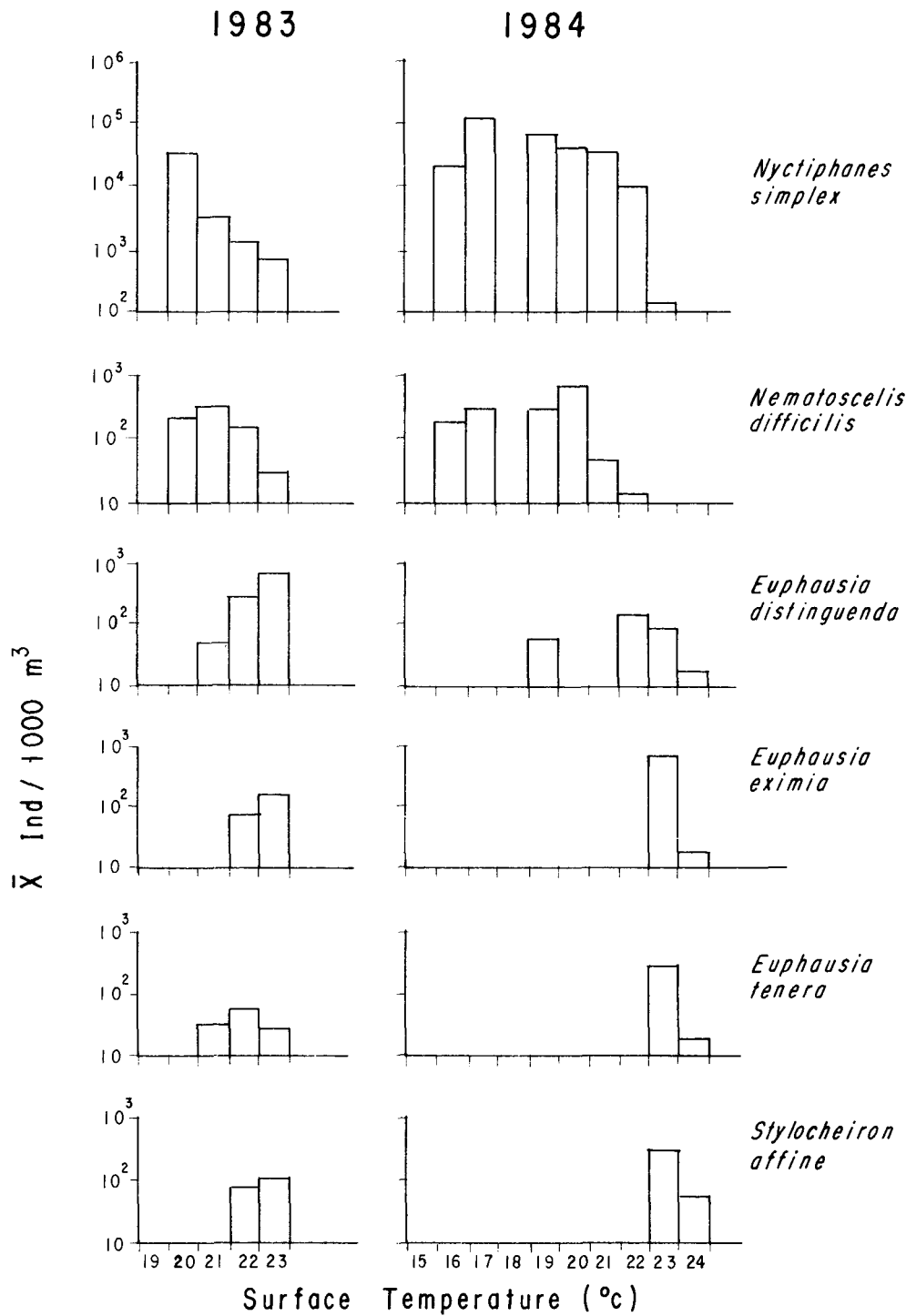


Figure 14. Mean abundances of calyptopis larvae versus surface temperature.

Therefore, the springs of 1957 and 1984 can be considered as transition states—to a warm period in 1957 and to a cool period in 1984. This generally corresponds to conditions reported for the California Current, where longer time series are available (Bernal 1981; Brinton and Reid 1986).

Increased tropical characteristics of gulf water in

1983 were associated with surprisingly indistinct differences in abundance and reproduction of the dominant, widespread species (*Nyctiphanes simplex*) compared with 1984, although there are suggestions of possible differences in abundances of calyptopes and postlarvae (table 2). However, those tropical waters seem to be related to an increased 1983 pres-

ence of *Euphausia eximia*, *E. distinguenda*, and *E. tenera*, species that belong to eastern tropical Pacific adaptative groups (Brinton 1962, 1979). In the following spring (1984), as climatic conditions changed, the *Euphausia* species contracted their distribution somewhat southward.

Between-year differences in euphausiid abundance and distribution suggested by the data can be explained by the changing surface circulation, which is coupled to the large-scale Pacific Ocean circulation (Wyrtki 1966; Baumgartner and Christensen 1985). When El Niño occurs, the North Equatorial Countercurrent is strengthened, causing the Costa Rica Current to reach northward into the Gulf of California. This process resembles an extension into spring of the usual summer-autumn gulf circulation pattern (Baumgartner and Christensen 1985). Northward incursions of the tropical species, interpreted as seasonal, were observed in the summer of 1957 (July–August; Brinton and Townsend 1980) and in the autumn of 1967 (September–November; Mundhenke 1969), when water was transported northward, associated with maximum recorded temperatures for those years.

In the California Current system, *E. distinguenda* and *E. tenera* rarely penetrate north of the tropics (Brinton 1960, 1962), and their occasional northward presence there has been related to El Niño, as in fall 1957 when the strong warming event of 1958–59 became evident in the eastern North Pacific. For example, at that time *E. distinguenda* was found off Punta Eugenia (28°N; Brinton 1960, 1967a). During winter 1982 many *E. distinguenda* and *E. tenera* adults were found off Magdalena Bay lagoons (23°26'–25°35'N), just to the north of the expected limit of the tropical fauna (Green-Ruiz 1986).

*E. distinguenda* is endemic to the eastern tropical Pacific, and postlarvae perform diel vertical migrations into and out of depths below 150 m, where oxygen concentrations are <1.0 ml/l in this water mass (Brinton 1979). Other species with this capability — *E. lamelligera*, *E. diomedae*, and *Nematoscelis gracilis* — were lower in abundance and steady in geographical range in March of 1983 and 1984 in the gulf. Brinton and Townsend (1980) reported that these species remained near the mouth of the gulf during the cool season of 1957 (February–April) but reached the central gulf and even the northernmost gulf during summer. The extent to which this northward penetration in 1957 may have been enhanced by the midyear onset of El Niño 1958–59 is not known.

All of the above equatorial species and the warm-water cosmopolite *E. tenera*, especially their post-

larval stages, had maximum densities where low concentrations of oxygen were present at shallowest depths (figure 7), while postlarvae of the temperate species *Nematoscelis difficilis* were absent in this region. Warm-water cosmopolite species such as *E. tenera* (40°N–40°S, but absent in eastern boundary currents) are not always good indicators of tropical water mass because of their large geographical ranges. However, the intrusion of *E. tenera* larvae into the gulf certainly results from transport by tropical water, since this species inhabits the eastern tropical Pacific but is usually absent from the adjacent southernmost part of the California Current (Brinton 1962, 1979).

In the spring of 1957, distributions of *Nematoscelis difficilis* and *Nyctiphanes simplex* extended southward to the mouth of the gulf (Brinton and Townsend 1980) as in 1983 and 1984. The summer data from 1957 showed both species still present almost to the mouth of the gulf, though in reduced numbers, even though surface waters were 10°C warmer than in spring. Both species, together with *Euphausia eximia*, are residents of the California Current (Brinton 1962, 1967a, 1973). However, *E. eximia* and *N. simplex* populations are centered in the southernmost part of that current, where they are considered to be midstream and coastal components, respectively, constituting their own subtropical group. On the other hand, *N. difficilis* is a conspicuous element all along the current to the tip of Baja California (23°N) (Brinton 1979). *N. difficilis* did not show strong interannual (1983, 1984) differences in its gulf distribution, despite its association with cooler waters than *Nyctiphanes simplex*. This may have been due to the generic behavior of *Nematoscelis*, whose postlarvae tend to stay beneath the mixed layer (below approximately 50–100 m in summer) day and night (Brinton 1967b, 1979).

Thus *Nematoscelis difficilis* may stabilize its range by avoiding the surface layer with its relatively variable temperatures. In March 1983, the mixed layer of the gulf was very stable, as can be observed in the 30-m temperature distributions (figure 5). There is some evidence, though inconclusive, that *N. difficilis* migrates vertically, possibly to 300–400 m in the California Current, but its migration may be restricted to well-oxygenated waters (Brinton 1967b, 1979). It is nevertheless probable that during spring 1983 many *N. difficilis* remained submerged beneath the warm surface layer of the gulf. This mechanism was observed in the copepod *Calanus pacificus californicus* during summer (Fleminger data in Brinton et al. 1986). However, Brinton and Townsend (1980) considered this possibility un-

likely for *N. difficilis* because they did not find significantly fewer adults in August 1957 than in April 1957, within the 0–140-m depths sampled. Because of the extensive presence of oxygen-deficient waters in the gulf, information on the depth distributions of gulf euphausiids is needed.

Among these species, *Nyctiphanes simplex* showed the longest reproductive period in 1957: at least February through June (Brinton and Townsend 1980). Even though 1983 larvae were found throughout a large range of surface temperature (20°–23°C), they were most abundant to the north, where temperature was lowest (figures 4, 14; appendix 1). This supports the possibility that the warming event of 1983 had a negative effect on calyptopis recruitment. Brinton and Townsend (1980) reported that the best calyptopis recruitment in 1957 occurred in waters of 17°–18°C (10-m depth), which is cooler than any part of the gulf covered in 1983. Calyptopis distribution in April 1957 was very similar to that of April 1984, but surface water temperature was slightly warmer in 1984. However, temperature distribution at 30-m depth in spring 1984 resembled that at 10-m depth in April 1957, with <19°C prevailing at those respective depths in the central and southeastern gulf.

Subsurface warming (down to 100 m) in spring 1983 could also help explain lower abundances of *N. simplex* postlarvae, since this species may perform short vertical migrations (150 m), as observed in the California Current (Brinton 1967b).

Feeding habits of *N. simplex* are not yet known. It seems unlikely that production of this species was limited in 1983 by available food, because much other plankton was then abundant in the gulf. Primary productivity and chlorophyll *a* concentrations were higher in the gulf during El Niño 1982–83 than during other times of observation (Valdez-Holguín and Lara-Lara 1987; Lara-Lara and Valdez-Holguín 1988), contrasting with generally decreased productivity observed in more oceanic, warm-temperate systems affected by El Niño (Dandonneau and Donguy 1983; Barber and Chavez 1983; McGowan 1983). Zooplankton biomass was also high, with March 1983 average amounts (displacement volumes) (Jiménez-Pérez and Lara-Lara 1988) being similar to March–April 1984 averages (Lavaniegos-Espejo 1988) and to those reported for April of 1956 and 1957 (Brinton et al. 1986).

Abundances of *Nyctiphanes simplex* in the gulf during spring 1983 were not low compared with most abundances found in the California Current, where, in uneventful years, this species usually is restrained within the region of about 20°N to 35°N

(Brinton 1962, 1979). During El Niño events this species proved to be a good indicator of northerly transport of coastal water of the California Current, reaching at least to Cape Mendocino (40°N) in 1958 (Brinton 1960) and at least to the Washington–Oregon border (46°N) in 1982–83 (Brodeur 1986). In the southern part of its distributional range, off Magdalena Bay (24°–25°N), *N. simplex* was not found in December 1982, whereas in summer of that year it had been present there in 40% of a set of zooplankton samples, constituting 95% of all euphausiid adults. In February 1983, warm temperatures persisted, and *N. simplex* continued to be scarce at that southern locality (Green-Ruiz 1986).

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APPENDIX 1  
 Abundances of Life Phases (Individuals/1000 m<sup>3</sup>), March 1983

Species	Life-history stage	Sampling stations (D = day; N = night)																
		D 75	N 70	D 64	D 68	N 66	N 58	D 50	D 56	N 53	D 44	N 41	D 34	D 38	N 27	N 14	D 24	N 20
<i>Nematoscelis difficilis</i>	Calypt.	843	2,190	2,831	3,038	2,170	1,822	6,390	1,844	2,744	628	1,795	308	1,812	994	461	840	78
	Furc.	211	313	786	640	723	1,325	3,630	1,418	3,659	63	3,740	231	680	1,293	1,077	2,648	0
	Postlar.	492	1,408	1,258	240	217	455	73	177	1,220	157	1,945	308	113	597	461	388	0
<i>Nyctiphanes simplex</i>	Calypt.	87,117	782	2,674	6,875	5,931	2,981	3,921	1,560	305	0	1,496	925	151	4,077	0	1,421	932
	Furc.	35,409	2,972	5,505	2,238	10,416	828	3,340	2,695	534	2,073	1,496	463	529	92,775	154	840	388
	Postlar.	9,836	352	315	0	615	248	109	71	457	188	1,496	0	151	1,790	231	258	39
<i>Euphausia eximia</i>	Calypt.	0	0	0	0	0	0	0	0	0	126	0	0	151	99	77	0	544
	Furc.	0	0	0	0	0	0	36	0	38	31	37	0	76	50	231	0	932
	Postlar.	0	0	39	0	72	83	0	35	38	0	75	0	0	199	461	0	155
<i>Nematoscelis gracilis</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78
	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78
<i>E. diomedea</i>	Calypt.	0	0	0	0	0	0	0	0	0	63	0	0	0	0	0	32	117
	Postlar.	0	0	0	0	108	0	0	0	0	0	0	0	0	25	0	0	117
<i>E. distinguenda</i>	Calypt.	0	0	0	0	0	0	0	142	145	126	449	0	154	1,094	538	65	1,320
	Furc.	0	0	39	0	0	41	109	0	38	63	0	0	227	398	231	388	1,476
	Postlar.	0	0	0	0	0	0	0	0	0	0	112	0	76	298	231	0	1,165
<i>E. lamelligera</i>	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	38	0	38	0	0
<i>E. tenera</i>	Calypt.	0	0	0	0	0	166	0	142	0	0	150	0	0	0	0	0	78
	Furc.	0	0	0	0	72	0	36	35	0	0	75	0	0	0	0	0	311
	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	0	99	0	0	1,243
<i>Nematobranchion flexipes</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	25	0	32	39	
<i>Stylocheiron affine</i>	Calypt.	0	0	0	0	0	0	0	0	0	0	0	0	0	398	0	0	233
	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	0	99	0	0	78
	Postlar.	0	0	0	0	0	0	0	0	0	63	0	0	0	75	0	0	272
<i>S. carinatum</i>	Postlar.	0	0	0	0	0	0	0	0	0	0	37	0	0	0	0	0	39
Total		133,908	8,017	13,447	13,031	20,324	7,949	17,644	8,119	9,178	3,581	12,903	2,235	4,158	104,385	4,191	6,912	9,712



APPENDIX 2  
 Abundances of Life Phases (Individuals/1000 m<sup>3</sup>) March–April 1984

Species	Life-history stage	Sampling stations (D = day; N = night)														Outside gulf	
		D 41	N 45	N 54	D 70	N 61	D 65	N 85	D 83	D 97	N 94	N 112	D 109	N 124	D 120	N 129	N 134
<i>Nematoscelis difficilis</i>	Calypt.	2,892	1,763	1,020	11,791	5,172	10,584	0	179	269	0	1,339	0	0	0	0	0
	Furc.	0	1,528	127	3,088	3,735	6,324	0	1,071	806	133	669	67	173	38	0	0
	Postlar.	263	1,763	2,677	0	1,473	161	0	2,142	168	1,339	0	135	138	0	17	85
<i>Nyctiphanes simplex</i>	Calypt.	143,286	25,746	115,615	115,098	9,769	5,679	4,751	3,213	134	18,102	105,774	0	0	0	412	0
	Furc.	1,117	12,343	2,422	10,668	5,172	42,593	82,121	1,071	873	31,279	14,728	0	104	0	6,201	0
	Postlar.	66	0	28,681	1,684	431	645	48,187	13,923	671	4,525	29,456	0	69	0	34	102
<i>Euphausia eximia</i>	Calypt.	0	0	0	0	0	0	0	0	34	0	0	0	1,526	0	0	
	Furc.	0	0	0	0	36	0	0	0	134	67	0	34	1,174	76	0	389
	Postlar.	0	0	0	0	0	0	0	0	0	116	0	0	553	0	189	761
<i>Nematoscelis gracilis</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	68
	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	481	68
<i>E. diomedea</i>	Furc.	0	0	0	0	0	0	0	0	0	33	0	0	0	229	69	17
	Postlar.	0	0	0	0	0	0	0	0	0	33	0	0	173	0	52	17
<i>E. distinguenda</i>	Calypt.	0	0	0	0	144	0	0	0	134	133	0	0	69	0	172	17
	Furc.	0	0	0	0	0	0	0	0	34	33	0	0	138	38	567	68
	Postlar.	0	0	0	0	0	0	0	45	269	532	0	0	760	38	756	541
<i>E. lamelligera</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	35	0	17	51
	Postlar.	0	0	0	0	0	0	0	0	0	33	0	0	0	0	0	17
<i>E. tenera</i>	Calypt.	0	0	0	0	0	0	0	0	0	0	0	0	207	458	120	17
	Furc.	0	0	0	0	0	0	0	0	0	0	335	0	0	229	120	118
	Postlar.	0	0	0	0	0	0	0	0	0	67	0	0	35	0	52	186
<i>Nematobrachion flexipes</i>	Furc.	0	0	0	0	0	0	0	0	0	33	0	0	69	0	0	0
	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
<i>Stylocheiron affine</i>	Calypt.	0	0	0	0	0	0	0	0	0	0	0	0	138	458	34	51
	Furc.	0	0	0	0	0	0	0	0	67	33	0	34	69	343	69	51
	Postlar.	0	0	0	0	0	0	0	0	0	67	0	34	173	114	206	118
<i>S. carinatum</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
Total		147,624	43,143	150,542	142,329	25,932	65,986	135,059	21,644	3,593	56,559	152,301	304	4,077	3,547	9,586	2,776

## ANALYSIS OF THE PATTERNS OF DISTRIBUTION OF ZOOPLANKTON AGGREGATIONS FROM AN ACOUSTIC DOPPLER CURRENT PROFILER

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### ABSTRACT

A test set of data of volume reverberation, measured from the R/V *New Horizon*, nominally from 12–240-m depth in 4-m intervals, was taken in April 1988 using a 307-kHz acoustic Doppler current profiler (ADCP). A vertical profile was produced each minute for three days over the San Diego Trough off southern California. The results show kilometer-scale zooplankton aggregations with somewhat larger gaps between them. The area profiles had about 10% coverage of zooplankton aggregations. Aggregation target strengths were usually stronger during the morning and evening migrations. Migration rates were of the order of 5–8 cm s<sup>-1</sup> during ascent and 3–4 cm s<sup>-1</sup> during descent. Zooplankton aggregations were of horizontal dimensions intermediate between fish schools and groups of schools.

### RESUMEN

En abril de 1988, a bordo del buque de investigación *New Horizon*, se colectó una serie de datos de volumen de reverberación, haciendo uso de un aparato de 307 kHz para perfilar la corriente doppler acústica (PCDA), abarcando una profundidad de 12 a 240 m en intervalos de 12 m. Se midió un perfil vertical cada 1 minuto, por un período de 3 días, en la Depresión de San Diego, frente al sur de California. Los resultados indican agregaciones de zooplancton en escalas de kilómetros, con espacios algo más grandes entre las mismas. Aproximadamente 10% del área de los perfiles presentaron agregaciones de zooplancton. Las fuerzas de blanco de agregaciones fueron, en general, más fuertes durante las migraciones matutinas y vespertinas. Las tasas de migración fueron del orden de los 5 a 8 cm seg<sup>-1</sup> durante el ascenso y de los 3 a 4 cm seg<sup>-1</sup> durante el descenso. Las dimensiones horizontales de las agregaciones de zooplankton fueron intermedias entre cardúmenes de peces y grupos de cardúmenes.

### INTRODUCTION

Distributional patterns in the pelagic habitat are known to exist at several time and space scales (Haury et al. 1978; Greenlaw and Percy 1985). Some spatial scales have been evaluated for some planktivorous pelagic schooling fish (Graves 1977; Fiedler 1978; Smith 1978b), zooplankton (Star and Mullin 1981; Haury and Wiebe 1982; Pieper and Holliday 1984), and mesopelagic micronekton (Greenlaw and Percy 1985). Two aspects of plankton sampling that must take account of these scales are (1) estimation of the abundance of a species and (2) an understanding of the interactions between planktonic organisms and their immediate environment, principal predators, competitors, and food organisms.

Vertical and horizontal integration can increase the precision of estimates of abundance of "patchy" organisms in the plankton sample (Wiebe 1972). The integrated sample, however, may underestimate the local density of an organism by sampling volumes at inappropriate depths, or may include species with which the target species never interacts. Resolving the patchy dispersion of prey within a fluid volume is important for estimating attack rates by predators (Ohman 1988a).

The space scales relevant to a particular population or process are invisible in the pelagic habitat. Pilot sampling studies are necessary to help formulate and constrain the questions to be answered (Andrews and Mapstone 1987). Acoustic methods can be useful for such preliminary surveys, as a means to obtain rapid, broad coverage, and as a tool to direct other, invasive sampling methods. Acoustic methods are not generally useful for identifying organisms or precisely estimating their biomass. A continuous acoustic record can be used to delineate spatial scales that must be encompassed or resolved (Holliday 1985).

Studies of the scale and intensity of fish schools have been used to design and interpret surveys of northern anchovy eggs (Smith 1970; Hewitt et al. 1976; Graves 1977; Fiedler 1978; Smith 1978a,b, 1981; Smith and Hewitt 1985a,b). Two major find-

ings of this work that depended on acoustic technology are that (1) on the small scale, within a school, the biomass of fish is on the order of 15,000 grams per square meter of horizontal surface, and their consumption of plankton would be approximately 750 grams per square meter of fish school horizontal surface per day; and (2) the fish schools of tens of meters in diameter are assembled in concentrations of shoal groups extending for tens of kilometers. We do not know the rules of assembly of shoal groups: one mechanism could be that schools' swimming speeds decrease and turning behavior increases when the school is in the upper ranges of plankton biomass. The lower ranges of plankton biomass could be a temporary result of foraging groups of schooled fish (Koslow 1981).

In addition to the spatial complexity of the pelagic habitat at several horizontal scales, rapid changes in the vertical distribution of organisms at dawn and dusk are well known (Enright 1977; Pieper and Bargo 1980). The impact of these migrators on the distribution pattern of their prey must be added to the direct effects of diel vertical migration on the distribution of plankton. Initial time and space scale information from acoustical methods may be useful in designing the most effective direct sampling procedures for studies of fine-scale processes and of geographic-scale population abundance.

Acoustic profiles may be used to estimate the scale and intensity of patchiness and to help specify the number, size, and placement of samples. The primary sampling design questions to be asked in pelagic studies are:

How many samples are needed?

How big should the sample units be?

At what separation distance can adjacent sample units be said to be effectively independent?

Over what spatial and temporal scales are processes operating?

What are limits of the temporal and spatial scales to be used for such studies?

It is the purpose of this study to report the qualitative spatial analysis from several days of continuous acoustical sampling. From these records, we will summarize the incidence of biological aggregations, their spatial dimensions, the dimensions of the spaces between aggregations, the depth distribution of aggregations, and the rates of change in depth.

## METHODS

The pilot study was conducted in a 5 by 15-n. mi. area oriented SE NW about 25 n. mi. west north-

west of San Diego (figure 1). The equipment used included a 307-kHz acoustic Doppler current profiler (ADCP)<sup>1</sup>, a multiple opening-closing net, and environmental sensing system (MOCNESS, Wiebe et al. [1985]), and standard hydrographic bottle casts. It is important to note that the ADCP had not been calibrated in the amplitude domain and that the effect of methods of conditioning the amplitude signal have not been studied. The Sea-Bird Electronics temperature sensor on the MOCNESS frame was calibrated against deep-sea reversing thermometers. Chlorophyll *a* and pheopigments retained on Gelman GF/F filters were extracted in refrigerated acetone and analyzed on a Turner Designs Model 10 fluorometer. Dissolved oxygen was determined by the Carpenter (1965) modification of the Winkler titration method. The MOCNESS (20 nets, 1-m<sup>2</sup> effective mouth area, 333- $\mu$ m mesh) was towed at about 50–75 cm s<sup>-1</sup>. A nighttime profile was made from 500 m to the surface in approximately 50-m intervals between 0131 and 0401 on April 6, 1988. A comparable daytime profile was made from 1330 to 1510 on April 6. Volume filtered per haul averaged 354 m<sup>3</sup> (range 156–927 m<sup>3</sup>). Samples were preserved in 10% Formalin buffered with sodium borate. Select copepod species were enumerated after subsampling with a Stempel pipette; when organisms were rare the entire sample was counted.

### Acoustical Methods

The primary function of the ADCP is to sense current direction and speed as a function of depth. It accomplishes this by detecting the Doppler frequency shift of backscattered sound from planktonic organisms, particles, and small-scale discontinuities in the water column. This frequency shift is proportional to the relative velocity between the backscattering source and the transducer. The change in frequency is measured by four transducers. Unlike echo sounders having the transducer aimed downward, or sonars (*sonically* determined azimuth and range) having the transducer directed laterally at any angle with reference to the bow, the four ADCP transducers are oriented at 30° from the vertical: approximately forward, aft, right abeam, and left abeam (figure 2). This means that the axes of the complementary beams are as far apart as the depth ( $2 \times \sin(30^\circ) = 1$ ) below the transducer. In

<sup>1</sup>Manufactured by RDI Inc. San Diego. (Mention of manufacturer does not imply endorsement by the U.S. government or the University of California). A more complete technical description is available in a manual from the manufacturer. See also Flagg and Smith (1989).

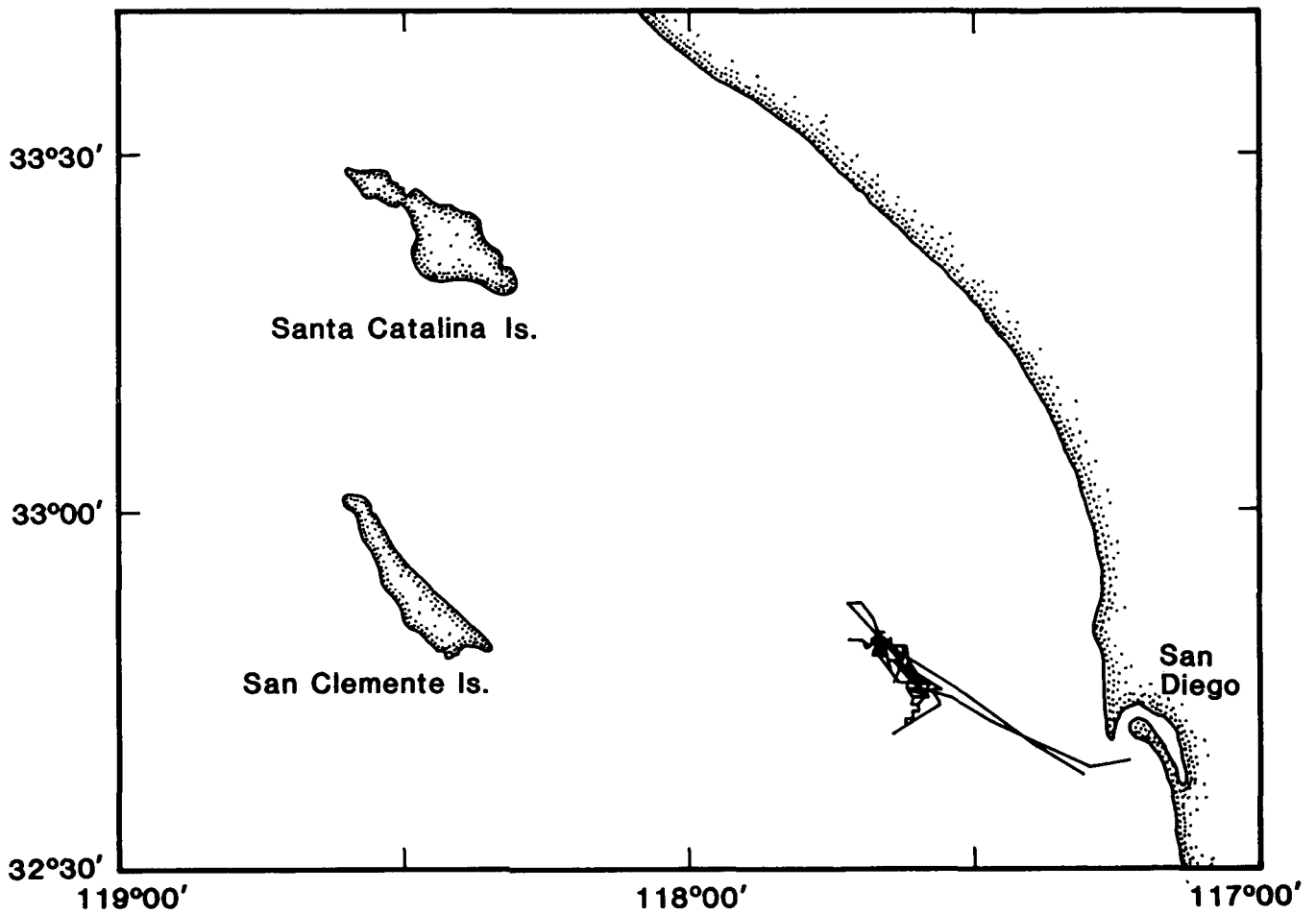


Figure 1. Track of R/V *New Horizon* during ZB1 cruise. Data were collected during the entire cruise. See figure 8.

this report we analyze the information content of the echo amplitudes, rather than their frequencies.

The speed of sound in water is approximately 1500 meters per second. Therefore a sound oscillation of 300,000 cycles per second (Hz) has a wavelength of 5 mm; in general, insonified objects much larger than 5 mm scatter sound more efficiently than objects equal to or smaller than 5 mm (Holliday 1980). The proportion of the sound transmitted through, reflected from, and scattered around the object is influenced by small contrasts between the compressibility and density of water and these features of the object. For example, an organism with a bony skeleton, scaly integument, and air bladder returns much more sound than an organism which is primarily protoplasm. Similarly, organisms that are aggregated into patches or layers return more scattered sound per unit of local volume than the same organisms would if distributed evenly throughout a larger volume.

The probability that the acoustic pulse will encounter a target increases with depth because the widths of each acoustic beam increase with depth (figure 2). The probability of detection of a given target decreases with depth because the sensitivity of the receiver is fixed but the sound available for reflecting or scattering is decreasing as the inverse square of the range. In addition, there is a frequency-specific attenuation of sound in water, with more sound lost as a function of range in the higher frequencies. To use the ADCP as an acoustic sampling system, we must be able to define the conditions of encounter and the probability of detection. Targets smaller than 240 m cannot be resolved at the deepest depths because of the transducer beam geometry.

The ADCP used in the April cruise operated at 307.2 kHz. The transducer installation on the R/V *New Horizon* was 4 m deep (the draft of the ship), and the outgoing pulse was set at 4-m length (2.7

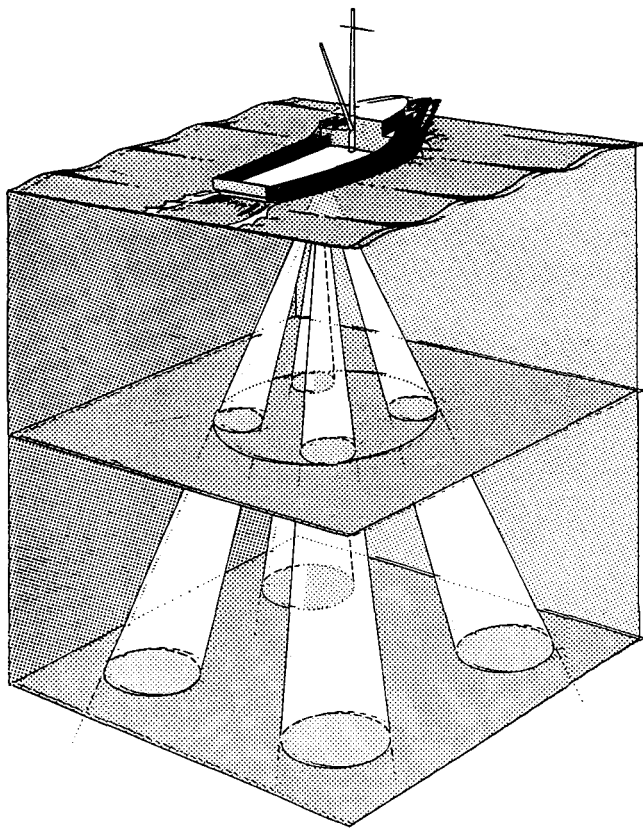


Figure 2. Diagram of the insonification pattern of an acoustic Doppler current profiler (RDI Inc. manual). Contrary to the diagram, the actual orientation of beams is 2 fore and aft and 2 left and right.

msec). Since the near-field return data (4 m) were not collected, the first data on the water column acoustic backscatter were obtained from a depth of about 12 m (figure 3). All graphical zero depths actually refer to 12 m. For each pulse, the amplitude of the return and the estimated velocity of the layer were stored in 60 depth "bins," each representing 4 m. Following nearly a minute of pulses at 1-second intervals, the ensemble average of each bin was calculated, and this average was stored as a compact binary record on a floppy disk. The ensemble averages of the previous profile were also displayed at the operator's console as the next ensemble was being taken (figure 3). Two of the four vertical profiles stored each minute are the velocities of the 4-m layers relative to ship's motion, as a function of depth. One of these profiles displays current speed at right angles to the ship's motion, and the other in the direction of the ship's motion.

There are two accessory profiles. One is the automatic gain control (AGC), which indicates echo amplitude with depth, and the second is the "percent good" value, which indicates the percentage of pings exceeding the signal-to-noise threshold. Note

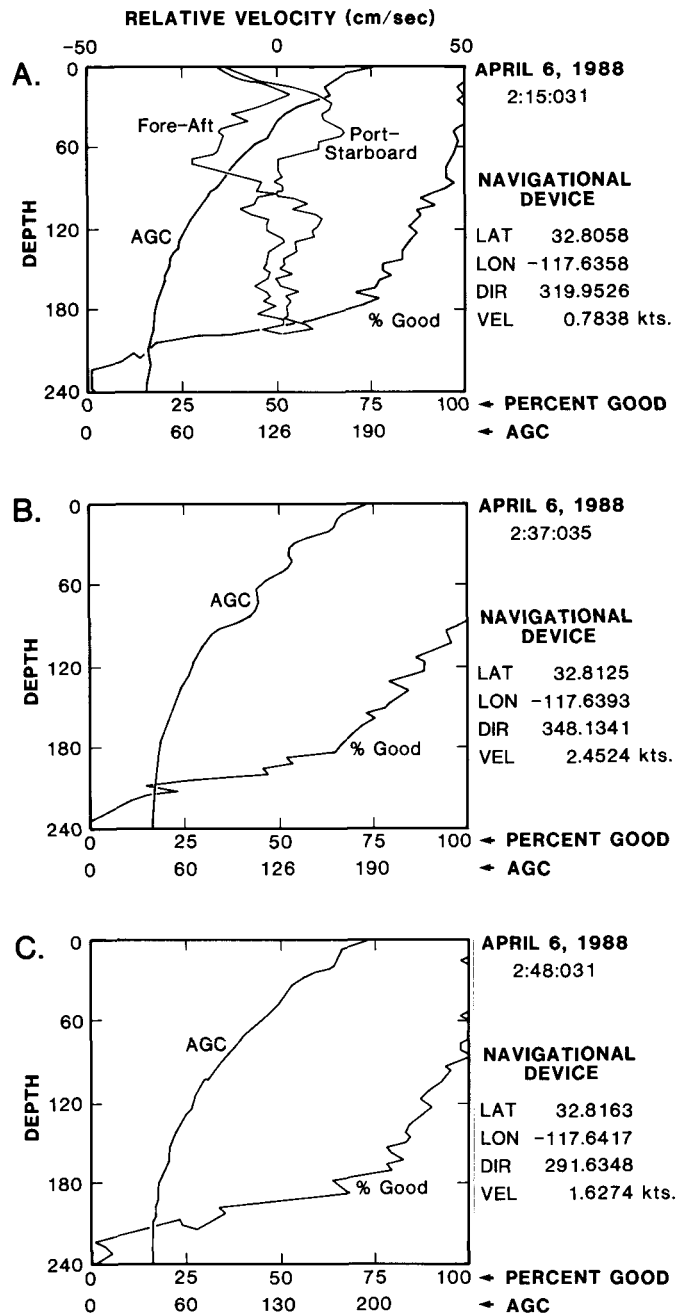


Figure 3. Specimen profiles. A, The velocity curves extend from 0 to 200 m and represent the water-layer motion after the effect of ship's motion in these planes has been removed. One velocity curve is the port-starboard velocity; the other is the fore-aft velocity. The curve labelled AGC is the automatic gain control. The last curve is the "percent good" value expressed as the percentage of pings in the ensemble that were analyzed for frequency at each 4-m depth interval. When this value drops below 25%, the analysis of velocities stops. B, Profile taken 22 minutes later, showing the effect of targets on the AGC profile. Velocity curves have been removed for clarity. C, Profile taken after the targets had passed.

in figure 3A that the AGC is primarily a decreasing function of depth and that "percent good" remains above 90% in the first 60 m below the ship, declines to 75% by 180 m, to 25% by 210 m, and to less than



10% below 220 m. The profile in figure 3B was taken 22 minutes after 3A and is an example of the display of targets in the AGC curve at approximately 50 m and 80 m. The profile in figure 3C was made 11 minutes after 3B, when the ship had passed over the target displayed in figure 3B.

The decline in "percent good" profiles in the ensemble decreases the precision proportional to the square of the number of good profiles. This means that at some depth below the ship, there will be essentially no information on the pattern of zooplankton distribution. The depth at which this happens has not been determined, and all nonrandom pattern has been analyzed no matter at which depth it was detected in the 12- to 250-m range.

The compact binary record also includes temperature of the water at the transducer, time of day, course and speed of the ship, geographic position of the ship, and the settings of the ADCP console at the time the ensemble average was taken.

The original binary record was converted to ASCII code for analysis. Two text files were constructed in the laboratory from each original file created at sea. One file contains 4 hours of AGC echo-amplitude data, 240 1-minute ensemble averages at each of 60 4-m depth intervals (figure 4A). The other file contains the date/time group, latitude, and longitude for the ensemble at half-hour intervals. The mean and standard deviation of the 240 values at each depth were calculated. Within each depth, the mean was subtracted from the value, and the difference was then divided by the standard deviation (figure 4B). Each data set was smoothed by the weighting matrix (figure 5), which was selected to speed the contouring process and limit the number of contour segments stored (Eber 1987). Contours were drawn at the unit-positive values of 1 or above. For the purposes of this study, small positive and all negative values were discarded as noise or assumed to represent the positions of continuous rather than aggregated sources of backscattering. Schott and Johns (1987) also contoured anomalies of echo amplitude in a moored ADCP.

Data collected over the continental shelf were not used for interpreting the mean and standard deviation for normalizing. In general, the volume reverberation was elevated in waters shallower than 240 m. Thus in the first and last panels of figure 8, the depth-specific means and standard deviations were assembled from data profiles in which the bottom echo was excluded.

We attempted to use the global mean and standard deviation for the entire data set rather than use

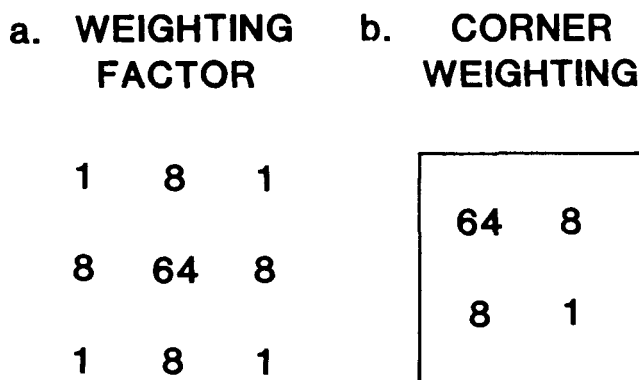


Figure 5. Weighting matrices for the smoothing operator that were used to prepare the grid of values for contour tracking. a. The contoured value replaces the central value in the 9 contiguous bins and consists of a weight of 64 for the central value, 8 for each on-side contiguous value, and 1 for each diagonal contiguous value. b. At corners or edges the weighting matrix is adjusted to the location.

4-hour averages. The effect was to pool heterogeneous data, increase the standard deviation, and reduce the sensitivity of the normalized values to spatial structure. It is possible that electronics drift, long-term instrument instability, or environmentally induced changes in the signal amplitude make the derivation of a representative global mean and standard deviation uninterpretable with the present amount of data. To study these instrumental problems further, one must convert to calibrated sound sources and receiver sensitivities (Flagg and Smith 1989).

The ship's velocity was estimated from the file of dates, times, and geographic position. The sequential geographic positions nearest to each half hour were evaluated for distance traveled in the elapsed time. The difference in latitude in degrees was multiplied by 60 to obtain nautical miles, and by 1852 to obtain meters in that plane. The difference in longitude in degrees was multiplied by 60 and the cosine of the latitude (about 0.85 at the latitude of this study) to obtain nautical miles, and by 1852 to obtain meters. The distance in meters was calculated as the square root of the sum of squares of the latitudinal and longitudinal differences.

Aggregations were arbitrarily defined as those shapes within the 1 standard deviation-contour, which contained a contour of 2 or more standard deviations. Aggregations were assigned an aggregation serial number. We also determined the shallowest and deepest depths of each aggregation.

To estimate the horizontal extent, we measured the proportion of the aggregation's horizontal extent relative to the half-hour interval of distance traveled. The aggregation was then assigned a horizontal width in meters. For example, if the aggrega-

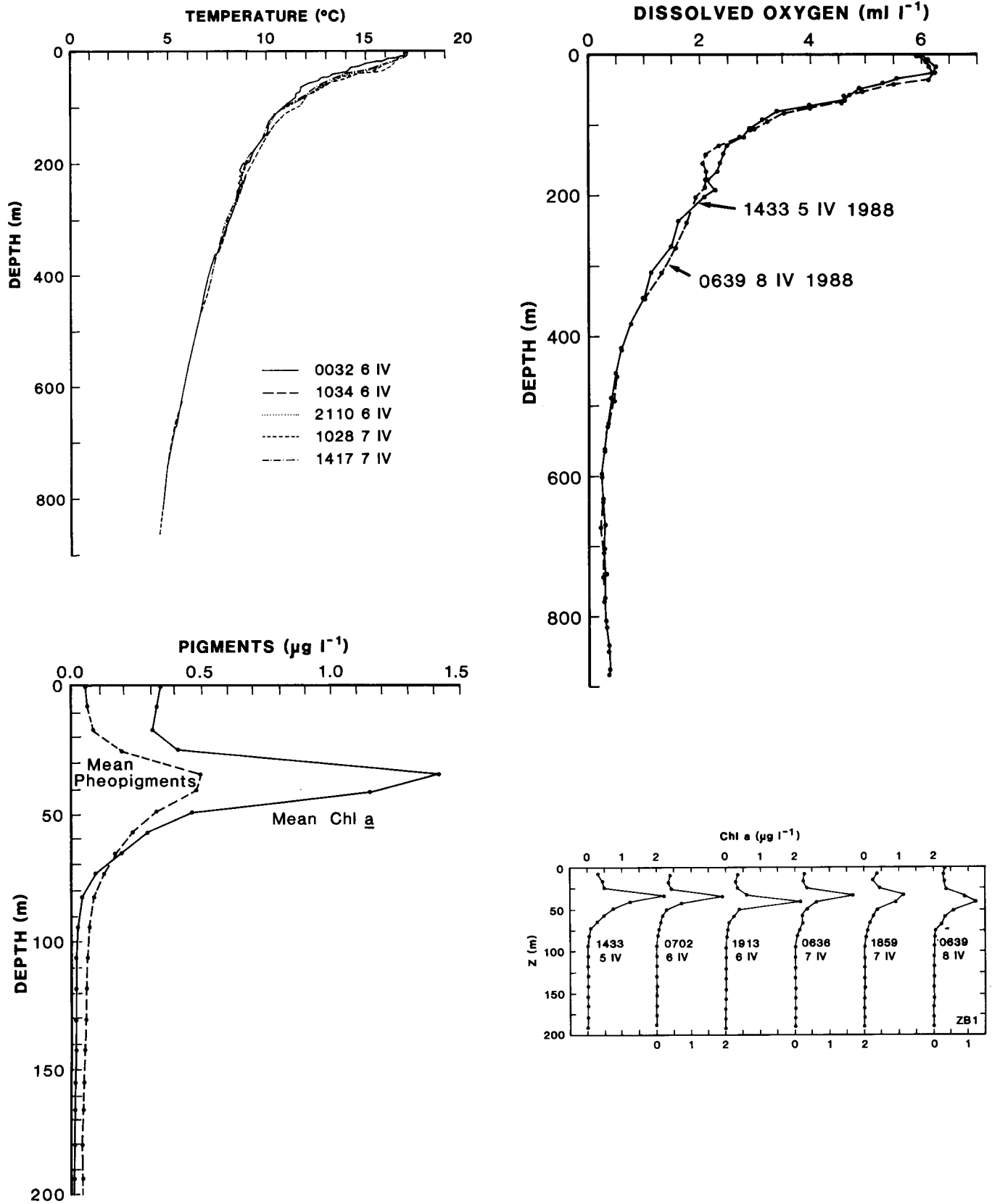


Figure 6. Vertical profiles: A, five temperature profiles; B, two dissolved oxygen profiles; C, means of six chlorophyll a and pheopigment profiles; D, six chlorophyll a profiles.



gation persisted for 10 minutes and the distance traveled in that half hour was 3200 m, the aggregation was said to extend 1070 m. The vertical plane area of each aggregation was estimated as the product of the vertical and horizontal dimensions. The sum of the vertical plane aggregation areas was estimated for each 4-hour period. The vertical plane area insonified was calculated by adding the ship's meters of progress in 8 half-hour intervals and multiplying by the depth of observation or 240 m. Comparison of the two values yielded an estimate of "coverage." Since there were no perfectly rectangular aggregations, the aggregation areas represent an overestimate varying from about 25% for inscribed circles to a factor of two or more for diagonally extended aggregations. Data exist for correcting this bias and for improving precision by more frequent evaluation of ship's speed.

## RESULTS

### Environmental Description

Vertical profiles of temperature, dissolved oxygen, and chlorophyll *a* can be characterized as exhibiting similarity in shapes and values among repetitions. Five temperature profiles taken between April 6 and 7 showed temperatures declining evenly, with some structure from 17°C at the surface to 5°C at 800 m (figure 6A). Deep oxygen profiles made near the beginning of the cruise (1433, April 5) and the end of the cruise (0639, April 8)

showed similar gradients, with a subsurface shallow maximum and a deep minimum at about 600 m (figure 6B). Vertical profiles of pheopigments showed maxima of about  $0.5 \mu\text{g l}^{-1}$  at or near the depth of the chlorophyll maximum layer (figure 6C). Six chlorophyll casts had distinct subsurface maxima of  $1-2 \mu\text{g l}^{-1}$  between 35 and 45 m (figure 6D).

Vertical distributions of adult females of three species of calanoid copepods illustrate different types of behavior that influence acoustic sampling methods (figure 7). Because all three species were relatively abundant and are known to store lipids (Ohman 1988b), they should have affected backscattering at 307 kHz. *Calanus pacificus californicus* Brodskii was nonmigratory, remaining in the upper 50 m within acoustic range day and night (figure 7A). If the finer-scale vertical distribution of this species were constant over time and distance, a *C. pacificus californicus* layer would influence the mean but not the standard deviation of echo amplitude. *Eucalanus californicus* Johnson was also nonmigratory, but remained between 200 and 400 m day and night (figure 7B). Slight shifts in vertical distribution of *E. californicus* of a few tens of meters would bring it into and out of acoustic range, primarily affecting the standard deviation of echo amplitude. *Metridia pacifica* Brodskii underwent a distinct vertical migration (figure 7C). A daytime population mode at 200–150 entered the upper 50 m at night. Such a pronounced shift in vertical distribution would influence both the amplitude mean and stan-

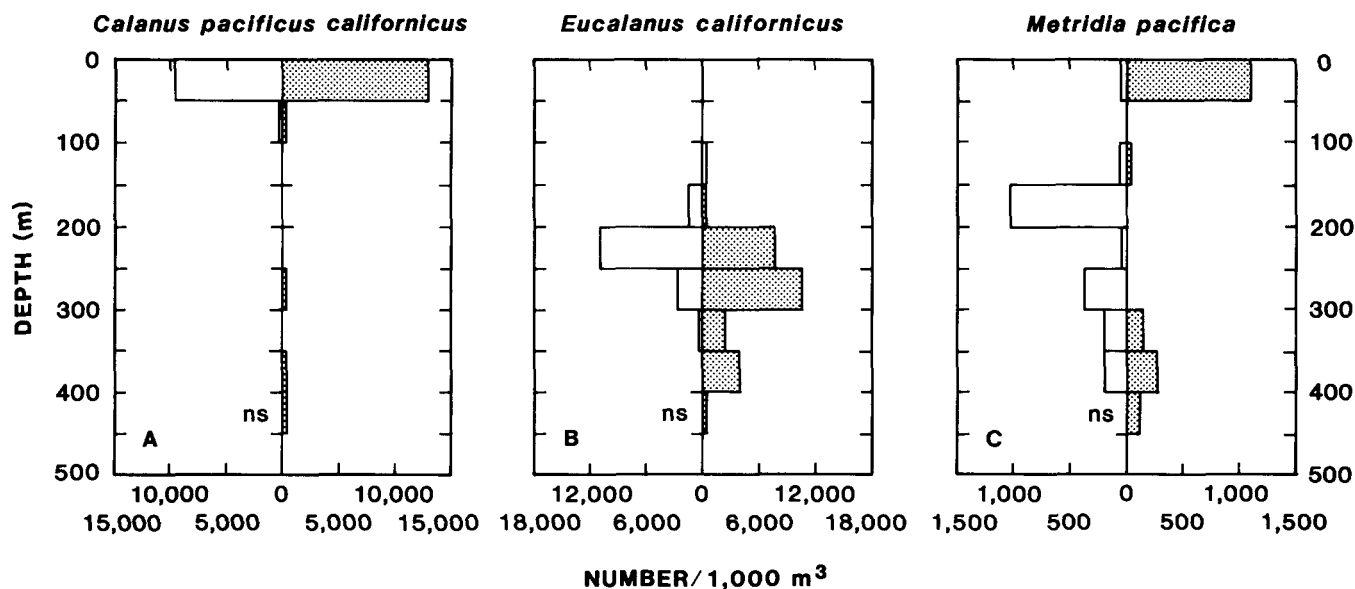


Figure 7. Day (open bars) and night (shaded bars) vertical distributions of adult females of the copepods *Calanus pacificus californicus* (A), *Eucalanus californicus* (B), and *Metridia pacifica* (C) on April 6, 1988. "ns" indicates that no sample was taken.

dard deviation. Note that a smaller segment of the *M. pacifica* population occurred at 400–300-m depth both day and night.

Euphasiid furciliae and adults, as well as other macrozooplankton taxa, also appeared in these samples.

### General Appearance of Aggregations

There were no pronounced differences in the general appearance of aggregations between day and night. Both seem characterized by the appearance of shattered layers, shattered patches, and relatively smooth-edged patches. The physical size of the patches ranged from the threshold of detectabil-

ity to relatively large at all depths at all times of day. The largest and most coherent aggregations were detected during the vertical migrations at dawn and dusk (figure 8C, F, I, L, O, R).

### Migration and Migration Rates

Coherent aggregations during the entire period of migration were observed in one of three dusk records and two of three dawn records. On the dawn of April 7 the descending layer bifurcated into distinct layers (figure 8L). Estimates of maximum ascent rate ranged from 5 to 8 cm s<sup>-1</sup>, and estimates of the maximum descent rate ranged from 3 to 4 cm s<sup>-1</sup>. Aggregation densities exceeded three standard

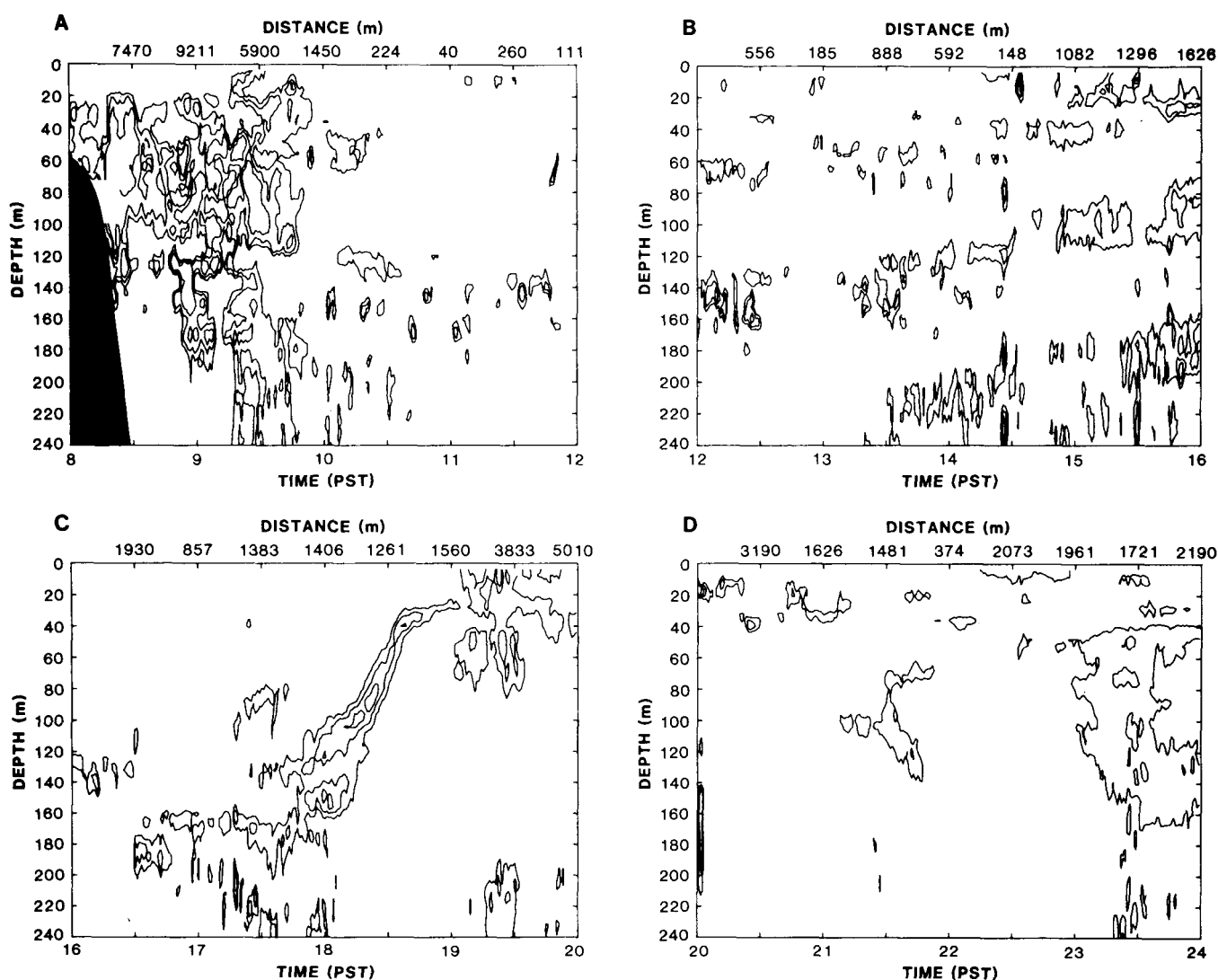


Figure 8 (continues on following three pages). A–S Each letter refers to a contoured data unit of 4 hours (less in 8S). The upper margin represents the straight-line distance between the ship's positions at the beginning and end of each half-hour interval. The figures are oriented on the page so that the day contours occupy the middle section, the dawn section for that calendar day is in the upper right, and the dusk section is in the lower left. The night contours are split between the upper left and the lower right. Contour interval is 1 standard deviation.

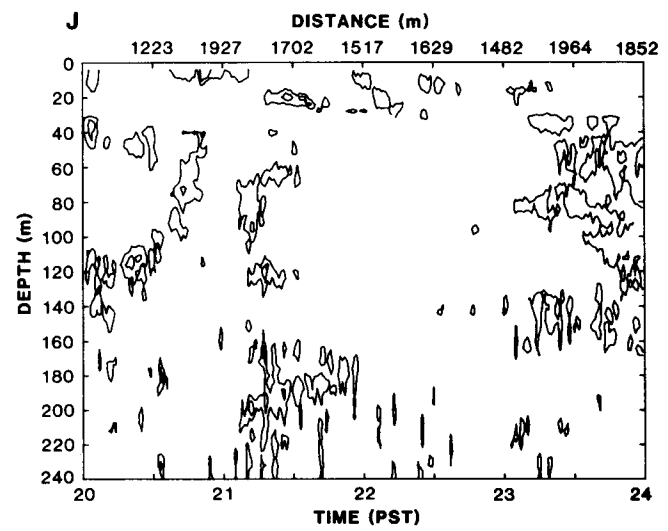
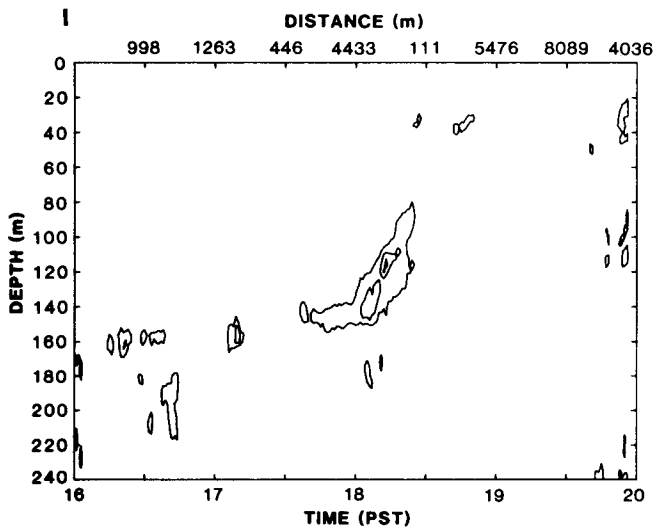
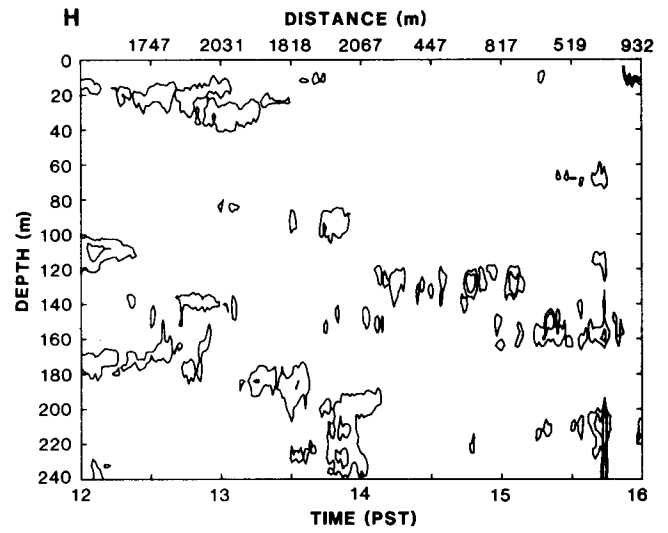
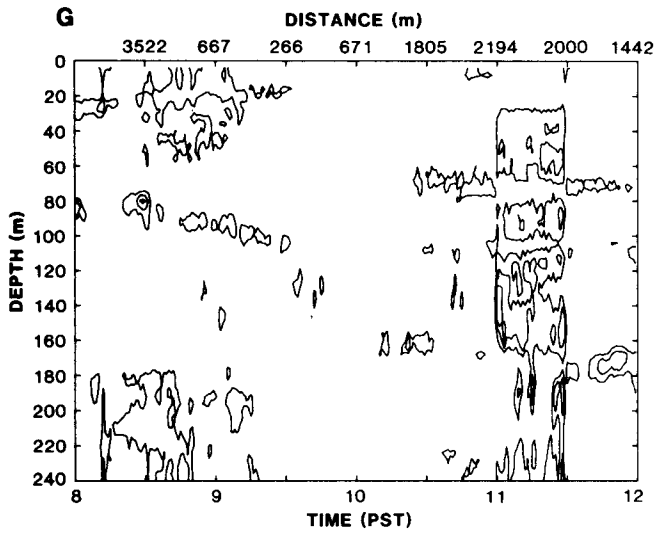
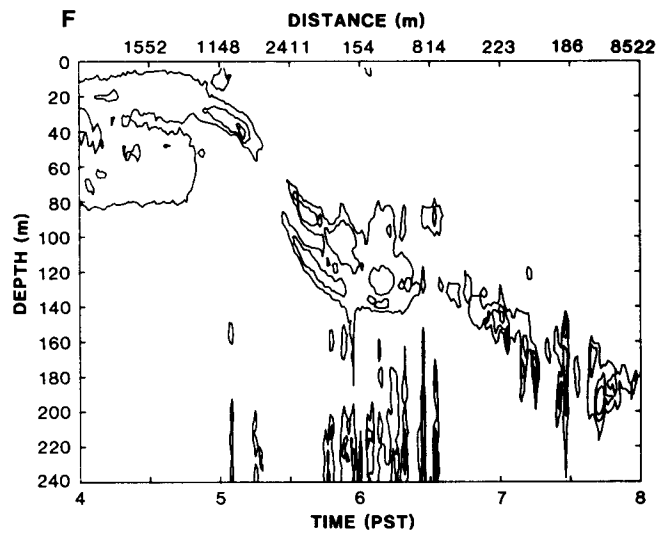
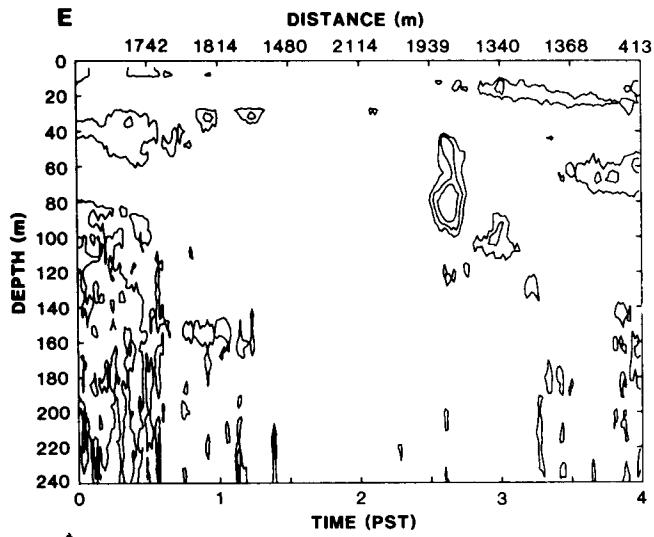


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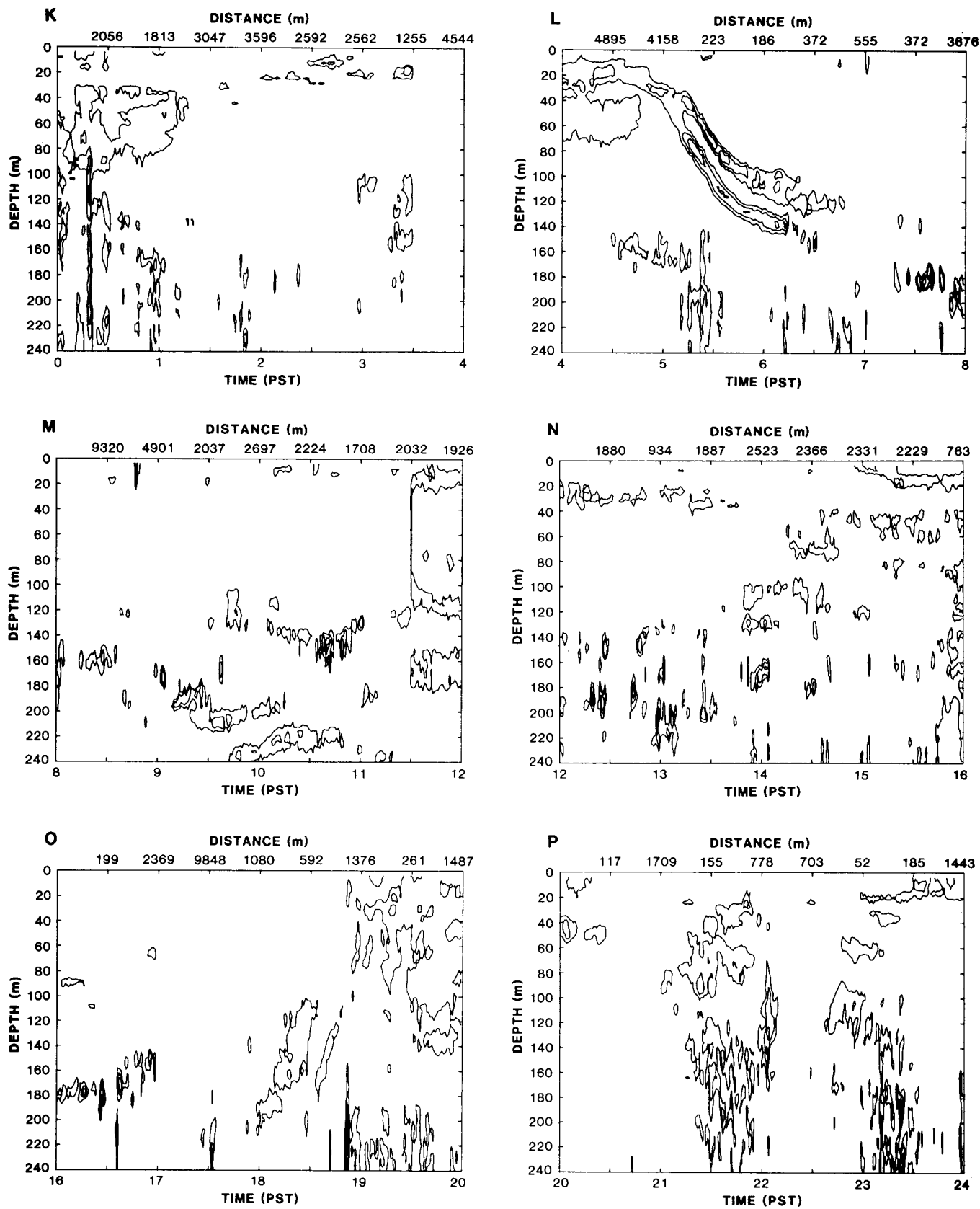


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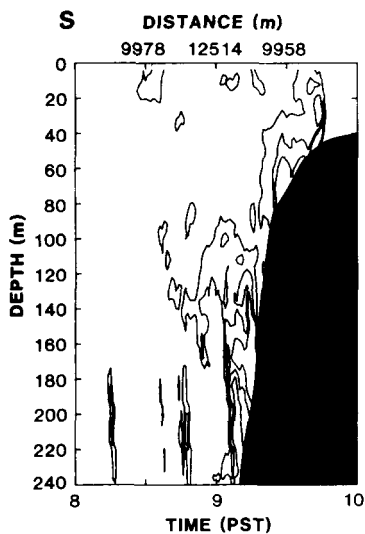
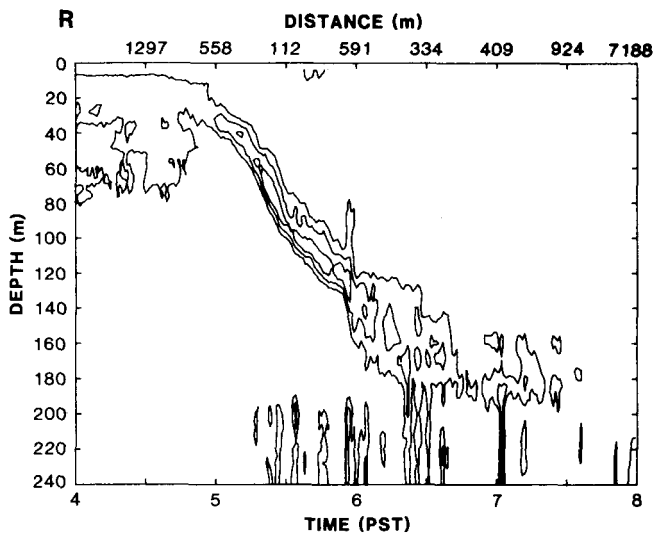
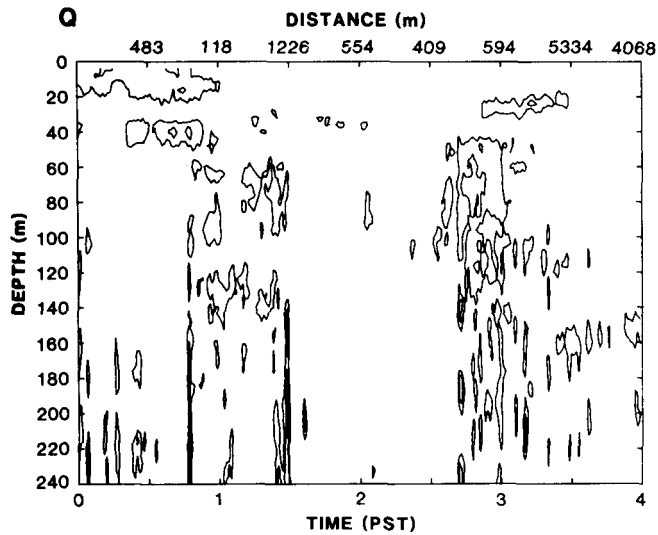


Figure 8 continued.

deviations above the mean in two of the three ascents and in all three descents.

**Depth Distribution of Aggregations**

Nearly twice as many of the 126 aggregations were detected at depth as near the surface (figure 9). The mean depth of aggregation is 134 m. At this stage of analysis it is not known if the cause of this distribution is simple or complex. The main cause of this imbalance is a surplus of aggregations at 180 m and 220 m and a deficiency of aggregations at 80 m and 100 m.

The simple explanation would be that this is the actual distribution of these aggregations. Complex explanations include (1) the width of the insonified volume increases at greater depths, increasing the chance of contact with patches; (2) some migrations from depth have destinations near the surface,

where the ADCP process does not insonify; (3) the fore-and-aft dimension of the insonified volume at depth detects aggregations that have been insonified many times during each ensemble average in the lower level but that are missed by insonifying the gaps among patches during their residence in the upper level; (4) the general level of reverberation in the upper level is higher, and the use of normalized detection is less effective there than in the lower level, where the aggregations stand out against a lower reverberation background level; and (5) the aggregation behavior of the organisms leads to compact aggregations at depth but more diffuse and less-detectable aggregations at the surface. The small value at 240 m may reflect the approach of the absolute depth for detection of aggregations from the surface with 307-kHz sound. At depths over 150 m there may be undetected aggregations owing to decreased signal-to-noise ratios.

**Vertical Dimensions of Aggregations**

More than half of the aggregations are less than 50 m in vertical dimension (figure 10). The mean vertical dimension of the aggregations was 54 m.

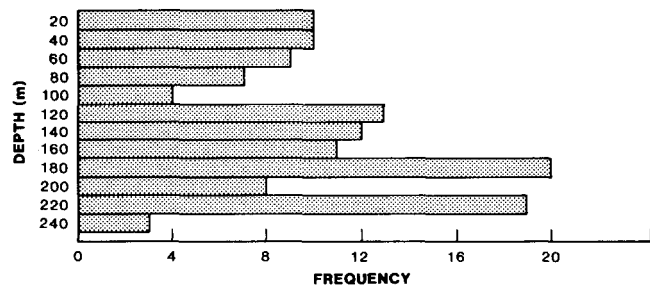


Figure 9. The depth distribution of aggregations.

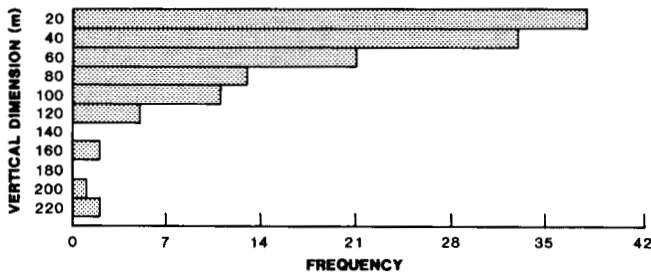


Figure 10. The vertical dimensions of aggregations.

Nearly 10% of the aggregations are more than 110 m in vertical extent. There has been no provision for excluding or estimating the incidence of aggregations that contact the upper or lower margin of the insonified volume; it appears unnecessary given the distribution of depths recorded here.

### Horizontal Dimensions of Aggregations

The median horizontal dimension of aggregation is less than 750 m in the survey, and about 10% of the aggregations exceed 2250 m (figure 11). The arithmetic mean of the horizontal dimensions is 1268 m; the geometric mean is 519 m. This distribution is suitably approximated as a log normal distribution with parameters 6.251 and 1.440 (mean and standard deviation of  $\ln$  values). The lower limit of detection of horizontal dimension is determined by ship's speed; at two knots ( $1 \text{ m s}^{-1}$ ) the lower limit would be 60 m; at 10 knots the lower limit would be 300 m. Much of this cruise involved the towing of plankton nets, and there was very little full-speed running between stations. Therefore the mode at horizontal dimensions less than 250 m may not be characteristic of cruise tracks at the higher speeds needed to cover wider geographic areas.

### Horizontal Dimensions of Gaps between Aggregations

The median dimension of gaps between patches is less than 1500 m (figure 12). The arithmetic mean

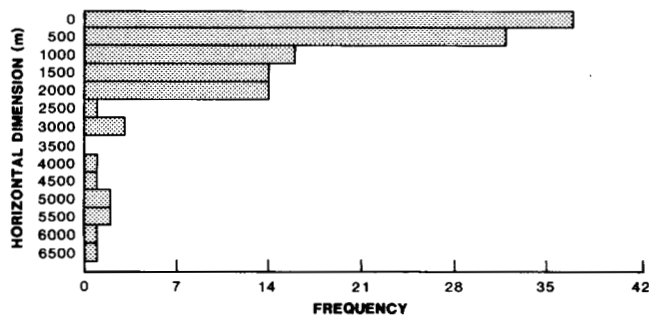


Figure 11. The horizontal dimensions of aggregations.

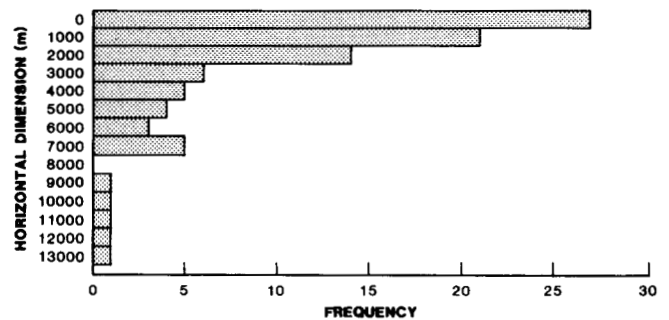


Figure 12. The horizontal dimensions of gaps between aggregations.

of gap is 2553 m; the geometric mean is 1120 m. The distribution is approximately log normal, with parameters 7.021 and 1.428. About 10% of the gaps are longer than 6500 m. Horizontal dimensions of gaps among patches appear to be about double the horizontal dimensions of the patches.

### Coverage

There is a clear mode in the coverage statistic at 10% (figure 13). Two-thirds of the 19 observations occurred in this interval. Two of the 19 4-hour segments were more than 25% covered with aggregations as defined.

### Continental Shelf and Slope

Plankton aggregations over the continental shelf, slope, and shelf-break area appeared in both crossings of that region. Since both passages occurred in daylight, this area may represent a special case for shallow daytime plankton aggregations. The points of contact of these aggregations and the bottom may be of considerable importance to the demersal organisms in those depth zones.

### Summary

Some important features of aggregations have been described with a sample of 126 aggregations measured in 19 4-hour segments. Limited data indicate that there are important plankton aggregations at the break between the continental shelf and slope. The vertical section of the aggregations covers approximately 10% of the water column in the upper 240 m. The mean thickness of aggregation is

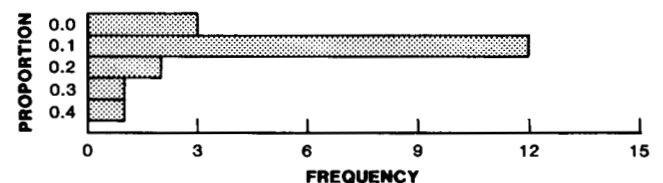


Figure 13. The distribution of proportion covered.

54 m, and about half of the aggregations are less than 50 m in vertical dimension. The mean horizontal dimension is 1268 m, and about half are less than 750 m across. In the horizontal plane, the gaps between aggregations are about twice as large as the aggregations. Vertical migration of the aggregations can usually be detected at dawn and dusk, but it is possible to be between aggregations at the time of migration in this locality.

## DISCUSSION

The primary results of this study are that a procedure for estimating the structure of plankton aggregations has been defined, and some preliminary data have been gathered in one habitat near the southern California coast over the San Diego Trough. Depth distributions, vertical and horizontal dimensions of the aggregations, and gaps between aggregations are relatively consistent. Although the number of sections is small, it is possible to estimate the coverage of the vertical section over this coastal area as about 10%. Some of the strongest and most clearly defined aggregations were detected at the time of vertical migration at dawn and dusk.

The 307-kHz sound used for this study is probably capable of detecting aggregations of larger copepods (Castile 1975), euphausiids, the gas bubble of physonect siphonophores, and mesopelagic fishes. The migration rates of the aggregations detected on this cruise are in the upper range for migrating copepods. Enright (1977) estimated migration rates of 1 to 5 cm s<sup>-1</sup> for the calanoid copepod *Metridia pacifica* from sequential net tows taken near the present study site. In laboratory respirometer chambers the euphausiid *Euphausia pacifica* has been clocked at up to 9.7 cm s<sup>-1</sup> (Torres and Childress 1983).

Several works have emphasized the interactions between the pelagic layers and the ocean bottom at the continental shelf, shelf-break, and slope (Isaacs and Schwartzlose 1965; Genin et al. 1988; Holliday 1987; and Pieper et al., in press). In the brief transects of the continental shelf and slope (figures 8A and 8S) in this paper, it would appear that this "enriched" region is worthy of more study. It is likely to be a region of high productivity of demersal fishes that depend on food advected in pelagic layers and the migrations of some of the biota.

Although the technique used for estimating the size of patches is fundamentally different from that used by Greenlaw and Percy (1985), the gross appearance and vertical and horizontal dimensions of the patches are similar. The Greenlaw and Percy

study was conducted with a single transducer and a fully calibrated system in the amplitude domain. Therefore the patches could be defined in absolute acoustic units by measuring contours at 5-dB intervals. From formal spatial spectral analysis, Greenlaw and Percy concluded that the vertical dimensions were of the order of tens of meters, and horizontal dimensions were km-scale. Our conclusions were based on statistical manipulation of unquantified amplitude domain acoustic signals, which appeared to be stable for short periods (4 hours). Our spatial scales were determined by direct measurement of arbitrary contour drawings, with contours placed at 1-standard-deviation intervals. In most of the drawings for this paper, this would involve 2–3-dB spacing for contours.

The horizontal dimension of plankton aggregations and of gaps between aggregations may be compared to fish schools, primarily the omnivorous planktivore northern anchovy (*Engraulis mordax*). In figure 14 are plotted the cumulative distributions of patch and gap dimensions from this study, a distribution of fish school sizes (Smith 1981), and the distribution of fish school group sizes (Fiedler 1978). Also, Star and Mullin (1981) described critical length scales for distributions of copepod stages and species, and found kilometer-scale aggregations to be the rule at a depth of 35 m. The slopes of the cumulative curves are lower for the patches and gaps than for the schools and school groups: one may infer from this that nekton spatial structures are under more behavioral control than the plankton aggregations.

It is clear from the size and intensity of the planktonic structures that considerable invasive sampling, with precise vertical and horizontal control of nets or pumps, will be necessary for studying the dynamics and interactions of these populations. The tactical deployment of such samplers directed by integrative acoustic devices like the ADCP will materially aid in understanding the primary interactions among schools and school groups of planktivorous fishes. In particular, the joint use of ADCP and directed sampling devices will be needed to model the foraging strategy of schooling fishes, and their search for, and effect on, the plankton aggregations to explain the relationship among spatial scales of primary production, secondary production, and the production of fishes.

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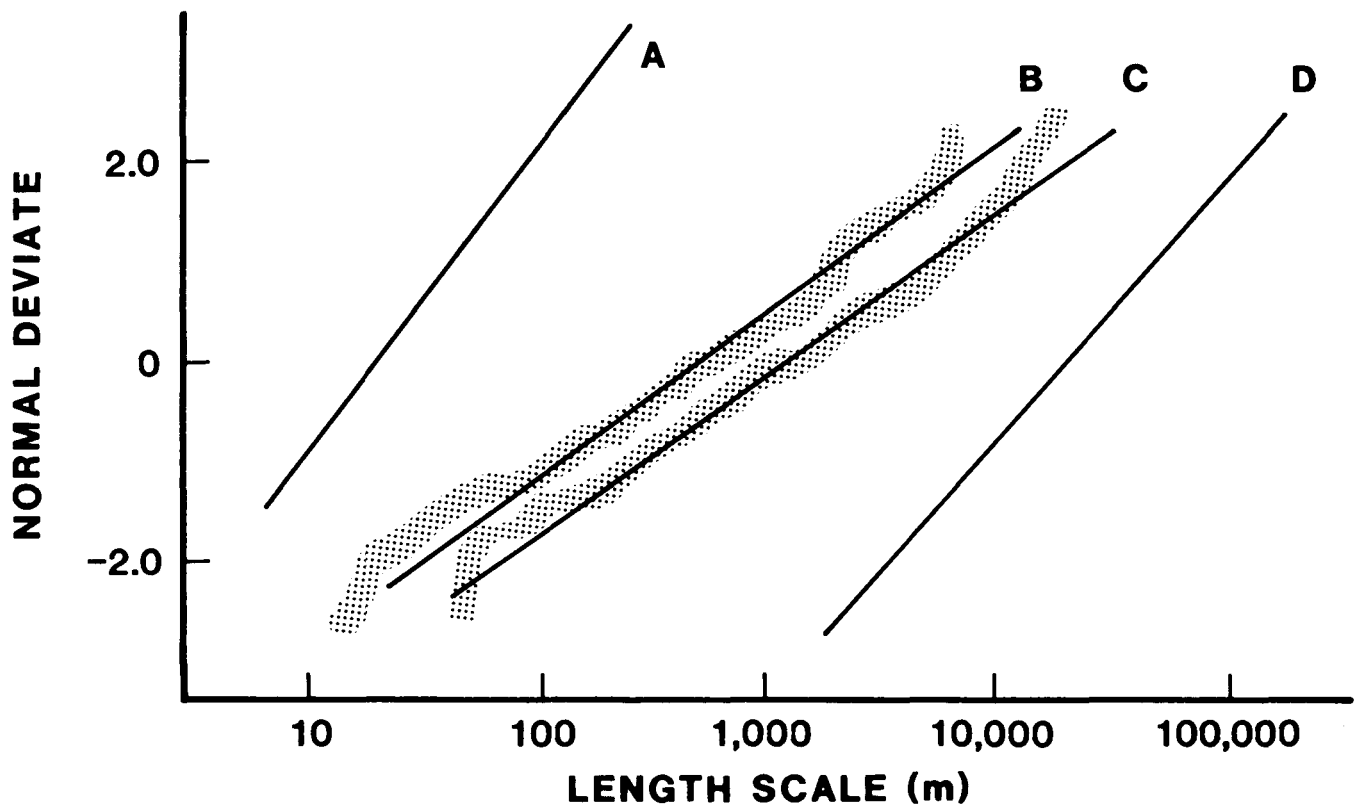


Figure 14. Comparison of the cumulative frequency distribution of horizontal dimensions of (A) fish schools (Smith 1981); (B) plankton aggregations; (C) gaps between plankton aggregations; and (D) fish shoal groups (Fiedler 1978). In curves B and C, a straight line has been fitted to the experimental data, which is represented with shading.

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## A CHECKLIST OF THE SPECIES OF PELAGIC SHRIMPS (PENAEOIDEA AND CARIDEA) FROM THE EASTERN PACIFIC, WITH NOTES ON THEIR GEOGRAPHIC AND DEPTH DISTRIBUTION

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### ABSTRACT

A checklist of the species of pelagic shrimps (Penaeoidea and Caridea) of the eastern Pacific based on published information and collections made off the coast of Mexico is presented. The list includes all species known from this region, including some records on seamounts 1250 km offshore. In total, 86 species have been considered (39 Penaeoidea and 47 Caridea). For each species, references to the original description and to more recent records and illustrations of the species are provided. Other information on geographic and bathymetric distribution is included. The zoogeographic affinities of the pelagic shrimps of the eastern Pacific are briefly discussed, with emphasis on the Mexican fauna. In total, 22 species (9 Penaeoidea and 13 Caridea) are endemic to the eastern Pacific; 24 species (8 Penaeoidea and 16 Caridea) are considered cosmopolitan; and 34 species (20 Penaeoidea and 14 Caridea) are also found in one or more geographical regions but are not cosmopolitan. Twenty-four species are found in the Pacific (throughout the Pacific, in the central Pacific, or in the western Pacific); 11 species are found in the Atlantic (6 are not found elsewhere); and 14 species are found in the Indian Ocean (2 are not found elsewhere). Four species extend their distribution to Japan (3) or to the Sea of Okhotsk (1). A small group of 2 species presents a peculiar distribution.

Of the 86 species reported, 51 (29 Penaeoidea and 22 Caridea) have been collected at least once off the coast of Mexico.

### RESUMEN

Se presenta una lista de especies de camarones pelágicos (Penaeoidea y Caridea) del Pacífico oriental sobre la base de informaciones publicadas y recolecciones realizadas frente a las costas de México. Esta lista comprende todas las especies conocidas para esta región, incluyendo algunas recolectadas en montes marinos, aproximadamente

1250 Km mar afuera. Se consideran 86 especies (39 Penaeoidea y 47 Caridea) y para cada una de ellas se hace referencia a la descripción original y a citas adicionales que incluyen observaciones recientes e ilustraciones de las mismas. Otros datos incluidos hacen referencia a la distribución geográfica y batimétrica de cada especie, tal como se conoce actualmente. Se discuten brevemente las afinidades zoogeográficas de los camarones pelágicos del Pacífico oriental con énfasis en la fauna mexicana. En total, 22 especies (9 Penaeoidea y 13 Caridea) son endémicas al Pacífico oriental, 24 (8 Penaeoidea y 16 Caridea) son consideradas cosmopolitas y 34 (20 Penaeoidea y 14 Caridea) han sido encontradas en una o mas regiones zoogeográficas, pero sin ser cosmopolitas. Se encuentran 24 especies en el Pacífico (en todo el Pacífico, en el Pacífico central o en el Pacífico oriental), 11 se encuentran en el Atlántico (de las cuales 6 no se encuentran en ninguna otra región) y 14 se encuentran en el Océano Indico (de las cuales 2 no se encuentran en ninguna otra región). Cuatro especies extienden su distribución hasta el Japón (3) o el Mar de Okhotsk (1). Un pequeño grupo de 2 especies presenta una distribución peculiar.

De las 86 especies reportadas, 51 (29 Penaeoidea y 22 Caridea) han sido recolectadas al menos una vez frente a las costas de México.

### INTRODUCTION

The pelagic decapod crustaceans of the Pacific coast of America have been little studied. This is particularly true in tropical and subtropical waters where local institutions have done little or no sampling of the fauna because, in most cases, it does not represent a readily available source of food.

The complex taxonomy of most genera of pelagic decapod crustaceans is another obstacle to their study. In particular, the identification of caridean shrimps and of certain groups of penaeoidean shrimps like *Sergestes* or *Gennadas* can be difficult because of the lack of comprehensive works on local fauna (the literature is widely dispersed and often

not available in countries where the species actually occur) or because of geographic variation of some morphologic features that only experts can evaluate by comparing large series of specimens from many localities.

As a general rule, pelagic or semipelagic species belonging to the Brachyura—e.g., *Portunus xantusii* (Stimpson), *Euphyllax dovii* Stimpson—and Anomura—e.g., *Pleuroncodes planipes* Stimpson—are well known. Their distribution and behavior (seasonal benthic and pelagic phases) are well understood because only a few species are involved (Jerde 1970; Mathews et al. 1974; Alvariño 1976; Blackburn 1977).

The biology of pelagic shrimps in the ocean was reviewed by Omori (1974), who also emphasized the importance for some countries of species of the genera *Acetes* H. Milne Edwards and *Sergia* Stimpson, which can be used as food (Omori 1978). It should be clearly understood, however, that in many cases the capture of pelagic shrimps for food is not worth the tremendous fishing effort necessary to obtain catches of commercial size.

One of the basic limitations to understanding the biology of pelagic shrimps is the lack of accurate sampling data regarding their vertical distribution in the water column. Although some species migrate diurnally over distances of up to 800 m (Omori 1974), a detailed study of this movement is available for only a few Pacific species. Many authors have emphasized the necessity of using automatic opening-closing nets to capture large planktonic or micronektonic species (see Omori 1974; Kensley 1981), but these expensive and sometimes difficult-to-operate instruments (see for example Roe and Shale 1979) are not as common as they should be, especially in countries with economic problems.

The study of the fauna of a given geographic area is made easier if a checklist of the species known for the region is available. In fact, a regional checklist for any given group of species is generally the first step toward a more detailed monographic study. During our study of pelagic shrimps available in the collections of various institutions in Mexico or recently collected by the R/V *El Puma* of the Instituto de Ciencias del Mar y Limnología, UNAM, we compiled a list of all species of pelagic shrimps that have ever been reported in the eastern Pacific. In this paper we present this list, with up-to-date information related to the geographic and depth distribution of each species, with the hope that it will serve as a basic tool for the study of the pelagic shrimps of the region.

## METHOD OF STUDY

The information in this paper was obtained from the literature on pelagic shrimps of the Pacific coast of America and of the world oceans. Indeed, many species of pelagic shrimps have a cosmopolitan distribution, and students of western American species often have to refer to literature dealing with other geographic regions in order to find adequate descriptions and illustrations.

Some original data regarding geographic and depth distribution were obtained during the revision of recent material obtained by the R/V *El Puma* (SIPCO, CORTES, and CICIMAR cruises); by the R/V *Antonio Alzate* (PESCA, México); or during CalCOFI cruises. These data are included in the text.

## RESULTS

This paper includes all species collected to date in the eastern Pacific, including the species reported by Hanamura (1983) on seamounts located 800 to 1500 km off the coast of Mexico and not previously known for the region—*Bentheogennema intermedia* (Bate), *Gennadas capensis* Calman, *Acanthephyra eximia* Smith, *Eupasiphae gilesii* (Wood-Mason). It should be clearly understood, however, that no original taxonomic considerations are included in this paper, and readers must therefore refer to the literature cited in the text in order to fully understand the viewpoints of some authors regarding the taxonomy of the genera and the synonymies.

Although there is still much to be learned on this particular point, it would seem that some benthic shrimps—e.g., *Hymenopenaeus doris* (Faxon)—are occasionally caught during midwater trawls and must therefore be included in a checklist such as the one presented here. Regarding depth distribution, however, it clearly appears that the most common problem is with pelagic shrimps that are captured during the descent or ascent of epibenthic trawls or sledges, because no residence depth can be determined. Many of the species included in the list are undoubtedly strictly pelagic (they have been captured repeatedly in midwater trawls), but some might have to be excluded in the future when more is learned about their biology.

A total of 86 species (39 Penaeoidea and 47 Caridea) have so far been reported for the eastern Pacific. They are all included in the following taxonomic list. The classification of the genera into families was made according to de Freitas (1984), Crosnier (1985), and Abele and Kim (1986). Within each genus, species have been ordered alphabetically. The restricted synonymy includes the origi-

nal description and often one or more references that include a good description of the species, with illustrations.

## PENAEOIDEA

### Family Benthescymidae

#### Genus *Bentheogennema* Burkenroad 1937

1. *Bentheogennema borealis* (Rathbun 1902).  
*Gennadas borealis* Rathbun 1902: 887; 1904: 147, figs. 88–89.  
*Bentheogennema borealis*. Butler 1980: 41 (illustrated).

*Geographic distribution*: From Japan and the Bering Sea to Isla Coronado, Baja California (Hanamura 1979; Butler 1980).

*Depth distribution*: Mostly from 200 to 1500 m and to 2560 m (Butler 1980). Krygier and Pearcy (1981) reported this species from 100 to 1000 m off Oregon, with maximal density from 600- to 1000-m depth.

2. *Bentheogennema burkenroadi* Krygier and Wasmer 1975.

*Bentheogennema burkenroadi* Krygier and Wasmer 1975: 737, figs. 1–3. Butler 1980: 43 (illustrated).

*Geographic distribution*: From the northeastern Pacific (52°N–142°W) south to Seamount 350, off Baja California (23°05'N–124°57'W) (Hanamura 1983).

*Depth distribution*: Mostly between 100 and 500 m, and down to about 1200 m (Butler 1980; Hanamura 1983). From surface to 2000 m off Oregon, with a population maximum between 300 and 1000 m (Krygier and Pearcy 1981).

3. *Bentheogennema intermedia* (Bate 1888).  
*Gennadas intermedius* Bate 1888: 343, pl. 58, fig. 3.  
*Bentheogennema intermedium*. Tirmizi 1960: 368, figs. 36–38.  
*Bentheogennema intermedia*. Crosnier 1978: 30, figs. 13a–b, 14a–c.

*Geographic distribution*: Recorded off Baja California (13°29'N–119°54'W and 23°05'N–124°57'W) by Hanamura (1983). Also recorded in the Atlantic Ocean (east and west), the Pacific Ocean (Japan and Hawaii), and the Indian Ocean (Crosnier 1978, 1985; Hanamura 1983).

*Depth distribution*: Probably only below 800 m and to 4000 m (Crosnier 1978). Records along the coasts of America are from about 500–950 m, 1000–1200 m, and 3386 m (Foxton 1970b; Hanamura 1983;

Abele and Kim 1986); from 1000- to 2020-m depth (Kensley 1981).

4. *Bentheogennema pasithea* (de Man 1907).  
*Gennadas pasithea* de Man 1907: 146.  
*Bentheogennema pasithea*. Crosnier 1978: 31, figs. 13c–d.

*Geographic distribution*: Southern California and off Baja California (13°29'N–119°48'W) (Hanamura 1983). Indo-Pacific (Crosnier 1978, 1985).

*Depth distribution*: The upper bathymetric limit is ill-defined. It probably occurs below 1000 m (Crosnier 1978; Hanamura 1983).

5. *Bentheogennema stephensoni* Burkenroad 1940.  
*Bentheogennema stephensoni* Burkenroad 1940: 37. Crosnier 1985: 859, figs. 9h, 11a.  
*Bentheogennema stephenseni*. Hanamura 1983: 55, fig. 3c–e.

*Geographic distribution*: Off Baja California (13°29'N–119°54'W) and New Zealand (Hanamura 1983). Indian Ocean (1°43'N–87°08'E) (Crosnier 1985).

*Depth distribution*: The depth of capture of the unique specimen reported by Hanamura (1983) is unprecise (0–1617 m). The unique specimen cited by Crosnier (1985) was obtained with a nonclosing beam trawl operating at a depth of 4360 m.

#### Genus *Gennadas* Bate 1881

6. *Gennadas capensis* Calman 1925.  
*Gennadas capensis* Calman 1925: 5, pl. 1, figs. 1–2. Kensley 1972: 14, figs. 5c, 5g. Crosnier 1978: 36, fig. 18c.

*Geographic distribution*: Off Baja California (23°00'N–125°02'W); Atlantic Ocean (east and west) and Indo-Pacific (Crosnier 1978, 1985; Hanamura 1983).

*Depth distribution*: Varies considerably from as little as 250 m (Kensley 1981) to 3517 m (Gore 1985). In midwater trawls, the depth ranges from 250 to 630 m (Kensley et al. 1987).

7. *Gennadas bouvieri* Kemp 1909.  
*Gennadas bouvieri* Kemp 1909: 726, pl. 74, figs. 1–4, pl. figs. 6–7. Crosnier 1978: 34, figs. 15a, 18a–b.

*Geographic distribution*: Recorded off Baja California (23°05'N–125°02'W) by Hanamura (1983). Also found in the Indo-Pacific, and in the South and West Atlantic Ocean (Kensley 1981; Gore 1985).

*Depth distribution:* From 250 to 3400 m (Kensley 1981). According to a study of the vertical distribution of *G. bouvieri* in the Gulf of Mexico, Hefferman and Hopkins (1981) found a range of 250 to 475 m at night and 750 to 875 m by day. In midwater trawls, from 250 to 630 m (Kensley et al. 1987).

8. *Gennadas incertus* (Balss 1927).  
*Amalopenaeus incertus* Balss 1927: 265, figs. 24–29.  
*Gennadas incertus*. Kensley 1972: 12, 14, figs. 4i, 5j. Crosnier 1978: 37, figs. 15b, 19a.

*Geographic distribution:* Off Oregon (Krygier and Percy 1981) and Baja California (23°05'N–125°02'W) (Hanamura 1983). Indo-Pacific (Kensley 1972; Crosnier 1978).

*Depth distribution:* Maximal range is provided by Aizawa (1974), who observed this species in samples taken at night between 100 and 200 m and in samples taken by day between 400 and 900 m.

9. *Gennadas propinquus* Rathbun 1906.  
*Gennadas propinquus* Rathbun 1906: 907, fig. 61a–b. Crosnier 1978: 38, figs. 16b, 18d–e.

*Geographic distribution:* Off Oregon and California (Krygier and Percy 1981), off Baja California (23°05'N–125°02'W) (Hanamura 1983), and in the Indo-Pacific (Crosnier 1978; Kensley 1981).

*Depth distribution:* Kensley (1981) gives a range of 200 to 3400 m, and Krygier and Percy (1981) reported this species between 50 and 700 m, with the highest night catches obtained below 500 m and the highest day catches obtained above 100 m. Pelagic, from surface to 1200-m depth (Kensley et al. 1987).

10. *Gennadas scutatus* Bouvier 1906.  
*Gennadas scutatus* Bouvier 1905 (1906): 748; 1908: 42, pl. 8. Kensley 1972: 12, 16, figs. 4d, 6g. Crosnier 1978: 43, figs. 17a, 19c.

*Geographic distribution:* *Gennadas scutatus* was reported from Isla Clarion by Burkenroad (1938) and later considered a cosmopolitan species (Indo-Pacific, from Africa to America; East and West Atlantic) (Crosnier 1978). Méndez (1981) found the species off Peru. It also occurs off the southeastern part of Baja California (pers. obs.).

*Depth distribution:* From 200 to 3400 m (Kensley 1981), in midwater tows at 130–2000 m (Crosnier and Forest 1973), and occasionally collected at the surface (Crosnier 1978). Méndez (1981) reports one sample of this species taken in tows made in the depth range of 0–50 m. Pelagic, from surface to 600-m depth (Kensley et al. 1987).

11. *Gennadas sordidus* Kemp 1910.  
*Gennadas sordidus* Kemp 1910: 177, pl. 13, figs. 1–3. Tirmizi 1960: 349, figs. 40b, 48, 52–57. Hanamura 1983: 57, figs. 4d–f.

*Geographic distribution:* Gulf of California, off Baja California and Islas Revillagigedo (Burkenroad 1938; Hanamura 1983). Throughout the Indian Ocean (Hanamura 1983). In the Gulf of California, the species occurs south of Isla Tiburón (28°25'N–112°44'W) (pers. obs.).

*Depth distribution:* Burkenroad (1938) gives a range of about 550–915 m, and the species possibly occurs in deeper waters (Hanamura 1983). In the Gulf of California, *G. sordidus* has been obtained in plankton samples between 0 and 300 m (pers. obs.).

12. *Gennadas tinayrei* Bouvier 1906.  
*Gennadas tinayrei* Bouvier 1906: 10, figs. 2–4, 14. Kensley 1972: 12, figs. 4b, 5c. Crosnier 1978: 44, figs. 17b, 19d.

*Geographic distribution:* Off Oregon and Baja California (Krygier and Percy 1981; Hanamura 1983). In the Indo-Pacific and the Atlantic Ocean (east and west) (Crosnier 1978; Kensley 1981).

*Depth distribution:* From 600 to 1400 m (Kensley 1981). It has been reported occasionally between 400 and 600 m (Crosnier 1978; Krygier and Percy 1981) and at a depth of 90 m (Kensley et al. 1987).

#### Family Penaeidae Genus *Funchalia* Johnson 1867

13. *Funchalia balboae* (Faxon 1893).  
*Penaeus balboae* Faxon 1893: 211; 1895: 181, pl. 47, figs. 1, 1a–c.  
*Funchalia balboae*. Crosnier and Forest 1973: 297, fig. 100.

*Geographic distribution:* Isla Cocos and Gulf of Panama; western Indian Ocean and Atlantic Ocean (east and west) (Crosnier and Forest 1973).

*Depth distribution:* Pelagic, from surface to 1609 m (Burkenroad 1936; Crosnier and Forest 1973).

#### Family Solenoceridae Genus *Hymenopenaeus* Smith 1882

14. *Hymenopenaeus doris* (Faxon 1893).  
*Haliporus doris* Faxon 1893: 214; 1895: 191, pl. 49, figs. 1, 1a–c.  
*Hymenopenaeus doris*. Pérez-Farfante 1977: 283, figs. 9, 17, 18a, 19–20. Hanamura 1983: 54, fig. 2.

*Geographic distribution:* From the southern tip of the Gulf of California to Costa Rica (Isla del Coco) (Burkenroad 1938; Pérez-Farfante 1977). Also re-

ported off Baja California (between 13°25'N–120°04'W and 13°27'N–120°07'W) (Hanamura 1983).

*Depth distribution:* Pelagic between 550 and 915 m; also captured in trawls operating at about 3600 m (Burkenroad 1938; Hanamura 1983) and at 4082 m (Faxon 1893).

### Family Sergestidae

#### Genus *Sergestes* H. Milne Edwards 1830

15. *Sergestes arcticus* Kroyer 1859.

*Sergestes arcticus* Kroyer 1859: 240. Hansen 1922: 62, pl. 1, figs. 1–2, pl. 3, figs. 3–5, pl. 4, figs. 1–2. Holthuis 1952: 8, fig. 1. Kensley 1971: 232, figs. 7a–f.

*Geographic distribution:* Off southern Chile; East and North Atlantic and Mediterranean; southern oceans, from Uruguay to Australia (Holthuis 1952; Kensley 1981; Astporssen and Hallgrimssen 1983).

*Depth distribution:* From about 100 to 366 m (Holthuis 1952; Omori 1974). Kensley (1981) reports the species from surface to 820 m.

16. *Sergestes brevispinatus* Judkins 1978.

*Sergestes brevispinatus* Judkins 1978: 13, figs. 2d, 5d–f, h, k, 6–8. Méndez 1981: 60, figs. 177, 177a–b, 182, 189.

*Geographic distribution:* Central tropical eastern Pacific, from about 10°N to 18°S (Judkins 1978).

*Depth distribution:* Ill-defined; the species has been caught in as little as 55 m (Méndez 1981) and probably occurs to 200 m (Judkins 1978).

17. *Sergestes consobrinus* Milne 1968.

*Sergestes (Sergestes) consobrinus* Milne 1968: 26, figs. 5–9.

*Sergestes consobrinus*. Judkins 1978: 16, figs. 9–11, 21b. Hanamura 1983: 67, fig. 9.

*Geographic distribution:* California Current and central Pacific between about 41°N and 17°N (Judkins 1978).

*Depth distribution:* From 20 to 400 m, with a maximal abundance at 120 m (Milne 1968).

18. *Sergestes erectus* Burkenroad 1940.

*Sergestes (Sergestes) erectus* Burkenroad 1940: 38.

*Sergestes erectus*. Hanamura 1983: 62, fig. 6.

*Geographic distribution:* Off Baja California (23°05'N–124°57'W) and in Pacific Ocean (Hawaii and Raratonga) (Hanamura 1983).

*Depth distribution:* Reported by Hanamura (1983) in plankton samples obtained in the range of 0–1236 m.

19. *Sergestes extensus* Hanamura 1983.

*Sergestes extensus* Hanamura 1983: 64, figs. 7–8.

*Geographic distribution:* Off Baja California (23°05'N–124°57'W, 23°01'N–125°02'W, and 23°10'N–124°51'W) (type material; Hanamura 1983).

*Depth distribution:* Collected in the water column between 0 and 1236 m (Hanamura 1983).

20. *Sergestes geminus* Judkins 1978.

*Sergestes geminus* Judkins 1978: 25, figs. 2a–c, 7, 16f–j, 17, 18, 21a.

*Geographic distribution:* Eastern tropical Pacific, from about 12°N to 8°S (Judkins 1978).

*Depth distribution:* Taken in plankton samples between 0 and 200 m (Judkins 1978).

21. *Sergestes gibbilobatus* Judkins 1978.

*Sergestes gibbilobatus* Judkins 1978: 27, figs. 2g, 4c, 7, 19a–h, 20, 21a.

*Geographic distribution:* Throughout the central Pacific, from about 6°N to 20°S (Judkins 1978).

*Depth distribution:* All type material came from micronekton samples obtained at an unknown depth (Judkins 1978).

22. *Sergestes halia* Faxon 1893.

*Sergestes halia* Faxon 1893: 217. Burkenroad 1937: 320, figs. 4, 5. Hanamura 1983: 64, fig. 6d–g.

*Sergestes edwardsii*. Faxon 1895: 212, pl. 51, fig. 1 (in part, not *S. edwardsii* Kroyer).

*Geographic distribution:* Off California, southwestern Baja California (near and offshore), at the entrance to the Gulf of California, and in the Gulf of Panama (Burkenroad 1937; Hanamura 1983; Krygier and Wasmer 1988).

*Depth distribution:* Collected in trawls and dredges operating between 428 and 1000 m (Burkenroad 1937) and in midwater trawls at 240–256 m and between 0 and 1617 m (Hanamura 1983). Also taken in tows between surface and 200 m (pers. obs.).

23. *Sergestes pectinatus* Sund 1920.

*Sergestes pectinatus* Sund 1920: 24, figs. 42–43. Kensley 1971: 240, figs. 13a–g; 1972: 16, figs. 11h–j.

*Geographic distribution:* Off Baja California (23°05'N–124°57'W) (Hanamura 1983). Atlantic and Indo-Pacific (Kensley 1981; Hanamura 1983).

*Depth distribution:* From surface to 1170 m (Kensley

1981). Foxton (1970b) reported day catches at 580–700 m and night catches at 100 m or less.

24. *Sergestes pestifer* Burkenroad 1937.  
*Sergestes pestifer* Burkenroad 1937: 318, figs. 1–3.

*Geographic distribution:* Eastern Pacific, from Baja California (24°N–112°22'W and 31°30'N–16°10'W) to Islas Galápagos (Burkenroad 1937).

*Depth distribution:* The upper limit is ill-defined; the deepest record is about 1100 m (Burkenroad 1937).

25. *Sergestes sargassi* Ortmann 1893.  
*Sergestes sargassi* Ortmann 1893: 34, pl. 3, fig. 1.  
Hansen 1922: 148, pl. 9, fig. 2. Kensley 1972: 26, fig. 11k–m.

*Geographic distribution:* Off Baja California (23°05'N–124°57'W) (Hanamura 1983). Atlantic, Mediterranean, and Indo-Pacific (Kensley 1981; Hanamura 1983).

*Depth distribution:* From surface to 600 m (Kensley 1971); 75 to 750 m (Abele and Kim 1986). Taken at depths between 110 and 435 m (maxima at 150–200 m) at night, and between 300 and 950 m (maxima at 650 m) by day (Foxton 1970b).

26. *Sergestes similis* Hansen 1903.  
*Sergestes similis* Hansen 1903: 60, pl. 11, figs. 6a–d. Butler 1980: 47 (illustrated).  
*Sergestes (Sergestes) similis*. Milne 1968: 22, figs. 1–4.

*Geographic distribution:* From the Bering Sea to the Gulf of California, where it seems to be very common (pers. obs.). Also in Japan (Hanamura 1979; Krygier and Percy 1981).

*Depth distribution:* From about 50 to 2400 m. This species, however, is rarely found below 1000 m and has a maximal population density between 50 and 200 m at night and between 200 and 600 m by day (Omori and Gluck 1979; Krygier and Percy 1981).

27. *Sergestes tantillus* Burkenroad 1940.  
*Sergestes (Sergestes) tantillus* Burkenroad 1940: 42.  
*Sergestes tantillus*. Judkins 1978: 19, figs. 7, 12, 13b, 21b.

*Geographic distribution:* Central equatorial Pacific (20°N to about 5°S) and eastern Pacific, off Costa Rica to Ecuador (Judkins 1978). Méndez (1981) reports this species off Peru (10°54'S).

*Depth distribution:* The vertical distribution is ill-defined. It occurs between 0 and 200 m (Burkenroad 1940; Judkins 1978).

### Genus *Sergia* Stimpson 1860

28. *Sergia bigemnea* (Burkenroad 1940).  
*Sergestes (Sergia) bigemneus* Burkenroad 1940: 49.  
*Sergia bigemnea*. Hanamura 1979: 167; 1983: 68, figs. 10c–d.

*Geographic distribution:* Off Baja California (23°05'N–124°57'W), Tahiti, Hawaii, southwestern Japan, and northeastern Pacific (Hanamura 1983).

*Depth distribution:* Collected in tows made in the range of 0–1236 m (Hanamura 1983).

29. *Sergia filicta* (Burkenroad 1940).  
*Sergestes (Sergia) filictum* Burkenroad 1940: 52.  
*Sergia filicta*. Hanamura 1983: 71, figs. 11a–e.

*Geographic distribution:* Off Baja California (13°29'N–120°07'W) and in the Gulf of Panama (Burkenroad 1940; Hanamura 1983).

*Depth distribution:* Collected at 734–845 m with a closing net; also present in samples obtained between surface and 1632 m (Hanamura 1983).

30. *Sergia inoa* (Faxon 1893).  
*Sergestes inous* Faxon 1893: 216; 1895: 208, pl. 51, fig. 2. Hansen 1919: 8, pl. 1, figs. 1a–c.

*Geographic distribution:* Off Isla Malpelo, Colombia (4°03'N–81°31'W) (Faxon 1893) and in the central Pacific (Hansen 1919).

*Depth distribution:* Faxon (1893) reported specimens taken in a trawl operated at a depth of about 1650 m.

31. *Sergia laminata* (Burkenroad 1940)  
*Sergestes (Sergia) laminatus* Burkenroad 1940: 53. Kensley 1971: 251, figs. 18a–f; 1972: 28, figs. 12a–b.  
*Sergia laminata*. Hanamura 1979: 169; 1983: 72, fig. 11f.

*Geographic distribution:* Off southern California and Baja California (23°05'N–124°57'W) (Hanamura 1983). Indo-Pacific, including Japan (Kensley 1981; Hanamura 1983).

*Depth distribution:* The species has been collected between the surface and 1416 m, without further bathymetric precision (Kensley 1981; Hanamura 1983).

32. *Sergia maxima* (Burkenroad 1940).  
*Sergestes (Sergia) maximus* Burkenroad 1940: 47.  
*Sergia maxima*. Hanamura 1983: 70, figs. 10e–g.

*Geographic distribution*: Off Baja California (32°52'N–132°30'W) and in the Indo-Pacific (Hanamura 1983).

*Depth distribution*: At 717 m (bottom trawl) (Hanamura 1983).

33. *Sergia phorca* (Faxon 1893).  
*Sergestes phorcus* Faxon 1893: 217. Burkenroad 1937: 323, figs. 6–7.  
*Sergestes bisulcatus*. Faxon 1895: 210, pl. 52 (not *S. bisulcatus* Wood-Mason).

*Geographic distribution*: From the central Gulf of California and Baja California (about 22°30'N) south to Peru and Islas Galápagos, Ecuador (Burkenroad 1937; Méndez 1981).

*Depth distribution*: Recorded in tows made from surface to about 1100 m and in bottom trawls between 549 and 1000 m (Burkenroad 1937; Méndez 1981).

34. *Sergia profunda* (Bate 1888).  
*Sergestes profundus* Bate 1888: 428. Hansen 1903: 69, pl. fig. 3.

*Geographic distribution*: Off Valparaiso (33°42'S–78°18'W), Chile, and possibly in the Gulf of Guinea (eastern Atlantic) (Holthuis 1952).

*Depth distribution*: This species has been reported at 2516 m by Faxon (1895).

35. *Sergia scintillans* (Burkenroad 1940).  
*Sergestes (Sergia) scintillans* Burkenroad 1940: 43. Kensley 1971: 257, figs. 22a–f; 1972: 28, figs. 12f–h.  
*Sergia scintillans*. Hanamura 1979: 169; 1983: 67, figs. 10a–b.

*Geographic distribution*: Off Baja California (23°N–125°W), southeastern Africa, and in Pacific Ocean (Kensley 1981; Hanamura 1983).

*Depth distribution*: Collected between surface and 1236 m (Hanamura 1983). It has been reported by Omori (1974) in the depth range of 100–300 m at night and in the range of 500–700 m by day.

36. *Sergia kroyeri* (Bate 1881).  
*Sergestes kroyeri* Bate 1881: 193; 1888: 421, pl. 70, figs. 3, 4. Krygier and Wasmer 1988: 72.  
*Sergestes tenuiremis* Kroyer 1855: 10; 1859: 255, 278, 285, pl. 4, figs. 11a–b (established on a mastigopus stage of development).  
*Sergia tenuiremis*. Butler 1980: 49 (illustrated).

*Geographic distribution*: North central Pacific to Canada and Oregon, North Atlantic (Krygier and Percy 1981), Indian and Pacific oceans (Krygier and Wasmer 1988).

*Depth distribution*: From depths between 300 and 1500 m, with maximal density between 300 and 700 m at night and around 800–950 m by day (Krygier and Percy 1981, as *S. tenuiremis*).

#### Genus *Petalidium* Bate 1881

37. *Petalidium suspiriosum* Burkenroad 1937.  
*Petalidium suspiriosum* Burkenroad 1937: 325, figs. 8–12. Wasmer 1974: 160, figs. 1–8. Word and Charwat 1976: 27–28 (illustrated).

*Geographic distribution*: Off Baja California (13°28'N–120°07'W and 23°N–125°W) and Oregon, Clarion and the Hawaiian islands, and northeastern Pacific (Krygier and Percy 1981; Hanamura 1983).

*Depth distribution*: Collected in the ranges of 734–845 m and 1117–1233 m with midwater trawl (Hanamura 1983). This species is also reported between 150 and 1750 m off Oregon, with maximum population density between 600- and 1000-m depth (Krygier and Percy 1981).

#### Genus *Acetes* H. Milne Edwards 1830

38. *Acetes binghami* Burkenroad 1934.  
*Acetes binghami* Burkenroad 1934: 101, fig. 39. Omori 1977: 515, fig. 4.

*Geographic distribution*: Gulf of Panama and the Bay of Guayaquil, Ecuador (Burkenroad 1937; Omori 1977).

*Depth distribution*: Unknown.

#### Family Luciferidae

##### Genus *Lucifer* Thompson 1830

39. *Lucifer typus* H. Milne Edwards 1837.  
*Lucifer typus* H. Milne Edwards 1837: 469. Hansen 1919: 53, pl. 38, fig. 6.

*Geographic distribution*: Northeastern Pacific to Gulf of California (up to the northern gulf) and in Atlantic Ocean (Burkenroad 1937; pers. obs.).

*Depth distribution*: This species has been taken in tows made between surface and 200 m. (pers. obs.) and down to 730 m (Burkenroad 1937).

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##### Family Pasiphaeidae

##### Genus *Pasiphaea* Savigny 1816

40. *Pasiphaea acutifrons* Bate 1888.  
*Pasiphaea acutifrons* Bate 1888: 871, pl. 141, fig.



3. Boschma 1949: 302, figs. 12–16, pl. 1, figs. 3–4. Holthuis 1952: 10, fig. 2.

*Geographic distribution:* From southern Chile (Valparaiso) and around southern South America to Patagonia (48°41'S); Japan (Holthuis 1952; Vinuesa 1977).

*Depth distribution:* Recorded between 300 and 1400 m (Holthuis 1952). No indication of the methods of capture was provided.

41. *Pasiphaea affinis* Rathbun 1902.  
*Pasiphaea affinis* Rathbun 1902: 905; 1904: 24, fig. 6.

*Geographic distribution:* Known only from southern California (Schmitt 1921).

*Depth distribution:* Captured at 1800 m (Schmitt 1921).

42. *Pasiphaea americana* Faxon 1893.  
*Pasiphaeia cristata americana* Faxon 1893: 208.  
*Pasiphaeia americana*. Faxon 1895: 173, pl. 45, fig. 1–1d.  
*Pasiphaea americana*. Méndez 1981: 64, figs. 193–196.

*Geographic distribution:* Off Baja California (24°30'N) and in the northern Gulf of California (30°11'N) (pers. obs.), south to Isla Lobos de Tierra, Peru, including Islas Galápagos (Méndez 1981).

*Depth distribution:* This species has been collected from 150 to 576 m in bottom trawls off Peru (Méndez 1981). It is also reported in depths to 1000 m by Faxon (1893) and was taken in plankton samples from the surface to 225 m (total depth from 277 to 645 m in the Gulf of California and from 350 to 1700 m off Baja California) during this study.

43. *Pasiphaea chacei* Yaldwyn 1962.  
*Pasiphaea chacei* Yaldwin 1962: 18, figs. 1–19.  
Hanamura 1983: 77, fig. 15.

*Geographic distribution:* Off Oregon and southern California to Baja California (23°05'N–125°W) (Word and Charwat 1976; Krygier and Pearcy 1981; Hanamura 1983).

*Depth distribution:* In samples collected between 100 and 850 m (Krygier and Pearcy 1981). Hanamura (1983) reports the species between 0 and 1236 m.

44. *Pasiphaea corteziana* Rathbun 1902.  
*Pasiphaea corteziana* Rathbun 1902: 905; 1904: 24, fig. 5.

*Geographic distribution:* Known only off southern California (Schmitt 1921).

*Depth distribution:* Captured in the range of 1400–1630 m (Schmitt 1921).

45. *Pasiphaea dofleini* Schmitt 1932.  
*Pasiphaea dofleini* Schmitt 1932: 333, fig. 1. Holthuis 1952: 14.

*Geographic distribution:* Known only from the type locality (Punta Arenas, Strait of Magellan) (Schmitt 1932).

*Depth distribution:* Unknown (Holthuis 1952).

46. *Pasiphaea emarginata* Rathbun 1902.  
*Pasiphaea emarginata* Rathbun 1902: 905; 1904: 22, fig. 4. Word and Charwat 1976: 205–206 (illustrated).

*Geographic distribution:* Southern California to the Gulf of California (up to Bahía Concepción) (Chace 1937).

*Depth distribution:* Taken in bottom trawl samples made in the depth range of 395–1600 m (Chace 1937). In plankton samples between surface and 200 m (pers. obs.).

47. *Pasiphaea faxoni* Rathbun 1904.  
*Pasiphaea faxoni* Rathbun 1902: 905 (*nomen nudum*); 1904: 22.  
*Pasiphaea acutifrons*. Faxon 1895: 175 (not *P. acutifrons* Bate).

*Geographic distribution:* Galápagos Islands.

*Depth distribution:* Unknown. The material reported by Faxon (1895) under *P. acutifrons* was obtained in trawls operating at about 85 to 1400 m and at 1900 m.

48. *Pasiphaea magna* Faxon 1893.  
*Pasiphaeia magna* Faxon 1893: 24; 1895: 176, pl. 45, fig. 2.  
*Pasiphaea magna*. Méndez 1981: 64, figs. 190–192.

*Geographic distribution:* Off Peru (17°08'S); Gulf of Panama (Faxon 1893; Méndez 1981) to Oregon (Krygier and Pearcy 1981).

*Depth distribution:* Abundant in bottom trawls (off Oregon and Peru) and collected once in an oblique tow from 0 to 1000 m (Méndez 1981; Krygier and Pearcy 1981).

49. *Pasiphaea pacifica* Rathbun 1902.  
*Pasiphaea pacifica* Rathbun 1902: 905; 1904: 20, figs. 2–3. Word and Charwat 1976: 209–210 (illustrated). Butler, 1980: 55 (illustrated).

*Geographic distribution:* From Alaska (Butler 1980) to the Gulf of California (northern part only in this study); also in Australia, South Africa, and the eastern seas of the USSR (Krygier and Wasmer 1988).

*Depth distribution:* Known from depths between 96 and 730 m (mostly in bottom trawls) and between 75 and 500 m (in midwater trawls) (Rathbun 1904; Krygier and Percy 1981). Also taken in oblique tows from surface to 225 m at stations with a total depth of 295–628 m (pers. obs.).

50. *Pasiphaea tarda* Kroyer 1845.

*Pasiphaea tarda* Kroyer 1845: 434. Sivertsen and Holthuis 1956: 23, fig. 17. Butler 1980: 56 (illustrated). Krygier and Wasmer 1988: 76.

*Pasiphaea princeps* Smith 1884: 381, pl. 5, fig. 2.–Rathbun 1904: 23.

*Geographic distribution:* From Unalaska to Ecuador and in Atlantic Ocean (east and west) (Butler 1980).

*Depth distribution:* Taken in midwater trawls in the depth range of 640–730 m (Butler 1980); 200–850 m, 1750–2000 m, and 0–2400 m (Krygier and Percy 1981). The species has also been taken in bottom trawls operating between 251 and 3000 m.

#### Genus *Parapasiphae* Smith 1884

51. *Parapasiphae cristata* Smith 1884.

*Parapasiphae cristata* Smith 1884: 388, pl. V, fig. 3.

*Geographic distribution:* Known only from Oregon and in the North Atlantic (Krygier and Percy 1981).

*Depth distribution:* Taken in midwater tows made between 1250 and 1500 m and in tows made in the water column between 0 and 2870 m. It probably never occurs above 400 m (Krygier and Percy 1981).

52. *Parapasiphae sulcatifrons* Smith 1884.

*Parapasiphae sulcatifrons* Smith 1884: 384, pl. 5, fig. 4, pl. 6, figs. 1–7. Kensley 1972: 34, fig. 15f. Butler 1980: 58 (illustrated).

*Geographic distribution:* From Canada and Oregon to Baja California (23°N–125°W); Atlantic and Indo-Pacific oceans (Hanamura 1983).

*Depth distribution:* Between 500 and 1250 m off Oregon (Krygier and Percy 1981); at 1300 m (Kensley 1981). Taken in midwater trawls made in the range of 540–630 m (Kensley et al. 1987), also taken at a depth of 1300 m (Kensley 1981).

#### Genus *Eupasiphae* Wood-Mason and Alcock 1893

53. *Eupasiphae serrata* (Rathbun 1902).

*Parapasiphae serrata* Rathbun 1902: 904; 1904: 25, fig. 7.

*Eupasiphae serrata*. Burukovsky and Romensky 1979: 328.

*Geographic distribution:* Southern California (Schmitt 1921) and southeast Atlantic (Burukovsky and Romensky 1979).

*Depth distribution:* Collected at about 1800 m (bottom trawl) (Rathbun 1904) and reported from a range of 970–1050 m (Burukovsky and Romensky 1979).

54. *Eupasiphae gilesii* (Wood-Mason 1892).

*Parapasiphae gilesii* Wood-Mason 1892: pl. 3, fig. 8.

*Parapasiphae (Eupasiphae) gilesii*. Wood-Mason (in Wood-Mason and Alcock) 1893: 166.

*Eupasiphae gilesii*. Tirmizi 1969: 214, figs. 1–4. Hanamura 1983: 78, fig. 16a–b. Crosnier, 1988: 786, fig. 1, 5a.

*Eupasiphae gilesii*. Crosnier and Forest 1973: 150, fig. 44.

*Geographic distribution:* Off Baja California (23°05'N–125°W) (Hanamura 1983). Indian Ocean and northeastern Atlantic (Kensley 1981). The record of Bermuda needs to be confirmed (Chace 1940; Foxton 1970a), although the species is reported for the western Atlantic by Crosnier (1988). Also in northwest Pacific (Crosnier 1988).

*Depth distribution:* Found in depths ranging between 340 and 770 m (Kensley 1981). Foxton (1970a) reported specimens collected at 800 and 925 m. It has also been captured between 2000 m and surface (Crosnier and Forest 1973), and in midwater trawls between 0–600 m and 391–630 m (Kensley et al. 1987).

#### Genus *Psathyrocaris* Wood-Mason 1893

55. *Psathyrocaris fragilis* Wood-Mason 1893.

*Psathyrocaris fragilis* Wood-Mason (in Wood-Mason and Alcock) 1893: 171, pl. 10–11. Crosnier and Forest 1973: 138, fig. 40a–d. Méndez 1981: 68, pl. 25, figs. 203, 204, 205a–c.

*Geographic distribution:* Off Peru (06°13'S–81°17'W to 8°43'S–80°03'W) (Méndez 1981). Indo-Pacific and eastern Atlantic, between 44°N and 18°S (Crosnier and Forest 1973).

*Depth distribution:* Taken in midwater tows at a depth of 1000–1100 m (total depth, 4000 m) (Méndez 1981); from depths between 600 and 800 m; and in bottom trawls between 498 and 900 m (Crosnier and Forest 1973).

### Family Oplophoridae

#### Genus *Acanthephyra* A. Milne Edwards 1881

56. *Acanthephyra brevicarinata* Hanamura 1984.  
*Acanthephyra brevicarinata* Hanamura 1984: 65, figs. 1–2. Chace 1986, 18 (key and under *A. curtirostris*), figs. 2d, 4d, 6c, 8c.

*Geographic distribution:* Off Baja California (13°28'N–119°49'W) (Hanamura 1984). Hanamura (1984) suggests that *A. brevicarinata* might occur from the Gulf of Panama to the Gulf of California (reported as *A. curtirostris* by Faxon 1895). See Chace (1986) for discussion.

*Depth distribution:* Between 600 and 900 m; possibly down to 1600 m (Hanamura 1984).

57. *Acanthephyra brevirostris* Smith 1885.  
*Acanthephyra brevirostris* Smith 1885: 504; 1887: 670, pl. 14, fig. 2, pl. 15, figs. 2, 8, pl. 16, figs. 1, 6. Kensley 1972: 38, fig. 17m. Crosnier and Forest 1973: 41, figs. 8c–d. Chace 1986: 8 (key), figs. 2e, 4e, 5e, 6d, 8d.

*Geographic distribution:* Off Baja California (13°28'N–119°49'W) (Hanamura 1983) and south to Ecuador (Faxon 1895). Indo-Pacific and Atlantic (east and west) (Méndez 1981).

*Depth distribution:* Reported from a range of 1280–5394 m, mostly in bottom trawls (Méndez 1981; Kensley 1981).

58. *Acanthephyra carinata* Bate 1888.  
*Acanthephyra carinata* Bate 1888: 748, pl. 126, fig. 2. Chace 1986: 13, figs. 2f, 4f, 5f, 6e, 8e (and key).  
*Acanthephyra approxima* Bate 1888: 755, pl. 126, fig. 8.

*Geographic distribution:* Southern Chile (51°27'S–74°03'W), Indonesia, and the Philippines (Chace 1986).

*Depth distribution:* Chace (1986) reports the species from a range of 315–1469 m and considers it a benthic species. *A. carinata* has apparently never been caught in mid-water, and it is a large species (up to 120 mm total length; Bate 1888). *A. eximia*, an even larger species (up to 140 mm), however, has been caught in the water column (see text), hence our decision to include *A. carinata* in this list.

59. *Acanthephyra chacei* Krygier and Forss 1981.  
*Acanthephyra chacei* Krygier and Forss 1981: 96, figs. 1–2. Chace 1986: 9 (key), figs. 2g, 4g, 5g, 6f, 8f.

*Geographic distribution:* Off Oregon (44°22'N to 52°53'N) (Krygier and Forss 1981).

*Depth distribution:* Taken in midwater trawls made in the depth range of 1500–2400 m and fished by bottom trawls in depths of up to 3900 m (Krygier and Percy 1981).

60. *Acanthephyra cucullata* Faxon 1893.  
*Acanthephyra cucullata* Faxon 1893: 206; 1895: 167, pl. 44, fig. 1. Chace 1986: 15, figs. 2h, 4h, 5h, 8g (and key).

*Geographic distribution:* Pacific coast, from Baja California (13°25'N–120°04'W and 13°28'N–119°54'W) (Hanamura 1983) to Isla Malpelo, Colombia (Chace 1986). Indo-Pacific.

*Depth distribution:* Taken in midwater trawls at a depth of 1307 m and between 0 and 1617 m (Hanamura 1983). Also captured in bottom trawls, from a depth range of 1266–3342 m (Faxon 1893; Chace 1986).

61. *Acanthephyra curtirostris* Wood-Mason 1891.  
*Acanthephyra curtirostris* Wood-Mason (*in*: Wood-Mason and Alcock) 1891: 195. Wood-Mason and Alcock 1893: 364, fig. 5. Crosnier and Forest 1973: 39, fig. 8a. Hanamura 1983: 74, fig. 13. Chace 1986: 17, figs. 2i, 4i, 5i, 6g, 8h (and key).

*Geographic distribution:* From Vancouver Island to Peru; Indo-Pacific and Atlantic oceans (northeast and Caribbean) (Butler 1980; Kensley 1981).

*Depth distribution:* Reported from depths of 300–1500 m in midwater tows, with greatest catches between 600–900 m (Krygier and Percy 1981) and 1000–1250 m (Butler 1980). Captured between 735 and 865 m off Baja California (Hanamura 1983). Also found in nonclosing bottom trawl samples taken between 660 and 4970 m (Méndez 1981), between 800 and 3700 m, and in a vertical tow from a depth of 2000 m to the surface (Crosnier 1987a).

62. *Acanthephyra eximia* Smith 1884.  
*Acanthephyra eximea* Smith 1884: 376 (as *eximea* p. 376 and *eximia* p. 377); 1887: 667, pl. 14, fig. 1 (as *eximea*).  
*Acanthephyra eximia*. Crosnier and Forest 1973: 34, figs. 7c–d. Chace 1986: 18, figs. 2j, 4j, 5j, 6h, 9a (and key).

*Geographic distribution:* Off California (32°52'N–132°30'W) (Hanamura 1983). Indo-Pacific and Atlantic oceans (Chace 1986).

*Depth distribution:* Reported from depths between 700 and 1200 m (Kensley 1981). According to Chace (1986), only juveniles seem to be pelagic, while adults of *A. eximia* probably live on or near the bottom at depths of 200–4700 m. Crosnier (1987a) reports captures of this species from a depth of 680–700 m in bottom trawls, and from 720 to 760 m in bottom traps.

63. *Acantheephyra faxoni* Calman 1939.  
*Acantheephyra faxoni* Calman 1939: 191, fig. 1.  
Méndez 1981: 87, figs. 269, 270, 270a. Chace 1986: 9 (key), figs. 2k, 4k, 5k, 6i, 9b.

*Geographic distribution:* Indo-Pacific; in the eastern Pacific, it is known from the Gulf of Panama to Peru (Méndez 1981).

*Depth distribution:* Ill-defined; *Acantheephyra faxoni* has been found in bottom trawl samples from depth ranges of 45–4000 m and has occasionally been captured in the water column at 1000–1100-m depth (total depth, 4000 m) (Méndez 1981).

64. *Acantheephyra pelagica* (Risso 1816).  
*Alpheus pelagicus* Risso 1816: 91, pl. 2, fig. 7.  
*Acantheephyra pelagica*. Chace 1986: 8 (key), figs. 3e, 4q, 5q, 7d, 9g, and 21 (under *A. eximia*).  
Wasmer 1986: 41, fig. 7. Crosnier 1987a: 702.

*Geographic distribution:* Off Chile and in subantarctic waters of the South Pacific (Wasmer 1986). According to Chace (1986), *A. pelagica* could be a synonym of *A. eximia* Smith, although it has generally been recognized as a valid species occurring in the North Atlantic and the Mediterranean (and possibly also panantarctic) (Holthuis 1977; Crosnier 1987a). Kensley (1981) reports this species for the Indo-Pacific. Takeda and Tanaka (1984) report *A. pelagica* off Uruguay (40°S).

*Depth distribution:* Reported from a range of 800–2166 m (Kensley 1981), this species probably never occurs above 350 m (Crosnier and Forest 1973). Roe (1984) reports small catches from depths of 450 and 600 m at night and between 700 and 800 m during the day.

65. *Acantheephyra prionota* Foxton 1971.  
*Acantheephyra prionota* Foxton 1971: 35, figs. 1–2. Crosnier and Forest 1973: 28, figs. 6b–c. Chace 1986: 10 (key), figs. 3f, 4r, 5r, 6e, 10a.

*Geographic distribution:* Off Baja California

(23°05'N–125°W) (Hanamura 1983). Indo-Pacific and northeastern Atlantic (Kensley 1981).

*Depth distribution:* The species is distributed from 750 to 1750 m (Kensley 1981). It has also been recorded in a vertical tow between 2000 m and the surface (Crosnier 1987a).

66. *Acantheephyra quadrispinosa* Kemp 1939.  
*Acantheephyra quadrispinosa* Kemp 1939: 571.  
Chace 1986: 26, figs. 3h, 4t, 5t, 7g, 10c, 14 (and key). Wasmer 1986: 39, fig. 5.

*Geographic distribution:* Oregon (Krygier and Pearcy 1981). Indo-Pacific and Atlantic oceans (Chace 1986).

*Depth distribution:* Known from depths between 250 and 1700 m (Kensley 1981). Krygier and Pearcy (1981) report a single specimen at 400–500 m; Chace (1986), referring to the material of the *Albatross*, notes that this species probably migrates between 180 and 1500 m and has been collected once at 27 m. Also taken in bottom trawls between 3700 and 5040 m and in a vertical tow between 2000 m and the surface (Crosnier 1987a).

67. *Acantheephyra trispinosa* Kemp 1939.  
*Acantheephyra trispinosa* Kemp 1939: 577. Chace 1986: 9 (key), figs. 3m, 4y, 5y, 6l, 10h.

*Geographic distribution:* Eastern Pacific (7°N to 4°S) and westward to 116°W (Chace 1986).

*Depth distribution:* “Mesopelagic” (Chace 1986).

### Genus *Ephyrina* Smith 1885

68. *Ephyrina hoskynii* Wood-Mason 1891.  
*Ephyrina hoskynii* Wood-Mason (*in*: Wood-Mason and Alcock) 1891: 194. Crosnier and Forest 1973: 79, figs. 24a–b. Chace 1986: 33 (key).

*Geographic distribution:* Indian Ocean (Chace 1986). Eastern Pacific (Hanamura, *in litt.*).

*Depth distribution:* Taken between 900 and 950 m (Foxton 1970a).

### Genus *Hymenodora* Sars 1972

69. *Hymenodora acanthitelsonis* Wasmer 1972.  
*Hymenodora acanthitelsonis* Wasmer 1972: 87, figs. 1–8. Chace 1986: 42 (key), figs. 21a–e.

*Geographic distribution:* North Pacific off Oregon and Japan; northeast Atlantic (Krygier and Wasmer 1988).

*Depth distribution:* Below 2400 m and probably to 3000 m (Krygier and Pearcy 1981). Reported from a depth range of 2400–5440 m by Krygier and Wasmer (1988).

70. *Hymenodora frontalis* Rathbun 1902.  
*Hymenodora frontalis* Rathbun 1902: 904; 1904: 28, fig. 8. Butler 1980: 70 (illustrated). Chace 1986: 42 (key), figs. 21f–j.

*Geographic distribution:* From the Sea of Okhotsk and the Bering Sea to southern California (Chace 1986).

*Depth distribution:* Reported from a range of 200–2400 m, with maximal abundance between 600 and 1300 m (Krygier and Pearcy 1981).

71. *Hymenodora glacialis* (Buchholz 1874).  
*Pasiphae glacialis* Buchholz 1874: 279, pl. 1, fig. 2.  
*Hymenodora glacialis*. Butler 1980: 72 (illustrated). Chace 1986: 42 (key), figs. 21k–o. Wasmer 1986: 48, fig. 10a.

*Geographic distribution:* From the Sea of Okhotsk and the Bering Sea to the Gulf of Panama (Butler 1980). Gulf of California (Rathbun 1904). Arctic region, North Atlantic to 30°N, and South Atlantic (west part) (Chace 1986). Off Chile and in subantarctic waters in the South Pacific (Wasmer 1986). Southwestern Indian Ocean (Crosnier 1987a).

*Depth distribution:* Rare above 2000 m and abundant in midwater trawls between 2000 and 2400 m; also in bottom trawls at a depth of 2800–3000 m (Krygier and Pearcy 1981). Taken in depths to 3900 m (Butler 1980) and in bottom trawls at 5610–5595 m (Crosnier 1987a).

72. *Hymenodora gracilis* Smith 1887.  
*Hymenodora gracilis* Smith 1887: 680, pl. 12, fig. 6. Crosnier and Forest 1973: 83, fig. 25a. Chace 1986: 43 (key), figs. 21p–t. Wasmer 1986: 49, figs. 10b–c.

*Geographic distribution:* From Oregon to Baja California (Hanamura 1983). Indian and Atlantic oceans (Chace 1986). Off Chile and in subantarctic waters of the South Pacific (Wasmer 1986).

*Depth distribution:* The species is distributed from 600 to 2400 m (one capture at 300–400 m), with a maximal abundance between 1250 and 2000 m (Krygier and Pearcy 1981). It is also reported from a depth of 2200–3000 m (Kensley 1981) and in bottom trawls at a depth of 4730–4589 m (Crosnier 1987a).

### Genus *Meningodora* Smith 1882

73. *Meningodora mollis* Smith 1882.  
*Meningodora mollis* Smith 1882: 74, pl. 11, figs. 8, 8a, 9, pl. 12, figs. 5, 5a, 6–9. Crosnier and Forest 1973: 44, fig. 10c. Chace 1986: 50, figs. 26a–k.  
*Notostomus fragilis* Faxon 1893: 207; 1895: 170, pl. 44, figs. 2, 2a–b.

*Geographic distribution:* Islas Galápagos and Panama to Oregon; Indian and Atlantic oceans (east and west) (Chace 1986).

*Depth distribution:* Recorded from depths between 500 and 1150 m (Krygier and Pearcy 1981), from 1400 m (Faxon 1893; *N. fragilis*), and in vertical tows between 2000 m and the surface (Crosnier 1987a).

### Genus *Notostomus* A. Milne Edwards 1881

74. *Notostomus japonicus* Bate 1888.  
*Notostomus japonicus* Bate 1888: 830, pl. 135, fig. 1. Stevens and Chace 1965: 277, figs. 1–4. Butler 1980: 63 (illustrated). Chace 1986: 53 (key), figs. 28j–l, 29h–i.

*Geographic distribution:* Off Oregon, Hawaii, and Japan (Krygier and Pearcy 1981).

*Depth distribution:* It has been taken in the range of 200–850 m (Krygier and Pearcy 1981).

75. *Notostomus elegans* A. Milne Edwards 1881.  
*Notostomus elegans* A. Milne Edwards 1881: 8. Crosnier and Forest 1973: 56, figs. 15, 16a–b. Chace 1986: 56, figs. 28d–f, 29c–e, 30 (and key).  
*Notostomus westergreni* Faxon 1893: 208; 1895: pl. f. Crosnier and Forest 1973: 60, fig. 17. Méndez 1981: 87, figs. 263–268.

*Geographic distribution:* Pacific and Atlantic (east and west) oceans; off Ecuador, Chile, and Peru (Méndez 1981; Chace 1986).

*Depth distribution:* Between 750 and 1170 m (Kensley 1981). Also taken in trawls between 1417 and 3931 m (Chace 1986) and between 450 and 5380 m (Crosnier and Forest 1973).

### Genus *Oplophorus* H. Milne Edwards 1837

76. *Oplophorus novaezeelandiae* de Man 1931.  
*Hoplophorus novae-zeelandiae* de Man 1931: 369, figs. 1–20.  
*Oplophorus novaezeelandiae*. Crosnier and Forest 1973: 26, fig. 5. Chace 1986: 59 (key), figs. 32f–j. Wasmer 1986: 37, figs. 3a–c.

*Geographic distribution:* Off Chile; in the South Pacific, and East Pacific. Atlantic Ocean, New Zealand, and southwestern Australia (Chace 1986; Wasmer 1986). Southwest Indian Ocean (Kensley et al. 1987).

*Depth distribution:* Mesopelagic (Chace 1986), the species is distributed from 90 to 725 m; it is reported in pelagic trawls between 630 m and the surface (Kensley et al. 1987).

77. *Oplophorus spinosus* (Brullé 1839).  
*Palaemon spinosus* Brullé 1839: 18 (illustrated).  
*Oplophorus spinosus*. Sivertsen and Holthuis 1956: 19, fig. 15, pl. 3, figs. 1–2. Chace 1986: 59 (key).

*Geographic distribution:* Off Baja California (23°N–125°W and 32°57'N–127°44'W) (Hanamura 1983). Indo-Pacific and Atlantic oceans (east and west) (Chace 1986).

*Depth distribution:* It has been recorded from depths between 400–500 and 1117–1233 m (Hanamura 1983), at a depth of 150 m (Abele and Kim 1986), and in bottom trawls at a depth of 2700 m (Crosnier 1987a). Also reported in midwater trawls operating from 90 m to the surface and between 60 and 630 m (Kensley et al. 1987).

#### Genus *Systellaspis* Bate 1888

78. *Systellaspis braueri paucispinosa* Crosnier 1988.  
*Systellaspis braueri paucispinosa* Crosnier 1987b (1988): 953, fig. 3–b (and key).  
*Systellaspis braueri*. Butler 1980: 65 (illustrated).  
Krygier and Percy 1981: 87, fig. 2.

*Geographic distribution:* Oregon and Central America (13°28'N–119°54'W) (Hanamura 1983). North and South Pacific, Indonesia (Crosnier 1987b).

*Depth distribution:* From 500 to 2000 m, with a maximum recorded in depths ranging between 900 and 2000 m (Krygier and Percy 1981).

79. *Systellaspis cristata* (Faxon 1893).  
*Acanthephyra cristata* Faxon 1893: 206; 1895: 162, pl. 43, fig. 1.  
*Systellaspis cristata*. Crosnier and Forest 1973: 94, figs. 26d, 27d. Butler 1980: 67 (illustrated), pl. 1, fig. e. Chace 1986: 64, figs. 34d–f, 35c. Crosnier 1987a: 711, figs. 6c–g, 7, 8c–d.

*Geographic distribution:* Off Canada, Oregon, and Baja California, and south to Central America (13°28'N–120°07'W). Indo-Pacific and Atlantic oceans (east and west) (Hanamura 1983).

*Depth distribution:* It has been captured from depths

of 200–300 m and 600–700 m (Krygier and Percy 1981) and from 250 to 900 m (Kensley 1981). In bottom trawls between 600 and 3241 m, in midwater tows between 700 and 930 m, and from the surface to a depth of 2500 m (Foxton 1970a, 1970b; Crosnier and Forest 1973).

80. *Systellaspis debilis* (A. Milne Edwards 1881).  
*Acanthephyra debilis* A. Milne Edwards 1881: 13.  
*Systellaspis debilis*. Crosnier and Forest 1973: 87, figs. 26b, 27b. Crosnier 1987a: 715, figs. 9a–h, 10. Chace 1986: 65, figs. 34g–i, 35e, f.

*Geographic distribution:* Off Oregon (Krygier and Percy 1981). Indo-Pacific and Atlantic oceans (east and west coast) (Chace 1986). Chace does not include the records for Oregon; these are, however, confirmed by Krygier and Wasmer (1988).

*Depth distribution:* The species has been reported from a range of 150–1500 m (Kensley 1981) and was captured at 80 m during a night haul (Krygier and Percy 1981). It concentrates between 650 and 800 m by day and at 150 m at night (Foxton 1970a). Other information obtained by Roe (1984) indicates that *S. debilis* concentrates at 450–600 m by day and at 100–250 m at night. Also taken in midwater tows in depths ranging between 0 and 1200 m (Kensley et al. 1987).

81. *Systellaspis eltanini* Wasmer 1986.  
*Systellaspis eltanini* Wasmer 1986: 52, figs. 13–15.

*Geographic distribution:* Off Chile (33°S), south to the subantarctic waters around South America, and in the western Atlantic (Wasmer 1986).

*Depth distribution:* Captured in midwater trawls between the surface and 1550–2330 m (never found in shallowest trawls) (Wasmer 1986).

#### Family Pandalidae Genus *Plesionika* Bate 1888

82. *Plesionika beebei* Chace 1937.  
*Plesionika beebei* Chace 1937: 114, fig. 2. Wicksten 1978: 84 (key).

*Geographic distribution:* From Punta Tosca, Baja California, to Mancora, Peru.<sup>1</sup>

*Depth distribution:* Captured between surface and 200 m, and in the water column between 549 and 914 m; also taken in bottom trawls from depths between 73 and 738 m.<sup>2</sup>

<sup>1</sup>Hendrickx, M. E., and M. K. Wicksten. MS. Los Pandalidae (Crustacea, Caridea) del Pacífico mexicano, con una clave para su identificación.  
<sup>2</sup>Ibid.

83. *Plesionika* aff. *P. rossignoli* Crosnier and Forest 1968.

Aff. *Plesionika rossignoli* Crosnier and Forest 1968: 113, fig. 6b; 1973: 218, figs. 67a, 68a–b.

*Plesionika* aff. *rossignoli* Hanamura 1983: 79, fig. 17.

*Geographic distribution*: Off Central America (13°29'N–13°25'N and 120°W) (Hanamura 1983).

*Plesionika rossignoli* is known from the eastern tropical Atlantic (Crosnier and Forest 1973).

*Depth distribution*: Between 734 and 845 m, and also recorded between the surface and 1617 m (Hanamura 1983). *Plesionika rossignoli* is known to occur between the surface and at least 650 m (Crosnier and Forest 1973).

84. *Plesionika sanctaecatalinae* Wicksten 1983.

*Plesionika sanctaecatalinae* Wicksten 1983: 138, figs. 1–3.

*Plesionika martia semilaevis*. Wicksten 1978: 85, fig. 1. Méndez 1981: 104, figs. 316–317.

*Geographic distribution*: From southern California (33°38'N) to Peru (12° to 18°S) (Wicksten 1983).

*Depth distribution*: Captured by Isaacs-Kid midwater trawls between 812 and 3877 m (Wicksten 1983).

#### Genus *Stylopandalus* Coutière 1905

85. *Stylopandalus richardi* (Coutière 1905).

*Pandalus* (*Stylopandalus*) *richardi* Coutière 1905a: 1115; 1905b: 18, fig. 6.

*Parapandalus richardi*. Chace 1940: 192, figs. 58–61. Crosnier and Forest 1973: 224, fig. 69b.

*Stylopandalus richardi*. Richard 1905: 11–13. Chace 1985: 136, fig. 62.

*Geographic distribution*: Isla Guadalupe and Baja California (23°N–24°42'N and 125°W) (Hanamura 1983). Indo-Pacific and Atlantic oceans (east and west) (Kensley 1981).

*Depth distribution*: Between 460 and 980 m (Kensley 1981). Also reported from depths of 30–490 m and 735–865 m (Hanamura 1983); from subsurface to 3600 m, but below 500 m at night (Crosnier and Forest 1973). Taken in midwater trawls between 60 m and the surface and between 216 and 630 m (Kensley et al. 1987).

#### Family Processidae

##### Genus *Processa* Leach 1815

86. *Processa pippinae* Wicksten and Méndez 1985.

*Processa pippinae* Wicksten and Méndez 1985: 16, figs. 1–4.

*Geographic distribution*: Gulf of California (north and central parts) (Hendrickx and Estrada-Navarrete 1989).

*Depth distribution*: In plankton samples collected between surface and 300 m (Hendrickx and Estrada-Navarrete 1989). The type material was obtained in bottom trawls (265–644 m) (Wicksten and Méndez 1985).

#### DISCUSSION

First of all, it seems necessary to remember that among the 86 species reported herein, some might not be regular members of the pelagic realm. This is probably the case of *Hymenopenaeus doris*, *Acanthephyra carinata*, and *A. eximia*, three species that have occasionally been caught in midwater trawls and must, therefore, be included in the checklist. In turn, species like *Plesionika mexicana* Chace and *P. trispinus* Squires and Barragan, two species of Pandalidae commonly found in bottom trawl catches in the Gulf of California and off the coast of Colombia/Peru, have never been recognized as pelagic species<sup>3</sup> although they are similar in size and morphology to *P. beebei*, a species found both in midwater and bottom trawls.

Some species, like *Benthesicymus tanneri* Faxon known from the Gulf of California to Peru, have sometimes been considered benthopelagic (Méndez 1981), although there is no precise record of their pelagic phase.

Caution should also be taken when considering species for which a single record (sometimes of a single specimen) is available for the eastern Pacific. *Bentheogennema stephensoni*, for instance, a species apparently never illustrated properly before 1985 (Crosnier 1985), was found by Hanamura (1983) off the coast of Baja California in only one sample with only one specimen (a male). Some species included in the checklist might also represent undescribed species (e.g., *Plesionika* aff. *P. rossignoli*).

Of the 86 species included in the checklist, 39 (45%) are members of the Penaeoidea and 47 (55%) of the Caridea. Five families of Penaeoidea with 9 genera, and four families of Caridea with 14 genera are present. The number of species per genus and family is quite variable, however, and as many as 12 species of Benthesicymidae, 24 species of Sergestidae, 16 species of Pasiphaeidae, and 26 species of Ophrophoridae are included in the checklist, totaling 90% of the species in just four families (table 1).

<sup>3</sup>Hendrickx, M. E., and M. K. Wicksten. MS. Los Pandalidae (Crustacea, Caridea) del Pacífico mexicano, con una clave para su identificación.

TABLE 1  
 Repartition of the 86 Species of Pelagic Shrimps from  
 the Eastern Pacific in Families and Genera of Penaeoidea  
 and Caridea

PENAEOIDEA (39)	CARIDEA (47)
Benthescymidae (12)	Pasiphaeidae (16)
<i>Bentheogennema</i> (5)	<i>Pasiphaea</i> (11)
<i>Gennadas</i> (7)	<i>Parapasiphaea</i> (2)
Penaeidae (1)	<i>Eupasiphae</i> (2)
<i>Funchalia</i> (1)	<i>Psathyrocaris</i> (1)
Solenoceridae (1)	Oplophoridae (26)
<i>Hymenopenaeus</i> (1)	<i>Acanthephyra</i> (12)
Sergestidae (24)	<i>Ephyrina</i> (1)
<i>Sergestes</i> (13)	<i>Hymenodora</i> (4)
<i>Sergia</i> (9)	<i>Meningodora</i> (1)
<i>Petalidium</i> (1)	<i>Notostomus</i> (2)
<i>Acetes</i> (1)	<i>Oplophorus</i> (2)
Luciferidae (1)	<i>Systellaspis</i> (4)
<i>Lucifer</i> (1)	Pandalidae (4)
	<i>Plesionika</i> (3)
	<i>Stylopandalus</i> (1)
	Processidae (1)
	<i>Processa</i> (1)

The analysis of the currently known distribution of pelagic shrimps reported herein permits division of the 86 species into three major groups according to their zoogeographic affinities (table 2). The first group comprises species endemic to the eastern Pacific, with 22 species and a majority of Caridea (9 species of Penaeoidea versus 13 species of Caridea). The 3 species of pelagic *Plesionika*, most species of *Pasiphaea* (7 out of 10), and a fair proportion of Sergestidae (7 out of 24 species) known from the eastern Pacific are endemic. But there are no endemic species of *Gennadas*, a genus well represented in the region (7 species).

A second group of 25 species comprises pelagic shrimps with a cosmopolitan distribution. Here again, a strong majority of Caridea is to be found, with 17 species versus only 8 species of Penaeoidea, the former including 12 species of Oplophoridae of a total of 23 known for the entire zoogeographic region (table 2).

The third major group of shrimps comprises species found elsewhere (e.g., in the Atlantic, in the Indo-Pacific) but not cosmopolitan. Of the 34 species with such geographic distribution, 20 belong to the Penaeoidea and only 14 to the Caridea. Noteworthy is the high proportion of Sergestidae in this group (14 out of 24 species known for the area; table 2).

Four species are found along the west coast of America but extend their distribution limits to Japan (3 species) or to the Okhotsk Sea (1 species). All 4 species are considered by Krygier and Wasmer (1988) as part of the subarctic-transitional species

(subarctic species with ranges extending southward along the Pacific coast to Baja California) (table 2).

Two species are not included in the major groups cited above. *Pasiphaea acutifrons* presents a bipolar distribution limited to the northern Pacific and around South America; *Pasiphaea dofleini* is known only from the Strait of Magellan.

As many as 51 of the 86 species of pelagic shrimps occurring in the eastern Pacific are found in Mexican coastal and offshore waters, including 29 species of Penaeoidea and 22 species of Caridea (table 2).

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TABLE 2  
 Zoogeographic Affinities of Pelagic Shrimps Reported from the Eastern Pacific

Species endemic to the eastern Pacific	Species with cosmopolitan distribution	Species also present in other regions but not cosmopolitan	Species extending their distribution to	
			Japan	Okhotsk Sea
* <i>Bentheogennema burkenroadi</i>	* <i>Bentheogennema intermedia</i>	* <i>Bentheogennema pasithea</i> (I-WP)	* <i>Bentheogennema borealis</i>	<i>Hymenodora frontalis</i>
* <i>Hymenopenaeus doris</i>	* <i>Gennadas capensis</i>	* <i>Bentheogennema stephensoni</i> (I-WP)	* <i>Sergestes similis</i>	
* <i>Sergestes extensus</i>	* <i>Gennadas bouvieri</i>	* <i>Gennadas incertus</i> (I-WP)	<i>Notostomus japonicus</i>	
<i>Sergestes geminus</i>	* <i>Gennadas scutatus</i>	* <i>Gennadas propinquus</i> (I-P)	(+ Hawaii)	
* <i>Sergestes halia</i>	* <i>Gennadas tinayrei</i>	* <i>Gennadas sordidus</i> (I)		
* <i>Sergestes pestafer</i>	* <i>Sergestes pectinatus</i>	<i>Funchalia balboae</i> (I-A)		
* <i>Sergia filicta</i>	* <i>Sergestes sargassi</i>	<i>Sergestes brevispinatus</i> (CP)		
* <i>Sergia phorca</i>	<i>Sergia kroyeri</i>	* <i>Sergestes erectus</i> (CP)		
<i>Acetes binghami</i>	* <i>Parapasiphaea sulcatifrons</i>	* <i>Sergestes consobrinus</i> (CP)		
<i>Pasiphaea affinis</i>	* <i>Eupasiphae gilesii</i>	<i>Sergestes gibbilobatus</i> (CP)		
* <i>Pasiphaea americana</i>	<i>Psathyrocaris fragilis</i>	<i>Sergestes tantillus</i> (CP)		
* <i>Pasiphaea chacei</i>	* <i>Acanthephyra brevispinata</i>	<i>Sergestes arcticus</i> (P-A)		
<i>Pasiphaea corteziana</i>	* <i>Acanthephyra curtirostris</i>	<i>Sergia inoa</i> (CP)		
* <i>Pasiphaea emarginata</i>	<i>Acanthephyra eximia</i>	* <i>Sergia laminata</i> (I-WP)		
<i>Pasiphaea faxoni</i>	<i>Acanthephyra pelagica</i>	* <i>Sergia bigemina</i> (P)		
* <i>Acanthephyra brevicarinata</i>	* <i>Acanthephyra prionota</i>	* <i>Sergia maxima</i> (I-WP)		
<i>Acanthephyra chacei</i>	<i>Acanthephyra quadrispinosa</i>	<i>Sergia profunda</i> (A)		
* <i>Plesionika beebei</i>	* <i>Hymenodora glacialis</i>	* <i>Sergia scintillans</i> (I-WP)		
<i>Plesionika aff. P. rossignoli</i>	* <i>Hymenodora gracilis</i>	* <i>Petalidium suspirosum</i> (CP)		
<i>Plesionika santaecatalinae</i>	<i>Oplophorus novaezeelandiae</i>	* <i>Lucifer typus</i> (A)		
* <i>Processa pippinae</i>	* <i>Oplophorus spinosus</i>	* <i>Pasiphaea pacifica</i> (I-P)		
	* <i>Systellaspis cristata</i>	* <i>Pasiphaea tarda</i> (A)		
	<i>Systellaspis debilis</i>	<i>Parapasiphaea cristata</i> (A)		
	* <i>Stylopandalus richardi</i>	<i>Eupasiphae serrata</i> (A)		
		<i>Acanthephyra carinata</i> (WP)		
		* <i>Acanthephyra cucullata</i> (I-P)		
		<i>Acanthephyra faxoni</i> (I-WP)		
		<i>Acanthephyra trispinosa</i> (CP)		
		<i>Ephyrina hoskynii</i> (I)		
		<i>Hymenodora acanthitelsonis</i> (P-A)		
		* <i>Meningodora mollis</i> (I-A)		
		<i>Notostomus elegans</i> (P-A)		
		<i>Systellaspis eltanini</i> (A)		
		* <i>Systellaspis braueri paucispinosa</i> (P)		

A = Atlantic Ocean; I = Indian Ocean; P = Pacific Ocean; CP = central Pacific; WP = west Pacific; \* indicates species reported off the coast of Mexico. Two species are not included in this table (see text).

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## CALIFORNIA SEA LION INTERACTION AND DEPREDATION RATES WITH THE COMMERCIAL PASSENGER FISHING VESSEL FLEET NEAR SAN DIEGO

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### ABSTRACT

California sea lions depredate sport fish caught by anglers aboard commercial passenger fishing vessels. During a statewide survey in 1978, San Diego County was identified as the area with the highest rates of interaction and depredation by sea lions. Subsequently, the California Department of Fish and Game began monitoring the rates and conducting research on reducing them. The sea lion interaction and depredation rates for San Diego County declined from 1984 to 1988.

### RESUMEN

Los leones marinos en California depredan peces colectados por pescadores a bordo de embarcaciones pesqueras deportivas. La investigación llevada a cabo en el estado de California en el año 1978, identificó al condado de San Diego como el área con la tasa de interacción y depredación más alta. En consecuencia, el departamento "California Department of Fish and Game" inició un programa de monitoreo de las tasas y condujo una investigación con el objeto de reducirlas. Los valores de las tasas de interacción y depredación del león marino en el condado de San Diego declinaron desde 1984 a 1988.

### INTRODUCTION

California's largest commercial passenger fishing vessel (CPFV) fleet operates from San Diego County with boats ranging in size to about 100 feet. The boats make scheduled trips for various lengths of time: half-day, three-quarter-day, full-day, multi-day, and twilight or evening. Passengers pay a fee to ride these boats and catch, with rod and reel, a variety of fish species, depending on the trip length, season, and fish availability.

California sea lions, *Zalophus californianus*, and occasionally Pacific harbor seals, *Phoca vitulina richardsi*, swim near or follow these boats and may take (depredate) the fish that have been caught and are being reeled in. In addition to taking the angler's catch, these marine mammals eat the fish used for chum. Chumming is done mainly with northern

anchovies, *Engraulis mordax*, which are thrown from the fishing boat to lure surface and mid-depth fish within casting range. Although depredation behavior has not been observed along the California coast among other marine mammals, it has become a serious problem with sea lions, and is less serious with harbor seals. The behavior is generally not appreciated by the boat operators or the anglers, even though some crew and anglers encourage it by hand-feeding the sea lions.

During depredation, sea lions usually surface some distance from the boat, dive to swim under the boat, take a fish, and then reappear a safe distance away to eat the fish, tear it apart, or just throw it around on the surface of the water. The angler or observer may never see the sea lion take a fish off the hook. What the angler experiences after hooking a fish and starting to reel it in is a tremendous tug and rush of line as the sea lion takes the fish. Occasionally, the sea lion itself may get hooked and get away by breaking the line, but it then carries the fishing hook until the hook rusts away.

In 1978, the California Department of Fish and Game (CDFG) began studying sea lion-fisheries interactions, and determined that the fishery off San Diego County was one of the most adversely affected in the state (Miller et al. 1983). The adverse effects included interactions (presence near a fishing vessel) and depredations. Since that time, CDFG biologists have investigated methods of reducing the interaction and depredations. Additionally, they have continued to monitor the rates while aboard the vessels to identify and measure the fish caught.

Some methods that have been tried for reducing or eliminating the interactions are small explosives, rockets, noise emitted through underwater transducers, slingshots, guns, and chemical deterrents. An additional method of stopping troublesome sea lions from bothering a particular fishing vessel was to move the boat to a new area and, while moving, pass close enough to another fishing boat so the sea lion becomes interested in the second vessel's operation and "drops or passes off" on it. Each method has limitations, and none works in every case or

against individual sea lions that repeatedly depredate catch (Scholl 1987; Scholl and Hanan 1987a, 1987b).

In 1986, despite negative findings about the effectiveness of nonlethal deterrents, the Sportfishing Association of California (an organization of CPFV operators) applied for and received a general permit from the National Marine Fisheries Service allowing CPFV operators to obtain certificates of inclusion. The certificates gave the operators permission to use nonlethal methods of harassment to keep sea lions away from their fishing activities. Recently a number of CPFV operators have stated that they have stopped using the deterrents.

Sea lion interaction and depredation rates are summarized and analyzed for the San Diego County CPFV fleet during the 1984–88 period to determine trends in those rates.

### MATERIALS AND METHODS

Field data were gathered by CDFG observers aboard CPFVs to investigate deterrents or to identify and measure the fish catch. For this study, we used only information from half-day, three-quarter-day, and twilight trips, which limits this study to fishing areas near the mainland and does not include any trips to the offshore islands, where sea lion interactions and depredations are reported to occur more frequently. Because harbor seals were rarely involved, they are not included in the summaries or analyses. The specific boats and the types of trips observed were chosen randomly, but space availability and crew cooperation played a part in the selection.

Observers completed specially developed data forms when they saw a marine mammal interaction or depredation. The forms included port of landing, fishing area by complex (figure 1), Fish and Game boat identification number, boat name, date, name of stop (fishing spot), number of marine mammals involved, number of marine mammals taking fish, kind of fish taken, the length of time spent at the stop, total time for the trip, and whether the same mammals followed the boat and appeared at each fishing stop.

We defined an interaction as a sea lion swimming within 100 yards of the boat, because some boat operators claim that the mere presence of a sea lion will “shut down the bite” (discourage fish from feeding and often scare them away from the boat). A depredation was defined as a sea lion taking one or more hooked fish (including part of a fish, since sea lions will often take the body and leave just the fish head on the hook) or a sea lion itself becoming

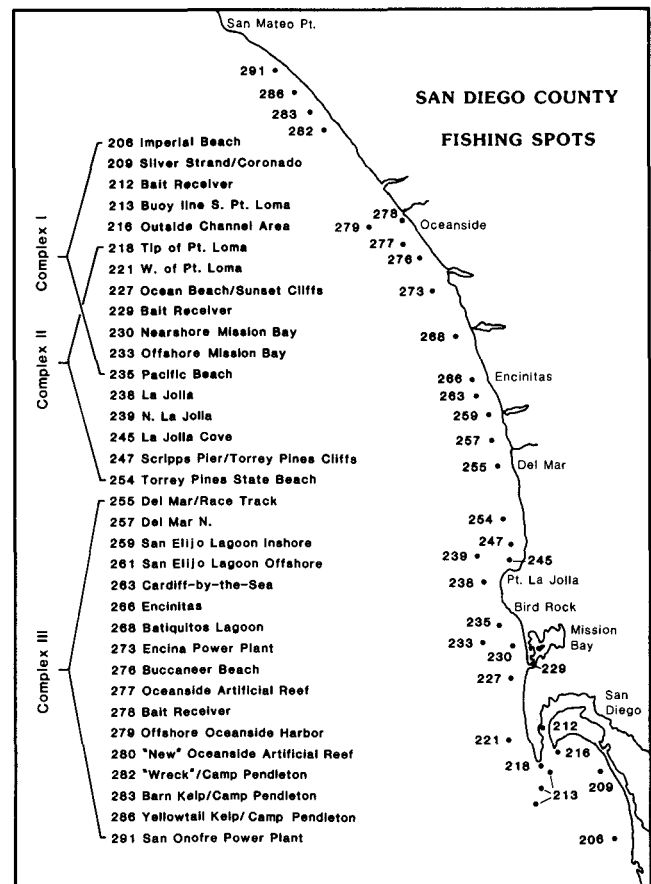


Figure 1. San Diego fishing spots used by commercial passenger fishing vessels (partyboats) are divided into three complexes depending on home port of the vessels using the fishing spots.

hooked (this implies that it ate a fish). The observer counted one sea lion taking multiple fish as a single depredation. Eating the chum or being hand-fed was not considered depredation.

CPFVs often made several fishing stops during a trip; when sea lions appeared at more than one stop, the observer was asked to determine whether they were the same animals at each stop. Skippers often attempted to “pass off” sea lions that were following them. If the technique was unsuccessful, a single sea lion could have several interactions or depredations involving a particular fishing vessel during one fishing trip. Each interaction or depredation was recorded as a separate incident for the summary and analysis.

Field data were entered into a microcomputer data base for summary and analysis. The data were grouped by area into three overlapping regions (referred to as complexes by the CDFG project that samples these fishing vessels) based on home port of the CPFV: San Diego Bay (Pacific Beach, Point Loma, and Imperial Beach); Mission Bay (La Jolla,

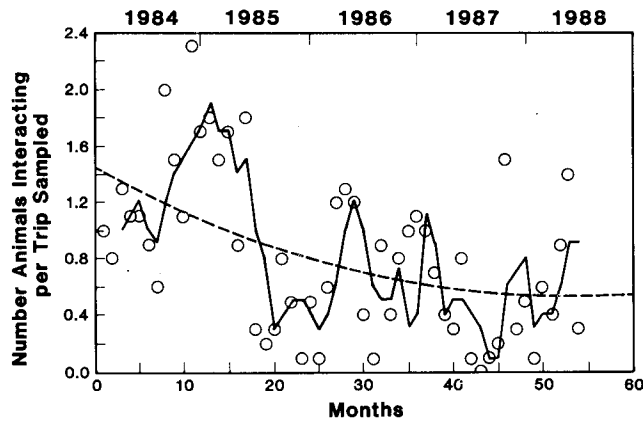


Figure 2. Average number of sea lions interacting (within 100 yards of the boat) per trip sampled with commercial passenger fishing vessels plotted by month, 1984 through 1988 (open circles), fit with a three-month running mean (solid line) and polynomial regression (broken line).

Pacific Beach, and Point Loma); and Oceanside (north San Diego County) (figure 1). There is overlap because boats from one complex occasionally fished in another, but the data were still grouped with the home port. Interaction and depredation rates are presented on a per trip basis.

Two models, polynomial and exponential, were used to describe the interaction and depredation data. The first model used a least squares fit of the polynomial regression:

$$y = a_0 + a_1x + a_2x^2$$

where  $a_0$ ,  $a_1$ , and  $a_2$  are the regression coefficients (figures 2–4). A polynomial regression was chosen for the interaction and depredation rates because we assumed that these rates would only approach zero if the sea lion population was reduced toward zero. In the second or exponential model, the data were

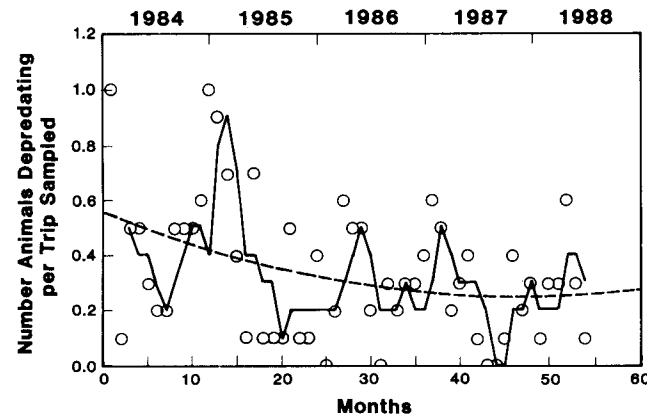


Figure 3. Average number of sea lion depredations (taking hooked fish) from commercial passenger fishing vessels plotted by month, 1984 through 1988 (open circles), fit with a three-month running mean (solid line) and polynomial regression (broken line).

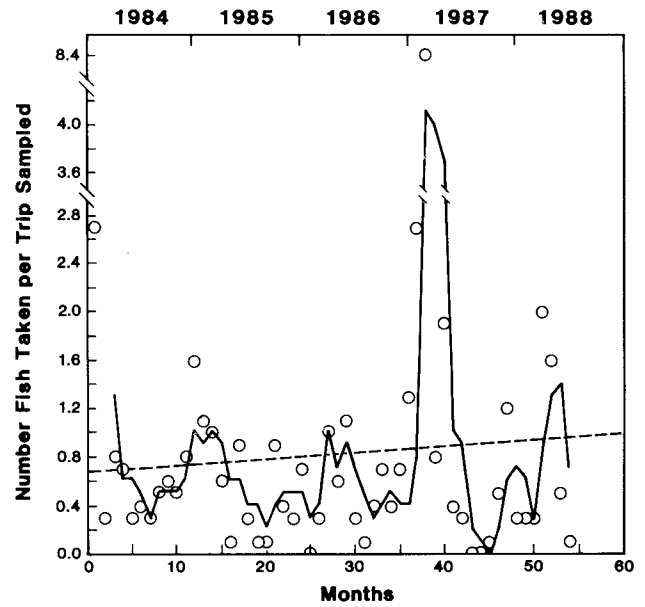


Figure 4. Average number of fish depredated by sea lions per trip plotted by month, 1984 through 1988 (open circles), fit with a three-month running mean (solid line) and least squares regression (broken line).

log-transformed, and a least squares linear regression was fit using

$$y = a_0 \exp(a_1x).$$

## RESULTS AND DISCUSSION

The data indicate seasonal trends in the interaction and depredation rates (figures 2–4). The rates decreased in the spring and early summer, possibly because sea lions congregate at the southern California Channel Islands for pupping and breeding during this period. Rates increased each year in midsummer along coastal San Diego County, coinciding with the end of the breeding season.

The data also show that the number of interactions and depredations per trip were decreased during the five-year period (table 1, figures 2 and 3). The mean number of fish depredated by sea lions per sampled trip appears to increase slightly (figure 3), but an ANOVA test of the slope indicates that it was not significantly different from zero ( $f = 0.25$ ;  $DF = 1, 52$ ;  $p > .05$ ). Therefore we assume that the average number of fish taken per depredation remained constant, while the numbers of interactions and depredations declined.

Potential explanations for these trends are (1) sea lions are more likely to depredate surface and mid-water fish, which may have been more available during and immediately following the 1983–84 El Niño event than during recent years; (2) the non-lethal deterrents used by the CPFV operators are

TABLE 1  
 Summary Output from Regression Analyses for 1984–88 Mean Sea Lion Interactions, Depredations, and Fish Taken per CPFV Trip Sampled

	Sample size	Regression coefficient			f	P > f
		a <sub>0</sub>	a <sub>1</sub>	a <sub>2</sub>		
<b>Polynomial</b>						
Interactions	54	1.45	-0.034	0.0003	7.5	0.0014
SE		0.22	0.018	0.0003		
t		11.36	-1.9	1.01		
Depredations	54	0.56	-0.013	0.0001	3.93	0.0259
SE		0.099	0.008	0.0002		
t		15.76	-1.56	0.94		
Number of fish depredated	54	0.673	0.005	—	0.25	0.6184
SE		0.338	0.011	—		
t		1.99	0.50	—		
<b>Exponential</b>						
Interactions	54	0.803	-0.009	—	13.94	0.0005
SE		0.077	0.002	—		
t		10.47	-3.73	—		
Depredations	54	0.379	-0.004	—	6.22	0.0159
SE		0.047	0.002	—		
t		8.13	-2.49	—		
Number of fish depredated	54	0.484	0.0004	—	0.01	0.91
SE		0.111	0.0035	—		
t		4.37	0.12	—		

working on all but a few of the more aggressive and successful sea lions; or (3) the total number of sea lions is decreasing, and the numbers of interactions and depredations are approximately proportional to sea lion numbers.

Based on CDFG studies of nonlethal deterrents (Scholl 1987; Scholl and Hanan 1987a, 1987b), we do not expect that those deterrents are affecting interaction or depredation rates. Because the number of sea lions does not appear to be declining (Demaster et al. 1982), we conclude that declining interaction and depredation rates are a function of fish availability and the desirability of the fish targeted by the CPFV fishery. This inference is consistent with anecdotal information gathered from CPFV skippers and anglers. Their impression is that sea lions prefer to depredate more desirable sport fish such as yellowtail, barracuda, or bonita. Sea lions rarely interact or depredate when CPFVs are fishing for rockfish or other bottomfish. This inference is further supported by findings that anchovies are the major diet component of free-ranging sea lions in the Southern California Bight, while bottomfish are a minor component (Lowry and Oliver 1986; Lowry et al. 1986; Lowry and Folk 1987; Lowry et al.<sup>1</sup>).

The "rogue animal" concept suggests that most CPFV/sea lion interactions and depredations are

caused by relatively few sea lions that have learned to follow the fishing boats and take the hooked fish. Since the studies of sea lions' food habits mentioned above show that the natural diet rarely includes fish caught in CPFV fisheries, we postulate that a few rogue sea lions have learned that it is easier or more satisfying to follow fishing boats and take a few good-sized sport fish than to catch a large number of free-swimming anchovies.

#### ACKNOWLEDGMENTS

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## REPRODUCTIVE CYCLE AND BATCH FECUNDITY OF THE BAY OF BISCAY ANCHOVY (*ENGRAULIS ENCRASICHOLUS*) IN 1987

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### ABSTRACT

In the 1980s, the anchovy fishery of the Bay of Biscay suffered a deep decline, with landings reaching historical low levels. A revision of the stock management is needed. Understanding the reproductive biology of the anchovy is essential for the rational management of the fishery. This study examines the reproductive cycle and the batch fecundity of this species.

The spawning season for the Bay of Biscay anchovy was found to be from April to July, with a peak spawning period in May and June. The estimate of mean relative batch fecundity, 517 eggs per body gram, is within the range of estimates reported for the Peruvian anchovy and the northern anchovy.

### RESUMEN

En la década del 80, la pesquería de la anchoveta del Golfo de Vizcaya ha experimentado un pronunciado declive, alcanzando sus capturas valores mínimos históricos. Por ello, resulta necesario una revisión del manejo del stock.

Para lograr una ordenación piscícola racional es esencial comprender la biología reproductora de la anchoveta. Este estudio examina el ciclo reproductor y la fecundidad parcial de esta especie.

La temporada de desove para la anchoveta del Golfo de Vizcaya se extiende desde abril a julio, alcanzando un máximo en los meses de mayo y junio. La fecundidad relativa media por desove parcial, 517 huevos por gramo de hembra, se halla dentro del rango de valores publicados para la anchoveta del Perú y la anchoa del norte de California.

### INTRODUCTION

An important anchovy fishery has traditionally existed in the Bay of Biscay. This fishery is accessible during the reproductive period, when the anchovy migrate from the northern cold waters of the bay to the south and southwest, coinciding with the water's spring warming. The anchovy spawn in an area south of 47°30'N and east of 4°W (figure 1), all

along the Spanish and French continental shelf, as well as in oceanic waters.

Landing levels reached a maximum of 85,000 MT in the 1960s. The value of this fishery is due to the high price that anchovy brings in the market, since it is a popular food.

For the last several years the anchovy fishery has been suffering a serious crisis, with a deep decline in catches (figure 2). From 1981 to 1987, the mean annual landing was 14,000 MT. This enormous decline since the 1960s has been accompanied by a gradual decrease of the fishing fleet. Nevertheless, a substantial fleet remains, and suffers economically from the diminished anchovy resource. In 1987, 269 Spanish purse seines dedicated half of their annual fishing activity to the capture of this species. From the French side there were 9 purse seines and 42 pelagic trawls.

In 1988, for the first time, the Bay of Biscay anchovy was included among the species that are sub-

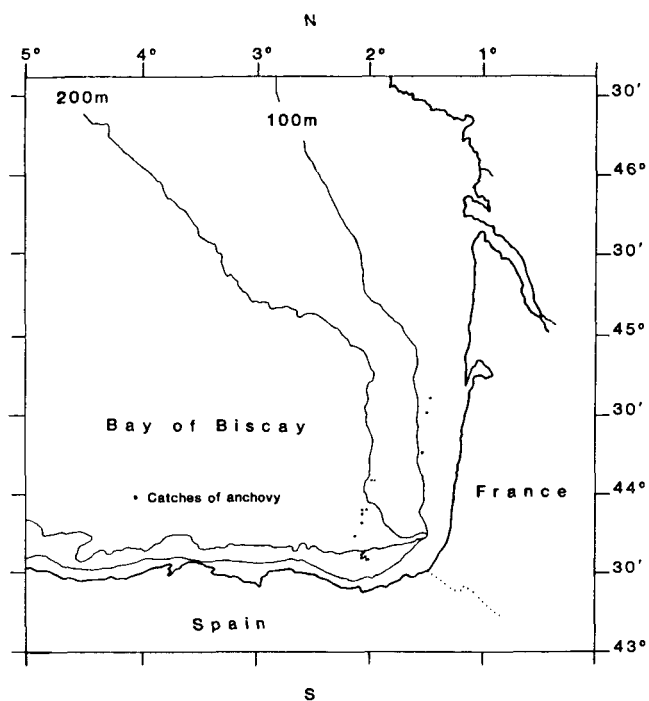


Figure 1. Anchovy spawning area in the Bay of Biscay, and location of anchovy catches for this study.

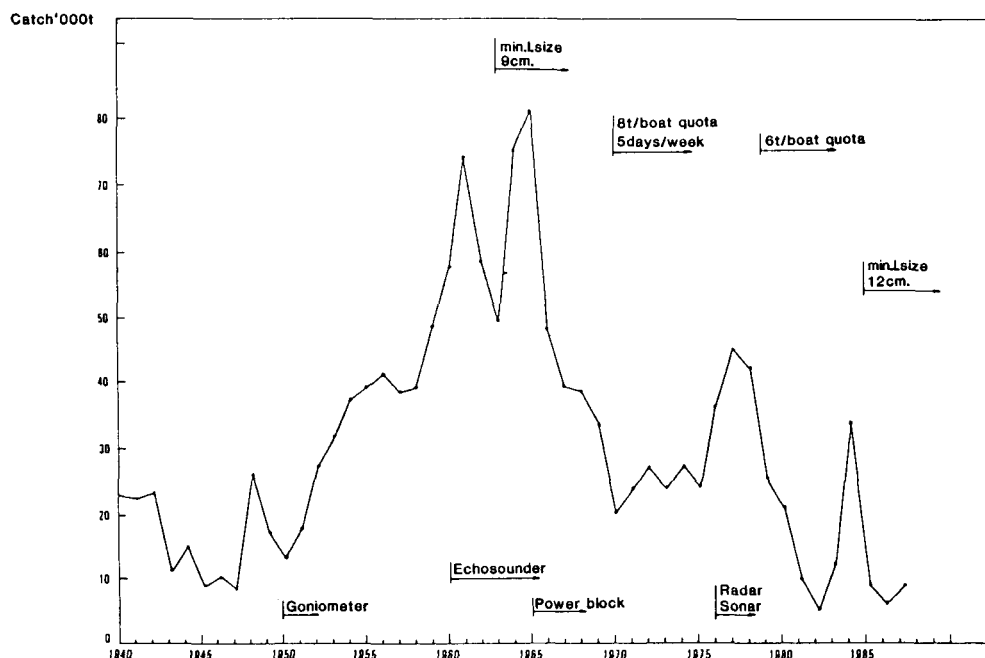


Figure 2. Historical evolution of anchovy fishery management (from Uriarte and Astudillo 1987).

ject to assessment by the International Council for the Exploration of the Sea (ICES). The state of the fishery was discussed, and there was concern that the stock may have collapsed (Anon. 1988), because biomass and recruitment levels are very low (Uriarte and Astudillo 1987). But there are great uncertainties because of the lack of precision in current stock estimates. The Council acknowledged the urgent need for more precise estimates.

Taking into account the studies made in other anchovy species from the same genus (Alheit et al. 1983), and similar studies on small pelagic species from European waters (Alheit 1987), it is now accepted that the Bay of Biscay anchovy has indeterminate fecundity (Anon. 1988).

The egg production method (EPM) of Parker (1980) is currently the best method for assessing stock size in indeterminate spawning fishes like the anchovy. This method is used to calculate the spawning biomass with a daily estimate of production and fraction spawning (Hunter et al. 1985).

It is the goal of the Oceanographic Investigation Service of the Basque Government to apply this method to the Bay of Biscay anchovy in the near

future. During the 1987 fishing season, one of our objectives was to develop the necessary techniques (sampling, histology, etc.) to obtain estimates of the different EPM parameters, and to determine some of them, such as batch fecundity.

It is preferable to apply the EPM during the peak of spawning activity. To determine the peak spawning period, it is necessary to examine the gonadal maturity cycle. The first part of this paper describes this subject; in the second part we test several assumptions of ovary subsampling and provide preliminary data on the batch fecundity of this species.

**METHODS**

**Gonad Maturity Cycle**

During the 1987 fishing season, we studied the maturity cycle to determine the spawning season and the peak spawning period. Fifty-one samples averaging 44 anchovies were collected from the landings. After the main spawning and catching season, in spring, the number of samples obtained drops considerably (table 1).

**TABLE 1**  
**Sampling Summary for the Gonad Maturity Cycle**

Month	March		April		May		June		July		October		November	
Day of month	1-15	16-30	1-15	16-30	1-15	16-30	1-15	16-30	1-15	16-30	1-15	16-30	1-15	16-30
Number of samples	1	4	7	9	4	8	5	5	0	3	0	2	3	0
Mean number of anchovies per sample	13	49	49	36	42	48	40	50		26		63	52	

Specimens were measured, total length (1 mm), and weighed (0.1 g). Both ovaries were excised, weighed (0.01 g), and classified according to a modified Holden and Raitt (1974) maturity index with seven stages: immature, virgin, early maturity, mature, spawning, partial postspawning, and final postspawning.

To simplify the analysis, these seven stages were grouped into three categories that included immature and virgin fish (stages 1 and 2); early maturity fish (stage 3); and mature, spawning, and postspawning fish (stages 4 to 7). Monthly percentages of the specimens in each group were calculated, for both males and females, to provide a preliminary estimate of size and endurance. The maturity cycle was also followed by the gonadosomatic index (GSI = gonad weight/gonad-free weight), males and females together.

**Batch Fecundity**

Twenty opportunistic collections of anchovy were taken at night from mid-April to late May 1987 (table 2 and figure 1), aboard several commercial purse seines of the Basque Country fleet.

After each set, hydrated females, which were identified by a swollen body cavity, were saved whenever encountered, according to a length-stratified sampling scheme that included females from 13 to 19 cm. We tried to include at least 10 specimens per cm increment in the total number of samples, so that the maximum number of different weights was covered.

The body cavity of freshly collected hydrated fe-

males was slit open along the side, and fish were preserved in buffered 4% Formalin. We preserved 3 adult anchovies per half-liter of Formalin (Hunter 1985).

At the laboratory, the hydrated females were blotted dry, measured to the nearest mm (total length), and weighed to the nearest 0.1 g. Then the ovaries were removed, blotted dry, weighed to the nearest 0.01 g, and placed in the Formalin solution.

Female weights and lengths were corrected for the effects of preservation during the two months of storage; 4% was subtracted from the weight value, and 3% was added to the length value (Hunter 1985).

All the ovaries were analyzed histologically to check for the presence of postovulatory follicles. Hydrated females with postovulatory follicles were rejected.

We have estimated the batch fecundity for the Bay of Biscay anchovy by the hydrated oocytes method (Hunter and Goldberg 1980; Hunter et al. 1985). One subsample each was sectioned from the anterior, middle, and posterior thirds of the biggest ovary. Samples were weighed (0.1 mg) and vialled for microscopic examination. Hydrated oocytes were identified and counted for each subsample.

Batch fecundity was determined from the mean number of hydrated oocytes per unit weight of the sample and the ovary weight.

*Statistical Analysis.* The hydrated oocytes method for estimating batch fecundity assumes that the oocytes are equally distributed along the ovary (Alheit et al. 1983). Before applying this method, we verified this assumption for the Bay of Biscay anchovy.

Therefore, we tested the effects that position of the ovary subsample and lobe of the ovary might have on the batch fecundity estimate. We estimated the ovarian density of hydrated oocytes (number of hydrated oocytes per gram ovarian tissue) in six subsamples (three from different locations in each ovary) in 25 females. A mixed trifactorial ANOVA was used, with two fixed factors — ovary (right and left) and position of the ovary subsample (anterior, middle, and posterior) — and one random factor — specimens (Sokal and Rohlf 1981).

The effect of position of the ovary subsamples inside the ovary was analyzed for 49 females. A mixed bifactorial ANOVA was used.

The optimum number of subsamples was determined according to the methods developed by Hunter et al. (1985), in which the optimum number of subsamples is the one that yields the better estimate of the variance ( $\sigma_A^2$ ) associated with the model that relates batch fecundity ( $F$ ) and body weight

TABLE 2  
 Summary of the Tows

Number	Date	Hour	Position	
			Lat. N	Long. W
1	29-4-87	01.00	44°07'	2°00'
2	29-4-87	02.00	44°07'	2°05'
3	6-5-87	02.30	44°18'	1°58'
4	6-5-87	05.30	44°31'	1°48'
5	7-5-87	01.00	44°38'	1°46'
6	18-5-87	20.30	43°45'	2°19'
7	19-5-87	20.30	43°50'	2°11'
8	19-5-87	08.15	43°54'	2°10'
9	20-5-87	23.30	43°34'	2°03'
10	21-5-87	01.30	43°36'	2°05'
11	21-5-87	03.45	43°34'	2°03'
12	21-5-87	06.30	43°40'	2°08'
13	25-5-87	22.00	43°53'	2°10'
14	26-5-87	03.00	43°49'	2°11'
15	26-5-87	01.45	43°49'	2°11'
16	26-5-87	04.00	43°49'	2°11'
17	26-5-87	05.00	43°53'	2°04'
18	26-5-87	24.00	43°37'	2°08'
19	27-5-87	02.00	43°35'	2°05'
20	27-5-87	04.15	43°35'	2°05'

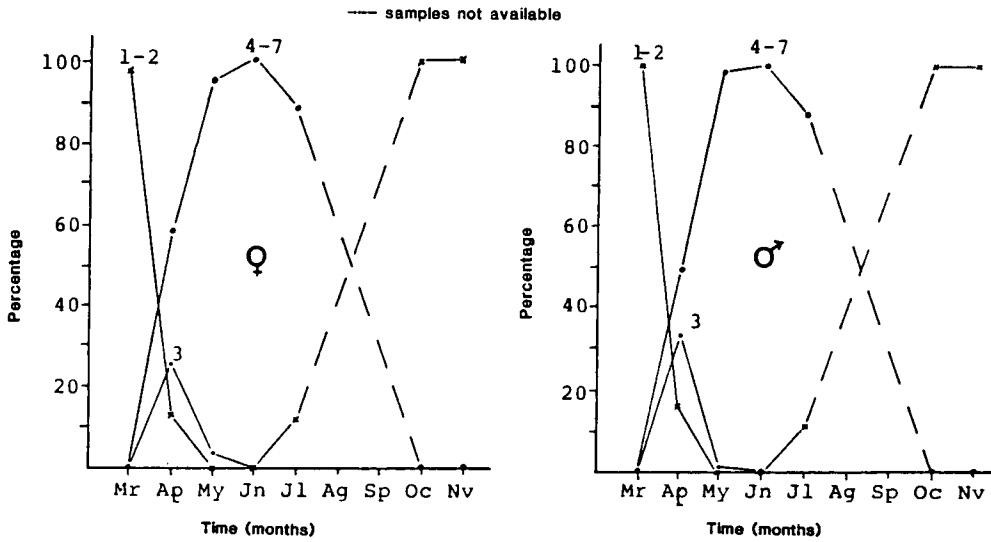


Figure 3. Monthly percentages of female and male grouped maturity stages during 1987 (1-2, immature; 3, maturing; 4-7, mature).

( $W$ ) when all eggs are counted. For a linear model (which fit the data, table 8):

$$F = f(W) + a$$

the error term ( $a$ ) has a mean equal to 0, and a variance equal to  $\sigma_A^2$ . When the number of hydrated eggs in a batch ( $F$ ) is not counted,  $f(W)$  are fitted to the estimated batch fecundities ( $\hat{F}$ ) calculated from  $m$  ovarian subsamples:

$$\begin{aligned} \hat{F} &= f(W) + a_i + e_i \\ &= f(W) + \xi_i \end{aligned}$$

the variance around the regression line ( $\sigma_\xi^2$ ) based upon data set ( $\hat{F}, W_i$ ) comprises two variance components:  $\sigma_A^2$  and  $\sigma_e^2$ , the within-ovary variance. The principal statistical parameter to determine the optimum number of subsamples is  $\theta = \sigma_e^2/\sigma_A^2$  (Lo et al. 1986), the ratio of the two error sources that determine the final error of the regression line.  $\theta$  is a measure of the relative variability within tissue samples. The ratio of  $\sigma_\xi^2$  (the real variance observed) and  $\sigma_A^2$ , i.e.,  $K = \sigma_\xi^2/\sigma_A^2$  evaluates the adequacy of the sample size, as compared to estimating batch fecundity by counting all eggs in a batch (Hunter et al. 1985).

In the EPM, batch fecundity must be expressed as a function of female weight. An appropriate model must be selected to describe the relationship between batch fecundity ( $F$ ) and gonad-free weight ( $W$ ). Four models were fit to our data:  $F = a + bW + e$ ;  $F = aW^b + e$ ;  $F = a e^{bW} + e$ ; and  $F = a + b \ln(W) + e$  ( $e$  = error).

In addition, batch fecundity must be expressed in terms of total weight to estimate the reproductive

biomass. Gonad-free weight was converted to total weight in the selected model, by the relation between the two weights for nonhydrated females (Hunter and Macewicz 1980).

## RESULTS

### Gonad Maturity Cycle

In figure 3 we have the gonad maturity cycle per month for males and females. The cycle was similar for both sexes.

In March, when the fishing season began, the anchovies were immature (figure 3), corresponding with minimum values of the GSI (figure 4). As can be seen in figure 3, the first increasing signs of ovarian activity were present from April onwards, with a certain proportion of fish maturing and mature. At the same time we can see an enlargement of the GSI (figure 4).

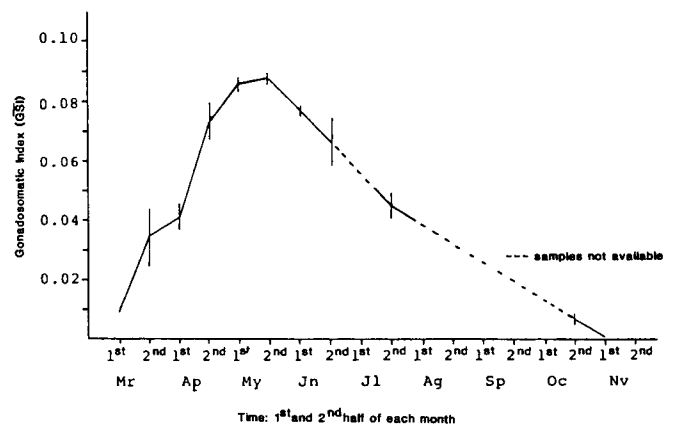


Figure 4. Evolution and standard error of the gonadosomatic index during 1987.

TABLE 3

ANOVA of the Hydrated Oocytes per Ovarian Gram, Obtained from the Right or Left Ovary, and as the Subsamples Are Located Inside the Ovary: in the Distal (I), Central (II), or Apical (III) Part (Fixed Factors), for 25 Anchovies (Aleatory Factor)

Source of variation	DF	SS	MS	F	sig. $\alpha = 0.05$
O ovary (right, left)	1	73084	73084	0.636	ns
P position (I, II, III)	2	329278	164639	2.665	ns ( $P < 10\%$ )
A among anchovies	24	8742486	364270	3.14	***
O $\times$ P	2	89459	44729	0.385	ns
O $\times$ A	24	2758578	114940		
P $\times$ A	48	2965280	61776		
O $\times$ P $\times$ A	48	5571519	116073		

Almost all the fish sampled during May and June were mature, with maximum GSI values in May. From July on, the percentage of mature anchovies declined, and GSI values decreased. Mature fish were absent in the samples taken in October and November, and GSI values descended to 0.

**Batch Fecundity**

From the 20 opportunistic collections, 79 hydrated females were obtained; 17 of them were rejected because of the presence of postovulatory follicles. So we counted 62 hydrated females for our study.

The statistical analysis to test the effects of the subsampling position indicated that there were no differences between the density of hydrated oocytes from the two sides of the ovary in the 25 hydrated females sampled (table 3). The differences in density of hydrated oocytes from the three subsample po-

TABLE 4

Variance Analysis of Two Factors to Verify the Effect of Subsample Position on the Number of Hydrated Oocytes per Ovary Gram

Bifactorial Variance Analysis: Effects of Inside-Ovary Position (Mixed Model)

Source of error	DF	SS	MS	F	sig. $\alpha = 0.05$
Inside-ovary position	2	261944	130972	2.140	ns
Between anchovies	48	9276640	193263	3.158	***
Residual error	96	5874742	61195		
Total	146	15413326			

Mean Number of Oocytes per Ovary Gram

Positions ( $n = 49$  females)

	I (distal)	II (central)	III (apical)	Total
Mean	2418	2320	2399	2379
SD	355	335	378	325

TABLE 5

Estimate of the Parameter  $\theta = s_e^2/s_A^2$  Used to Determine the Optimal Number of Ovarian Subsamples

Source of error	Formula	Estimation
Within-ovary ( $S_{eij}^2$ )	$S_{eij}^2 = \frac{\sum_i \sum_j (F_{ij} - F_i)^2}{n(m-1)}$	$2.7984 \times 10^6$
Residual value of $\hat{F} = f(W) + \xi: S_{\xi}^2$	$S_{\xi}^2 = \frac{\sum_i [F_i - f(W)]^2}{n-2}$	$7.7928 \times 10^6$
Residual value of $F = f(W) + a: S_A^2$	$S_A^2 = S^2 - \frac{S_{eij}^2}{m}$	$6.8600 \times 10^6$
Variance coefficient ( $\theta$ )	$\theta = S_{eij}^2/S_A^2$	0.41

$F_{ij}$  = estimated total number hydrated eggs in the ovary from the  $j^{\text{th}}$  tissue sample;  $F_i$  = estimated total number of hydrated eggs in the ovary;  $m$  = number of tissue samples from an ovary;  $n$  = number of anchovies.

sitions were not significant at  $\alpha = 0.05$ , but they were significant at  $\alpha = 0.10$  (the observed  $P$  was smaller than 10%). To be certain that the subsample position had no effects, 24 hydrated females were added to the 25 females sampled, and a bifactorial ANOVA was applied to the total of 49 females (table 4). This analysis indicated that no significant difference existed between the three subsample positions at either  $\alpha$  levels ( $\alpha = 0.05$  and  $\alpha = 0.10$ ).

Based on the analysis, we conclude that the density of hydrated oocytes in the ovary was homogeneous between ovaries of the same individual. All the ovarian sections of the anchovy were equally hydrated.

For the Bay of Biscay anchovy, the variance coefficient value ( $\theta$ ) was 0.41 (table 5). According to Hunter et al. (1985) and Lo et al. (1986), if  $\theta < 0.5$ , the optimum resource distribution is obtained by estimating the batch fecundity of each hydrated female from two ovarian tissue samples, assigning the rest of the effort (economic and work) to sample a larger number of hydrated females. With two subsamples per ovary  $K = 1.21$ ; i.e., the variance around the regression is increased 21% in relation to the one that would be obtained if we were counting the total number of hydrated oocytes in the total number of hydrated females (table 6).

Because the cost of the processing time for a new section is not too high and the increase in variance

TABLE 6

Effect of Number of Samples per Ovary ( $m$ ) on the Ratio  $K$  for the Linear Model

$m$	1	2	3	4	5
$K$	1.41	1.21	1.14	1.10	1.08

TABLE 7  
 Batch Fecundity of Bay of Biscay Anchovy

Number	Gonad-free weight (g)	Ovary weight (g)	Batch fecundity	Relative fecundity
0	19.07	3.86	10105	530
2	27.01	5.19	10769	399
3	31.18	6.51	16073	515
4	30.89	6.06	13550	439
5	34.54	7.01	16669	483
6	31.86	8.25	17325	544
7	40.52	8.52	23702	584
8	38.52	7.32	14662	381
9	37.51	9.75	22990	613
10	38.72	6.84	16006	413
11	38.69	9.99	24945	645
12	44.28	7.95	18126	409
14	23.25	4.75	12583	541
15	39.10	8.30	19206	491
16	31.94	6.21	18177	569
24	30.24	6.41	13160	431
25	27.02	3.84	9170	339
26	38.34	7.39	21690	566
27	35.86	7.84	17969	501
29	38.81	9.48	20676	533
30	40.14	6.79	17335	432
34	32.29	5.14	12577	389
35	31.91	6.54	15807	495
39	31.82	6.20	16957	533
40	24.67	4.88	10916	442
41	29.59	8.31	19811	669
42	23.85	4.97	12226	513
54	17.72	3.09	6050	341
55	15.53	2.76	7433	479
56	21.17	3.95	9579	452
57	16.55	3.60	7913	478
59	28.03	7.83	17398	620
60	24.55	6.44	10497	427
61	26.54	4.92	14341	539
62	30.26	7.10	15961	527
63	28.26	5.24	13571	470
64	23.37	4.68	10460	447
65	24.57	4.62	10714	436
66	29.61	7.08	18245	616
67	28.32	6.14	13974	493
68	28.34	7.19	14358	507
69	29.10	7.14	17307	595
70	33.52	8.40	18774	560
72	32.88	7.10	15229	463
77	33.00	7.53	19488	590
80	34.73	6.53	17520	504
82	41.07	10.78	23684	577
83	38.44	11.95	28453	740
86	39.66	10.74	22694	572
88	36.11	8.18	17014	471
89	42.54	12.91	24903	585
90	46.63	11.53	26311	564
91	48.00	11.20	21941	457
93	48.70	14.03	32629	670
104	27.20	6.52	16737	615
105	36.55	8.76	19254	527
117	30.70	7.39	18800	612
119	40.45	9.11	20743	513
121	30.36	6.54	15094	497
194	31.09	8.23	21028	676
239	24.24	6.05	13606	561
255	32.89	6.23	15002	456
	Mean		16772	517
	SD		5252	84
	CV		16.3%	31%

TABLE 8  
 Relation between Anchovy Batch Fecundity ( $F$ ) and Gonad-Free Weight ( $W$ ), Based on 62 Females with Three Subsamples

Model	Parameters		MSE ( $\times 10^{-6}$ )	$r^2$
	$a$	$b$		
$F = a + bW + e$	-2447.64	597.830	7.7928	0.722
$F = a + b \ln W + e$	-43695.10	17578.200	8.5241	0.696
$F = a W^b + e$	290.32	1.164	9.8323	
$F = a e^{bW} + e$	4643.92	0.038	8.5273	

about the regression is increased 14% ( $K = 1.14$ ), taking three tissue samples per ovary would be an easy and inexpensive way to increase precision in the estimation. There is no reason to increase the number of tissue samples beyond three because the reduction in  $K$  becomes negligible at a larger sample size (table 6).

Our value of  $\theta$  was within the range of the estimates for other species of small pelagic fish: for example, *E. mordax*, 0.5 or 0.6 (Hunter et al. 1985); and *Sardinops sagax*, 0.35 (Lo et al. 1986).

We used a data set of 62 hydrated females with no postovulatory follicles, in which three samples were taken from the right ovary to estimate batch fecundity. The different values for the 62 anchovies are listed in table 7. The mean value was 16,772 eggs per female. The relative fecundity, expressed as the number of hydrated oocytes per gram of ovary-free weight, ranged from 436 to 740, with a mean of 517.

Four regression models were evaluated to relate batch fecundity to ovary-free weight (table 8). Mean square error (MSE) was computed for all models and was used to select the most appropriate one. There was hardly any difference between the four MSE values; as Hunter et al. (1985) stated, the simple lineal model is preferable because the regression coefficient has a biological meaning, and batch fecundity for the females in the middle size range is better explained (figure 5).

$$F = -2447.64 + 597.83W^* \quad (1)$$

The conversion of gonad-free weight ( $W^*$ ) to a weight that included the active but not hydrated ovary ( $W$ ) was done through the relationship:

$$W = 0.025 + 1.086 W^*$$

If we reestimate equation 1 in terms of total biomass we obtain:

$$F = -2462.58 + 550.48 W$$

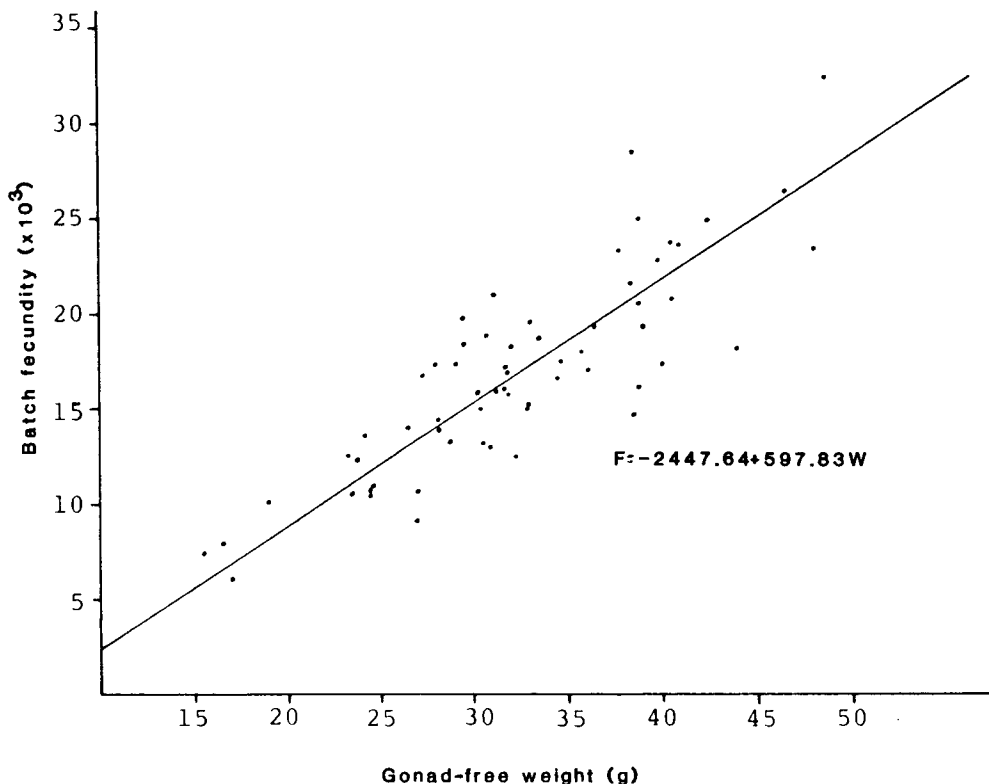


Figure 5. Point diagram of batch fecundity and female gonad-free weight, and the best model for our data set ( $F = a + bW$ ).

## DISCUSSION

Judging from the occurrence of grouped gonad stages and the pattern in GSI, it may be concluded that the spawning season for the Bay of Biscay anchovy in 1987 began in April and ended in July. These results confirm what was observed from egg and larval surveys (Arbault and Lacroix 1969, 1971, 1973; Suau and Vives 1979; Dicenta 1984; Santiago and Eltink 1988) and other studies of gonad maturity (Furnestin 1945; Andreu 1950; Cort et al. 1976, 1977, 1979). These studies have shown that the gonad maturity cycle parallels the warming process in spring, when the water goes from 12°C at the end of winter to 20°C at the beginning of summer.

The gonad maturity cycle was characterized by fast gonad development at the beginning of the reproductive period and slow absorption at the end of it. The peak spawning period is the most suitable time to obtain the adult reproductive parameters for the EPM. From the results obtained from the two maturity indices that were used (macroscopic and GSI), May appears to be the best time to conduct an EPM survey.

To determine batch fecundity, the subsamples can be taken from either of the two ovaries, because no significant difference was detected between the hydrated oocyte densities of the right and left ovaries. Also, no differences were seen between the

three subsampling positions in the ovary. The location of subsamples has no effect on the batch fecundity estimation for the Bay of Biscay anchovy. Hunter et al. (1985) found the same results for the northern anchovy. Hunter et al., like we did, sampled the anchovy during the night, when the females that were going to spawn were completely hydrated. But, as stated by Hunter et al., if females are captured during the day, position effects may be likely, because hydration does not proceed at a uniform rate throughout the ovary.

The optimum number of ovarian tissue sections is two, but we take three as suggested by Lo et al. (1986) when the cost of the processing time for a new section is not too high. This reduces the increase of variance around the regression to 14%, in relation to the regression based on counting all the hydrated oocytes in the ovary.

The mean batch fecundity was 16,772 eggs per female. The mean relative fecundity value (517 eggs per body g) was within the range of the estimates reported for other closely related species, such as the Peruvian anchovy and the northern anchovy (table 9).

Our data suggest that batch fecundity is linearly related to ovary-free body weight. As an example, we can consider that with a mean batch fecundity of 16,772 eggs, if the spawning frequency is between 3

TABLE 9

Relative Fecundity and Regression between Batch Fecundity and Gonad-Free Weight of Different Anchovy Species

Species	Sub-population	Year	Month	Sample size	Weight range	Relative fecundity		r	Slope
						Mean	SD		
* <i>E. ringens</i>	north + cent.	1981	Ag/Sp	437	15-18	580	139	0.806	981
* <i>E. ringens</i>	central	1981	Ag/Sp	254	15-38	637	134	0.769	1213
* <i>E. ringens</i>	north	1981	Ag/Sp	183	15-38	502	103	0.883	824
* <i>E. mordax</i>	central	1978		23	9-31	389	141	0.511	528
* <i>E. mordax</i>	central	1979		44	9-28	438	150	0.784	881
* <i>E. mordax</i>	central	1980		33	†17.11	444	80	0.903	624
* <i>E. mordax</i>	central	1981		127	†14.75	601	180	0.873	872
* <i>E. mordax</i>	central	1981		109	†16.54	606	151	0.724	852
* <i>E. carpensi</i>		1977		14	†17.24	‡644	153	0.451	1542
<i>E. encrasicolus</i>		1987	Ap/My	62	15-48	517	84	0.839	597

\*Data from Alheit et al. (1983)

†Mean weight

‡Parameter not calculated by the hydrated oocytes method

and 7 days, with a spawning period of approximately 90 days per anchovy, the total annual number of spawns per year would be between 12 and 30. These values turn out to be close to those given by Smith (1985) for *E. mordax*, according to different ages. This gives us an annual production range of 201,000-503,000 eggs. This approach is comparatively superior to the range of 23,000-173,000 eggs per spawning period given by Cendrero et al. (1981), who counted the total number of oocytes >250 μ in the ovary.

As we can see, the use of standing-stock oocytes underestimates the annual fecundity. For indeterminate spawners like the anchovy, annual fecundity must be calculated by both the batch fecundity and the number of spawnings per year (Hunter and Macewicz 1985).

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## SPERM CONCENTRATIONS AND EGG FERTILIZATION RATES DURING SPAWNING OF CAPTIVE ANCHOVY, *ENGRAULIS MORDAX*

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### ABSTRACT

The minimum sperm density needed for maximal fertilization success was determined for northern anchovy. On the average, 90% of anchovy eggs were fertilized in a concentration of 100 or more sperm per ml. These results were obtained by varying the number of hormone-treated male and female northern anchovy spawned in 3-m<sup>3</sup> tanks and examining the egg fertilization rate. These results were compared with two other studies.

### RESUMEN

Se determinó la densidad mínima de esperma necesaria para maximizar el éxito de fecundación de la anchoa del Pacífico norte. En promedio, 90% de los huevos de anchoa fueron fertilizados con una concentración de 100 ó más espermatozoides por mililitro. Estos resultados fueron obtenidos variando el número de machos y hembras de anchoa, desovados en tanques de 3 m<sup>3</sup> y previamente tratados con hormonas, y examinando posteriormente la tasa de fecundación de los huevos. Estos resultados fueron comparados con dos estudios previos.

### INTRODUCTION

Only a small percentage of the anchovy eggs collected during the CalCOFI cruises have been identified as being undeveloped. Thus the northern anchovy may have evolved a mode of spawning in which nearly every egg contacts sperm in sufficient numbers for fertilization. The concentrations of sperm required for high rates of fertilization, and the role of the male in establishing these concentrations have been observed in only a few fishes and never in pelagic spawners. This report presents laboratory observations on the concentration of sperm in the water at the time of anchovy spawning, and on how that concentration relates to the fertilization rate.

### MATERIALS AND METHODS

The concentration of sperm in the spawning tank, and the percentage of eggs fertilized were estimated for 19 spawning trials. Each trial consisted of a hor-

none-induced spawning and the collection of sperm and egg samples immediately after detection of eggs in the water. Collected anchovy were acclimated to the holding tanks for several months before hormone treatments, and the trials began only when the majority of fish had well-developed gonads.

The fish were induced to spawn with a procedure modified from Leong 1971; the females received 50 I.U. of human chorionic gonadotropin and 5 mg of carp pituitary, while the males received only 50 I.U. of human chorionic gonadotropin. The injection on the first day, 50 I.U. of human chorionic gonadotropin, was given to all fish. On the following day, all fish were squeezed, and males were identified by the secretion of milt. Fish that did not secrete milt when squeezed were assumed to be females and given the second injection. The number of males was reduced in some trials to lower sperm density.

Shedding of eggs began spontaneously 35 to 42 hours after the first injection. A strainer was passed through the water at half-hour intervals to determine when eggs were released. The spawning tank was slightly more than 3 m in diameter and contained 2.96 m<sup>3</sup> of water with a depth of .41 m. The flow-through tank had a water flow rate of 15 liters per minute, and the spawning temperature was about 17°C. The salinity averaged 32‰.

Three water samples provided an estimate of the average sperm concentration in the spawning tank during a trial. The samples, 100 ml in volume, were taken at mid-depth from different areas of the pool. Two drops of rose bengal stain and two ml of concentrated Formalin were added to each sample to stain and preserve the spermatozoa. Immediately after collection, each sample was passed through a millipore filter (0.25- $\mu$ m pore size and 25-mm diameter) under slight vacuum to separate and concentrate the spermatozoa, which have a head 4  $\mu$ m  $\times$  1.3  $\mu$ m and a tail about 55  $\mu$ m long (figure 1). The filter was placed on a microscope slide with immersion oil and warmed to clarify the filter and make the spermatozoa visible.<sup>1</sup> I estimated the

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<sup>1</sup>A brochure by the Millipore Corporation gives further details on the clarification and use of millipore filters.

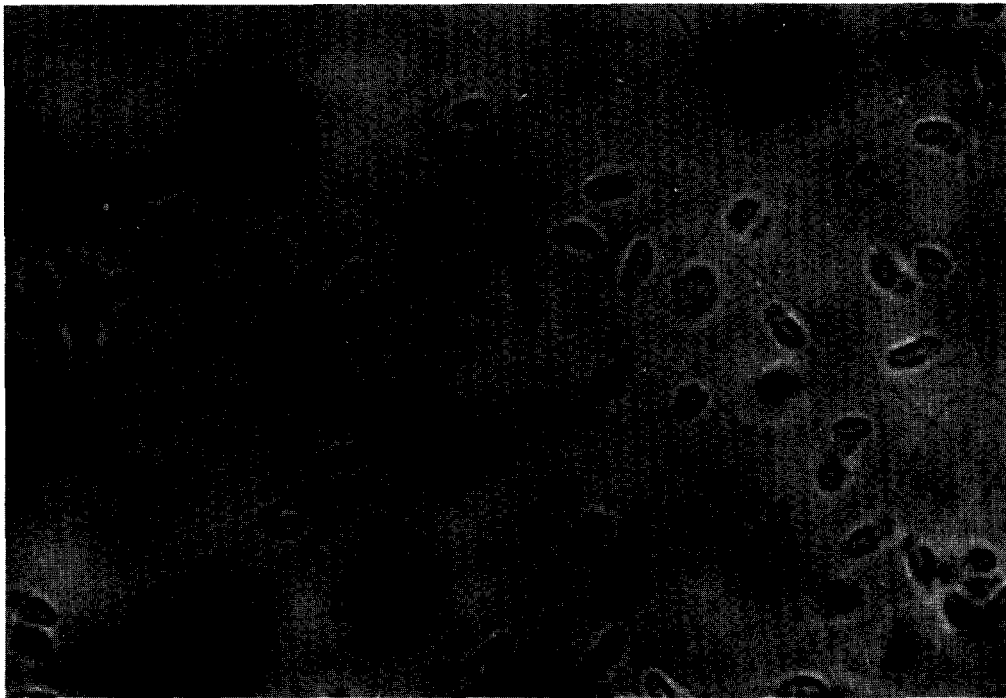


Figure 1. Anchovy sperm (photo by Bev Macewicz). Head  $4\ \mu\text{m} \times 1.3\ \mu\text{m}$ ; tail  $\sim 55\ \mu\text{m}$ .

number of spermatozoa on the filter by counting the number in several transects of measured lengths and widths with an inverted microscope at 400X magnification. I counted at least 300 sperm per filter except at the lowest concentration. Estimates made by the millipore filter method were compared to estimates made with a hemacytometer for five milt samples to test the technique (table 1). The milt were diluted 1:20,000 for counting with the hemacytometer and 1:20,000,000 for the millipore filter. The sperm densities estimated by the two methods did not differ statistically ( $t = 4.54$ ;  $p < .05$ ).

All fish in a trial were used only once and were killed at the end of the trial. Routine measurements on males included length, weight, testes weight, and gonadosomatic index (percentage testes weight of body weight).

The egg fertilization rate was determined by examining 200–300 eggs for signs of development. The eggs were collected soon after the detection of spawning and incubated in a beaker for an hour before examination. Developing eggs were easy to distinguish during the early stages of cell division, with pictures from Moser and Ahlstrom (1985) and Bolin (1936) as guides. Eggs that did not develop after the one-hour waiting period were assumed to be unfertilized.

## RESULTS AND DISCUSSION

The estimated density of sperm in the water of the spawning tank, percentage of eggs fertilized,

and other pertinent data from each of the 19 trials are given in table 2. The relation between the egg fertilization rate and density of sperm appears in figure 2. The figure shows the fertilization rate increasing with higher sperm density for densities up to  $100\ \text{ml}^{-1}$ ; maximum rates begin to appear near that level. The regression equation for observations with less than  $100\ \text{sperm}\ \text{ml}^{-1}$ ,  $Y = 1.00$ , indicates that the rise in egg fertilization was proportional to the density of sperm for the trials, and indicates a 50% level of fertilization for a sperm density of  $50\ \text{ml}^{-1}$ . The regression equation for observations with sperm density greater than  $100\ \text{ml}^{-1}$ ,  $Y = 88.1 + 0.0007$ , suggests a slight increase in fertilization rate with higher sperm density, but the slope was not significantly different from zero. The average fertilization rate for sperm densities above  $100\ \text{ml}^{-1}$  was 88.9%, with a range of 70.1% to 99.0%. Some of the lower rates were probably due to imperfec-

TABLE 1  
 Comparison of Two Methods Used to Count Sperm

Milt sample	Hemacytometer estimate ( $10^9$ )	Millipore filter estimate ( $10^9$ )	Ratio of millipore to hemacytometer estimate
1	6.76	4.00	.59
2	6.28	5.92	.94
3	7.88	6.74	.86
4	8.04	8.78	1.09
5	8.64	9.66	1.12
$\bar{x}$	7.52	7.02	.92

TABLE 2  
 Estimated Density of Sperm and Percentage of Eggs Fertilized When Anchovy Were Induced to Spawn in the Laboratory

Trial	Estimated sperm density in water of spawning tank (n/ml <sup>-1</sup> ) <sup>a</sup>	Percentage of eggs fertilized	Number of fish		Average male gonosomatic index (%) <sup>c</sup>
			Male <sup>b</sup>	Female	
1	9013	93.0	17	19	7.8
2	1435	98.0	4	19	6.4
3	862	98.0	18	—	4.7
4	744	80.1	14	11	6.1
5	337	99.0	14	18	10.9
6	268	90.0	25	35	8.7
7	217	70.1	6	20	10.1
8	165	80.0	1	16	8.6
9	141	84.6	17	14	7.3
10	122	96.4	18	17	8.3
11	97	97.0	19	16	3.7
12	87	84.0	11	22	6.9
13	86	89.2	27	14	7.9
14	78	70.0	8	10	8.0
15	66	60.2	13	—	9.4
16	55	80.0	8	16	8.3
17	50	54.2	2	14	4.8
18	25	18.5	11	16	5.1
19	4	4.4	2	15	13.0

<sup>a</sup>Estimated from three 100-ml water samples from spawning tank containing 2.96 m<sup>3</sup> water.

<sup>b</sup>Average male length was 116.6 mm; average weight was 21.0 g.

<sup>c</sup>Postspawning testes weight ÷ body weight × 100.

tions in the induced spawning procedure, which in some cases may have stimulated the release of immature gametes.

The rough relationships between sperm density and the number of males suggest that the number of sperm released per male was highly variable. The average concentration of sperm in the water may not be the same as the concentration surrounding newly extruded ova. In many species the male deposits sperm directly over the newly spawned eggs (Breder and Rosen 1966), and in those situations the eggs are surrounded by sperm at a much higher concentration than that surrounding the average egg in the water column. However, I did not see any close interaction between the sexes during the trials. Members in the spawning school usually milled about slowly and did not display any obvious behavior patterns such as pairing or posturing to indicate that spawning was in progress; yet my samples indicated that spawning had occurred. The sexes may have simply released gametes into the water, perhaps with some synchrony but without apparent change in behavior. If the spawning anchovy simply released gametes into the water without pairing and body contact, then the eggs were fertilized in water containing the observed sperm

concentrations. Whether the simple mode of spawning I observed in the laboratory also occurs in the sea is unknown. Anchovy spawn only at night (Smith and Hewitt 1985; Bolin 1936), and the dark conditions could possibly limit the use of visual cues in their spawning behavior.

The minimum sperm density needed for maximal fertilization success has been studied in only a few teleosts, and the results have been varied. Ginzburg (1972) studied the problem by placing roe with

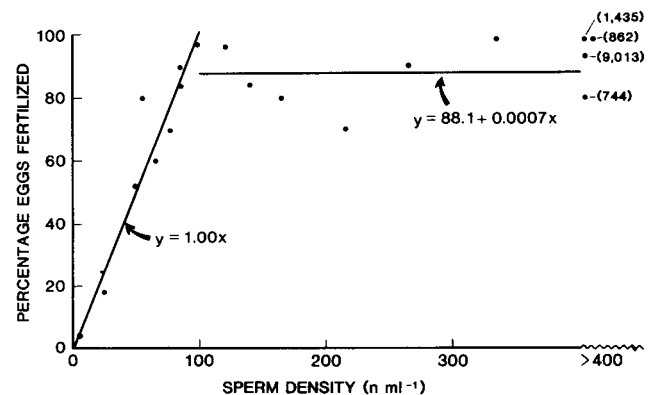


Figure 2. Percentage of eggs fertilized and sperm density during induced spawning of northern anchovy. Density is number of sperm ml<sup>-1</sup> water of spawning tank. Densities greater than 400 ml<sup>-1</sup> are in parenthesis.

stripped milt in various dilutions and found that concentrations of  $10^5$ – $10^6$  sperm  $\text{ml}^{-1}$  were necessary for maximum fertilization in certain salmonids and sturgeon. In a different setting Hourston and Rosenthal (1976) sampled surface water of milky discoloration above a school of spawning herring *Clupea harengus pallasii* and found concentrations of 148 and 129 sperm  $\text{ml}^{-1}$ , which they theorized to be more than ample for high fertilization success.<sup>2</sup> The sperm densities at which maximum fertilization occurred in the present study are close to those observed by Hourston and Rosenthal, but magnitudes lower than those observed by Ginzburg. Additional studies would be required to resolve these differences.

In any future work, other factors such as swimming speed and longevity, length of time ova are receptive to sperm, properties in the egg that may attract or activate sperm, and temperature should be considered as well as sperm density; only sperm density was considered in this study.

<sup>2</sup>Hourston and Rosenthal calculated that a herring egg would attract 24 sperm when the density is 150  $\text{ml}^{-1}$ , but P. E. Smith, NMFS, La Jolla, personal communication, found an error in their calculation; the number attracted should be corrected to 0.024.

## ACKNOWLEDGMENTS

I thank John Hunter, Paul Smith, and Gail Theilacker for reviewing the manuscript and making useful suggestions, and Eric Lynn for his help during the trials.

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## CORRIGENDUM

A personal communication attributed erroneously to me may have misled readers of *CalCOFI Reports*. I stated that "gelatinous zooplankton can have doubling times on the order of *days*," not weeks, as reported on p. 83 of Roesler and Chelton (1987).

Individuals of the aggregate generation of the salp *Thalia democratica* can double their carbon content in 3–4 days (Deibel 1982) and reportedly much more rapidly (Alldredge and Madin 1982; Heron and Benham 1984). Phorozoids of the doliolid *Dolioletta gegenbauri* can double their mass within 1 day (Deibel 1982). Individual *Oikopleura dioica* (larvaceans) can double body carbon in less than 1 day (King et al. 1980 combined with King 1982); during irruptions, population biomass can increase 100-fold within 5 days (King 1982).

This point influences interpretations of the mechanisms contributing to unusually high zooplankton

biomass. For some macrozooplankton taxa both individual and population growth can occur on relatively short time scales.

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*Text* style will in general follow that of the U.S. Department of Commerce (NOAA) *Fishery Bulletin*. Contributors who are not familiar with this publication will do well to follow *The Chicago Manual of Style* (1982). Authors are strongly urged to compare their typewritten equations with similar expressions in the printed literature, with special attention to ambiguity of the symbols for "one" and for "el," before submitting. Whenever possible, write in the first person, and use active verbs.

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(book):  
Odum, E. P. 1959. *Fundamentals of ecology*. 2d ed. Philadelphia: Saunders, 546 pp.

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*Acknowledgments*, if included, should be placed at the end of the text and may include funding source.

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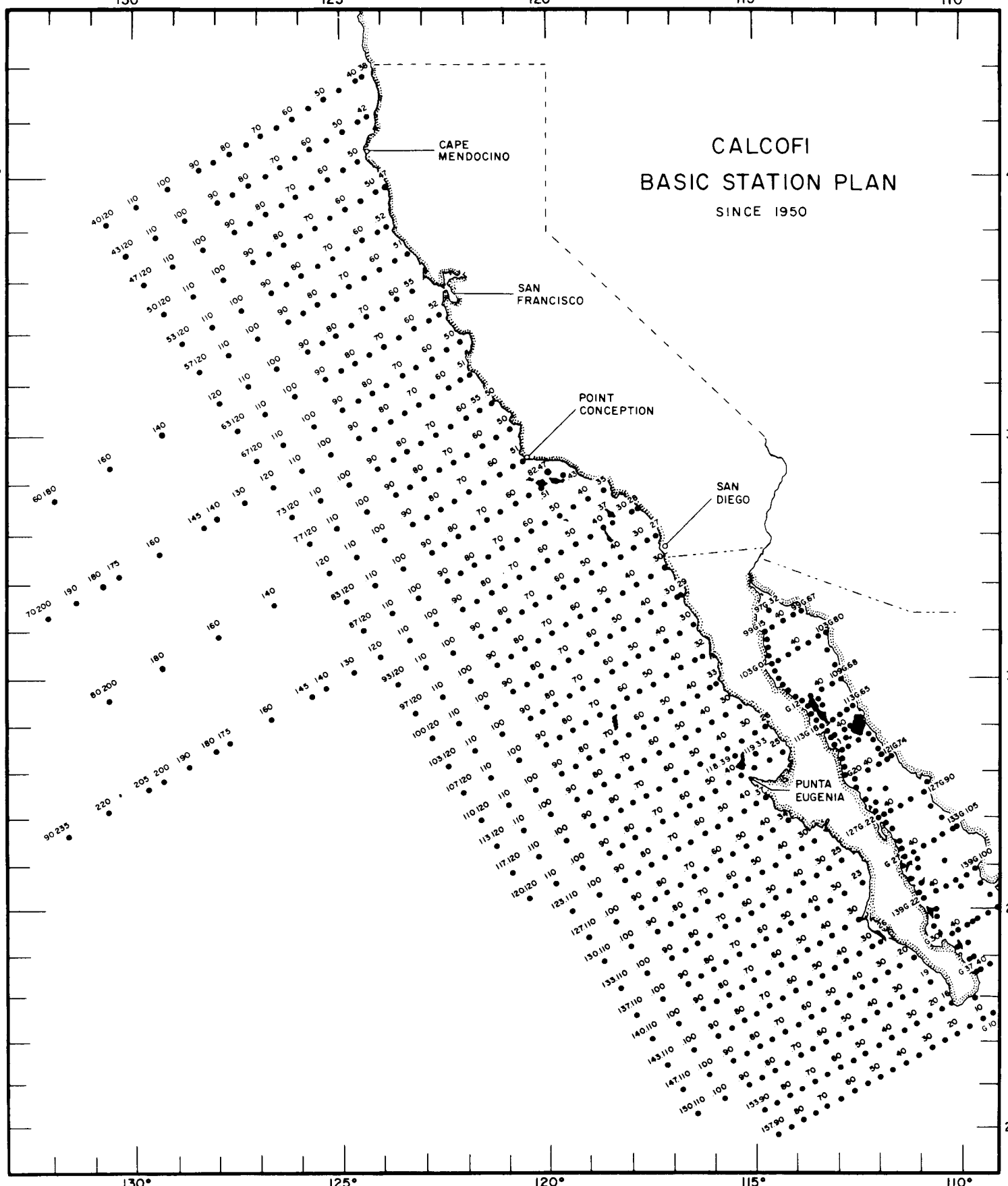
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- marine organisms
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- marine fishery modeling, prediction, policy, and management
- marine climatology, paleoclimatology, ecology, and paleoecology
- marine pollution
- physical, chemical, and biological oceanography
- new marine instrumentation and methods.



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