CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

CALIFORNIA

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In Memoriam

Elbert Halvor Ahlstrom
15 February 1910 – 27 August 1979

We are all saddened by the sudden death of our dear friend and honored colleague, Dr. Elbert Halvor Ahlstrom, on 27 August 1979, for on that day one of the world's outstanding fisheries scientists was no longer with us.

As a fishery biologist and Senior Scientist for more than 40 years with the National Marine Fisheries Service, and its previous titles the Fish and Wildlife Service and the Bureau of Commercial Fisheries, Dr. Ahlstrom's role was instrumental in developing a means of assessing stocks of marine fishes by systematically sampling the ocean for fish eggs and larvae. Through his strict discipline, extreme dedication and creativity, discovering and describing abundance and distribution of larval pelagic fishes and of spawning adult fish populations from ichthyoplankton surveys became a fundamental scientific tool and a foundation upon which the CalCOFI program was built.

Scientists from the world's fisheries and marine biological laboratories have come to the Southwest Fisheries Center to obtain ideas and information from Dr. Ahlstrom. He devoted much time to teaching formal courses in larval fish identification to students from various countries. Through his efforts, the Center now has the most extensive larval fish reference collection in the United States.

In 1959 Dr. Ahlstrom became the first director of the Southwest Fisheries Center in La Jolla. In this position the scope of his influence widened greatly. It was during his tenure as director of the Center that CalCOFI matured from a multi-agency group, with each smaller entity tugging to achieve somewhat different goals, to the truly cooperative and highly productive unit that it has become.

In 1965 Dr. Ahlstrom received the highest award of the U.S. Department of the Interior, its Distinguished Service Award, in recognition of more than 25 years of outstanding service in fisheries research and oceanography. In 1973 he won the U.S. Department of Commerce Gold Medal, their highest honor, for contributions of major significance to the Department and the nation.

He has authored about 80 scientific papers, which have been widely read and quoted. Together with co-author H. Geoffrey Moser, Dr. Ahlstrom received The Wildlife Society award for the outstanding publication of 1971 for their monograph on the development of lantern-fishes in the California Current.

Dr. Ahlstrom was much more than an outstanding scientist. Ahlie, as his friends called him, was a warm, affectionate, sincere human being who loved classical

Carl Leavitt Hubbs
18 October 1894 – 30 June 1979

Carl Hubbs was at the 1947 meeting at Stanford of fisheries representatives and scientists who created Cal-COFI. He was at almost every sardine conference for many years, where, as always at meetings, he offered judicious suggestions and served as a catalyst in bringing together people whose work he knew. He was on hand when the Isaacs-Kidd midwater trawl was being designed and tested, and it was at his urging that one of the first free-vehicle instruments was a fish trap.

Born in Williams, Arizona, raised in southern California, educated at Stanford University, Hubbs became established in science at the University of Michigan, where from 1920 to 1944 he enlarged the fish collection, organized the Institute of Fisheries Research, and pursued studies on systematics of fishes, on their distribution, on hybridization between species, and on relict fish faunas of the arid West. His publication output was prodigious.

Hubbs was enticed to Scripps Institution of Oceanograpy in 1944, where the Pacific Ocean beckoned. To his earlier projects he added studies of marine fishes and began the logarithmic increase in the institution's fish collection. Interest in distribution of fishes led him to taking ocean-temperature surveys along the rugged coast of Baja California, Mexico, which led to researches on past climates. Into that work he incorporated studies on aboriginal habitations in southern California and Baja California. Interest in the increasing numbers of gray whales migrating annually within his view led him to voicing conservation measures for those and for several other scarce marine mammals.

Often honored, always admired, was Carl Hubbs, a forthright man, dedicated to science. The breadth of his interests is represented in his bibliography of 700 publications and in his library of 80,000 catalogued entries, now the Hubbs Collection in the Scripps Institution Library.

Elizabeth N. Shor

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music, fine wines, and good food, and numbered many different people as friends. To many of us, Ahlie and his charming wife, Marge, were close friends, wonderful traveling companions, excellent hosts, and delightful company. We will sorely miss Ahlie. To his wife go our love and our deepest sympathy.

We are both saddened and honored to dedicate this volume to the memory of Dr. Elbert Halvor Ahlstrom.

John Radovich

Frontispiece. Photograph taken 14 March 1947 at Stanford University at a meeting of representatives from 1) the California Department of Fish and Game, 2) the California Academy of Sciences, 3) the South Pacific Investigations of U.S. Fish and Wildlife Service, and 4) Scripps Institution of Oceanography (University of California). *Front Row:* Milner B. Schaefer (3), John L. Kask (2), Frances N. Clark (1), John F. Janssen (1), Julius B. Phillips (1), Osgood R. Smith (3), and Donald H. Fry. *Back row:* Harald U. Sverdrup (4) , Oscar E. Sette (3), Wilbert M. Chapman (2), Carl L. Hubbs (4), Robert C. Miller (2), Elbert H. Ahlstrom (3), Richard S. Croker (1), and Kenneth M. Mosher (3).

PART I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE—1980

CalCOFI Reports is an annual publication, presenting papers on the physical and chemical environment of the California Current and its living resources. The scientific contributions are reviewed in order to maintain the quality of scholarly communication. Symposia of interest to CalCOFI member institutions also appear in the *Reports*. The CalCOFI Committee is especially grateful to the contributors and reviewers of this volume, and to Alex MacCall who graciously served as symposia reviewer.

The symposia included in this volume have in common a recognition of the relations of living things to each other and to the environment in which they live. In particular, the papers by Ainley, by Anderson et al., and by Hunt and Butler demonstrate how dramatically the increase or decrease of one stock can affect another. The papers on climate and ecological regimes emphasize the tremendous importance of collecting and maintaining data files of long duration and justify the concepts of the founders of CalCOFI.

Research that requires investment in a long-term data base is often hard to defend when compared with short-term programs that may yield more immediate, though limited, results. Relationships within the California Current system, which are just now being understood and appreciated, could not have been determined or even foreseen without the present data base; for example, the long-term correlation of sardine to anchovy abundance, seen both through the sedimentary record and through catch data; relationships between North Pacific sea-surface temperature and Arizona tree-ring width; the importance of storms in the spawning area to success of the anchovy year class.

A long-term data base is very useful to managers, since it may be employed to develop predictive and utilization models. Portions of the archived data base may become very valuable as the questions now being asked begin to change, as new technologies develop, and as needs evolve. The CalCOFI Committee pledges itself to the maintenance of the CalCOFI record and to its continuing quality and adequacy.

We note the deaths last year of Carl Hubbs and Elbert Ahlstrom, two of those who took prominent parts in the establishment of CalCOFI, and who planned for the long-term collections of physical, chemical, and biological data. Their labors, their wisdom, and their foresight will long be remembered.

Isadore Barrett, John Radovich,
Joseph Reid, and George Hemingway

REVIEW OF THE PELAGIC WET FISHERIES FOR 1978 AND 1979

Total commercial landings of pelagic wet fisheries declined in 1978 as a result of a virtual collapse of the anchovy reduction fishery. Jack mackerel landings also declined in 1978 from the 25-year high of the previous year, while Pacific mackerel, market squid, and Pacific herring fisheries recorded sizeable increases in landings (Table 1).

During 1979, the anchovy fishery made a moderate recovery, but jack mackerel landings continued to decline. The Pacific mackerel and market squid landings represented 22 and 33 year highs, respectively.

Pacific Sardine

The moratorium on sardines remained in effect during 1978, and their occurrence in mackerel landings was virtually nonexistent. Biomass levels continued to remain "very low" during the past few years when Pacific and jack mackerel had some apparently successful spawning seasons (1974 and 1976). Although live-bait fishermen in southern California seldom recorded the occurrence of adult sardines caught incidentally with anchovies, juvenile sardines, "firecrackers," were frequently encountered by several fishermen.

Although biomass levels remained low during 1979 and the moratorium remained in effect, some encouragement for the resource was gained from monitoring the species composition of mackerel landings. Whereas sardines rarely occurred in these landings in most recent years, during 1979 they were observed and sampled in all months from January through August. Although the majority of these occurrences were of trace quantities, it is estimated that 17 tons were landed. Also encouraging was the presence during April and May of a size class (160-200 mm), presumably 2-year olds, which has been

rarely observed in the last decade.

Although live-bait fishermen, in general, did not indicate any apparent increase in availability or occurrence of sardines, one fisherman, fishing off Palos Verdes Peninsula, indicated that 6-10-inch sardines made a "good show" on five successive nights in September, an event he considered rare.

Northern Anchovy

The total landings for 1978 reached 11,136 tons, the lowest in 14 years (Table 1).

The first half of the year saw very little fishing activity in either the northern or the southern areas. The lucrative herring and squid fisheries lured the entire Monterey fleet of nine boats from fishing anchovies, while southern area fishermen (47 permittees) encountered adverse weather and unavailability of commercial size fish schools, in addition to price disputes and labor union problems.

The 1978-79 reduction season was the first to be managed under the Pacific Fishery Management Council whose management plan was approved by the Secretary of Commerce on July 13, 1978. The regulations that implemented the plan define the procedures by which the United States reduction and nonreduction fisheries may harvest the anchovy resource. The regulations establish a total harvest quota for the anchovy fishery as well as a specific quota for the California reduction fishery. These quotas will be announced by Federal Register notice on or about August 1 of each year. The reduction fishery quotas for the 1978-79 season were 5,833 tons for the north and 52,500 tons for the south.

The season opened in the north on August 1, when interest in squid fishing was high. Boats did not catch any

TABLE 1

Landings of Pelagic Wet Fishes in California in Short Tons in 1964-79.

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1964	6,569	2,488	13,414	44,846	175	8,217	75,709
1965	962	2,866	3,525	33,333	258	9,310	50,254
1966	439	31,140	2,315	20,431	121	9,512	63,958
1967	74	34,805	583	19,090	136	9,801	64,489
1968	62	15,538	1,567	27,834	179	12,466	57,646
1969	53	67,639	1,179	26,961	85	10,390	105,307
1970	221	96,243	311	23,873	158	12,295	133,101
1971	149	44,853	78	29,941	120	15,756	90,947
1972	186	69,101	54	25,559	63	10,303	104,993
1973	76	132,636	28	10,308	1,410	6,031	150,489
1974	7	82,691	67	12,729	2,630	14,452	112,576
1975	3	158,510	144	18,390	1,217	11,811	190,075
1976	27	124,919	328	22,278	2,410	10,153	160,115
*1977	4	111,476	5,930	49,526	4,851	14,121	185,908
*1978	1	11,136	12,364	33,977	5,774	18,813	82,065
*1979	17	52,768	29,392	17,652	4,651	18,954	123,434

*preliminary

TABLE 2

Anchovy Landings for Reduction in the Southern and Northern Permit Areas for 1965-67 through 1978-79 Season, in Short Tons.

Season	Southern permit area	Northern permit area	Total
1966-67	29,589	8,021	37,610
1967-68	852	5,651	6,503
1968-69	25,314	2,736	28,050
1969-70	81,453	2,020	83,473
1970-71	80,095	657	80,752
1971-72	52,052	1,314	53,426
1972-73	73,167	2,352	75,519
1973-74	109,207	11,380	120,587
1974-75	109,918	6,669	116,587
1975-76	135,619	5,291	140,906
1976-77	101,434	5,007	106,441
1977-78	68,476	7,212	75,688
*1978-79	52,694	1,174	53,867

*preliminary

anchovies until late August, but the fish were very small and contained phytoplankton which created processing problems at the reduction plants. The abundance of squid and the absence of large fish eliminated any anchovy effort for the remainder of the year.

The 1978-79 season commenced in the south on September 15, but fishing effort was low and total landings through December 31 reached only 9,740 tons. Four Port Hueneme seiners caught over 50% of this total. Nine San Pedro-based seiners were actively fishing during the same period, landing fish at Terminal Island. The sharp decrease in fall 1978 anchovy landings might be attributed to the scarcity of legal-size fish (over 5 inches, total length) and a price dispute with the major cannery. Data analysis from this area indicated the presence of unusually high numbers of young fish (1978 year class) and the relative scarcity of older fish.

During 1978, an estimated 1,000 tons of anchovies were landed for nonreduction purposes, in addition to an estimated 6,600 tons for live-bait purposes.

As 1979 began, fishermen were still unable to locate good concentrations of anchovies, and on February 1, the reduction fisheries were closed for two months. However, fishing in the southern area began promptly on April 1, and on June 8 the fishery was closed when seasonal landings reached 52,694 tons (Table 2). In the north, landings remained minimal during the spring, as excellent squid fishing reduced effort towards anchovies.

The age composition of the 1979 spring fishery was marked by a strong appearance of one-year-old fish (1978 year class), which accounted for approximately 70% of sampled fish. The drastic decline in numbers of 3-year-old fish (1976 year class) was discomforting, since it was this year class that appeared to be relatively strong during the fall and winter of 1977.

On the basis of egg and larvae surveys by the National Marine Fisheries Service, the quotas for the 1979-80 season were set at 10,000 tons for the northern area and 146,100 tons for the southern area. For the first three and a half months of the season, northern area fishermen concentrated on squid, but by the end of December four seiners had landed 1,396 tons. In the southern area, catches occurred exclusively in the Santa Barbara Channel, with 5,813 tons landed by the end of the year. Of this total, 5,218 tons were landed at Port Hueneme by four seiners, whereas one San Pedro boat accounted for 600 tons landed at Terminal Island.

Age data based on Port Hueneme samples indicate the 1978 year class was dominant, representing 80% of the sampled fish. The 1977 year class accounted for 17%, whereas the 1976 year class contributed a meager 3%.

An estimated 1,000 tons of anchovies were landed for nonreduction purposes in 1979. Live-bait landings totaled an estimated 6,000 tons.

Pacific Mackerel

The year 1978 began with the California Department of Fish and Game establishing a 5,000-ton quota for the 1977-78 season, retroactive to October 1, 1977. As of January 1, 1978, approximately 1,000 tons of the quota had been landed. The remaining 4,000 tons were fished under permit restrictions of 15-ton daily limits when Pacific mackerel occurred in catches in percentages greater than 60% by weight. On February 22, when the season landings were approaching 4,000 tons, restrictions were tightened by allowing fishermen to land only catches containing less than 40% by weight. On March 10, the season was closed when the 5,000-ton quota was reached, and subsequent landings could only contain 18% Pacific mackerel by weight.

During the ensuing month, urgency legislation was introduced with the intent of increasing the 1977-78 season quota and allowing the Department more flexibility in establishing permit restrictions. This legislation became effective July 5 and established the quota formula at 20% of the total biomass over 20,000 tons. This allowed for an increase in the 1977-78 season quota from 5,000 to 9,300 tons.

On July 10, the fishery was reopened with restrictions limiting pure loads to three tons with larger loads allowed to contain up to 50% *by number* Pacific mackerel. Fishing was excellent during the next two months, and on September 18 the season was again closed when the final 9,300-ton quota was met.

On October 1, the 1978-79 season was opened with a 14,000-ton quota. Permit restrictions limited pure loads to eight tons with larger landings limited to 50% by number Pacific mackerel. By December 31, approximately 2,600 tons had been landed.

Preliminary analysis of age composition data during 1978 indicates that the 1976 year class contributed close to 70% of the tonnage landed. The 1977 year class accounted for most of the remaining tonnage with few fish 3 years old and older being represented in samples.

Several indicators suggest that Pacific mackerel had an excellent spawning season during the spring and summer of 1978. During mid- and late summer, San Pedro purse seiners, fishing for bluefin tuna, were "frequently" entering small spots of juvenile Pacific mackerel. These young-of-the-year fish also occurred frequently in nearshore live-bait catches from San Diego to Santa Barbara. In addition, the California Department of Fish and Game's nearshore midwater trawl survey during November of 1978 sampled "above average" numbers of juvenile fish. Prospects seemed good for the continued resurgence of the fishery and the resource. The 1978 catch of 12,364 tons was the highest since 1964 (Table 1).

As 1979 began fishermen were operating under permit restrictions that limited landings to 8-ton "pure

loads" with larger loads allowed to contain up to 50% Pacific mackerel by number. On January 22, when approximately 4,000 tons of the 14,000-ton seasonal quota had been caught, new permits were issued increasing the pure load limit to 25 tons. Landings increased dramatically during the ensuing months, partly as a result of the recruitment of an excellent 1978 year class.

On June 8, as seasonal landings were approaching 13,000 tons, the California Department of Fish and Game increased the quota to 18,000 tons. On June 18, permits were modified in an attempt to reduce the catch rate, and pure loads were again restricted to 8 tons. On July 5, permits were again modified to allow 40-ton weekly limits. Landings increased dramatically in July, and on July 20 the 1978-79 season was closed. Interseason restrictions were 18% by number tolerance and no pure loads.

On October 1 of 1979, the 1979-80 season began with the establishment of a 25,000-ton quota. Permits were issued without restrictions for the first time since the resource began its recovery in 1975. Fishing was relatively slow during the first few weeks of the new season because of local seiner effort on the tunas. Landings picked up at mid-October, and fishing remained good through December. Seasonal landings were approaching 11,200 tons by the end of December. The 1979 annual landings, estimated at 29,392 tons, represent the third highest catch since 1944 when 41,828 tons were recorded. Landings during 1957 were 31,022 tons.

The success of the 1979 fishery was largely the result of the excellent 1978 spawning season. Preliminary age composition studies indicate that the 1978 year class made up approximately 73% of the fish sampled during the year. Less encouraging is the fact that the 1979 year class of Pacific mackerel had not been detected by any form of sampling (purse seine fishery, research cruises, or live-bait fishery) by the end of the year.

Jack Mackerel

The landings for 1978 are estimated at 33,977 tons, a decrease from the 25-year high of 49,526 tons recorded during 1977 (Table 1).

The reduced catch might be attributed in large part to a dispute between boat owners, fishermens' unions, aerial spotters, and canneries, lasting from late April to early July. This was also the period of time that the Pacific mackerel season was closed, and many fishermen voiced the opinion that the 18% tolerance for Pacific mackerel inhibited their fishing for jack mackerel. On the other hand, a few independent fishermen indicated that both mackerels were generally unavailable for most of this period.

Whatever the case, the eventual settlement in early July resulted in an increase in price for "mackerel" from $100 to $130/ton, with an agreement that the price would be raised to $150/ton at the end of the year. Fishing turned out to be excellent for most of the remainder of the year, with 75% of the annual landings occurring from July through December.

Length-frequency analysis of 1978 samples suggests that the vast majority of tonnage landed was contributed by the 1976 year class. Fish older than two years are estimated to have made up less than 10% of the catch and one-year olds (1977 year class) were seldom sampled during the period when they normally are recruited into the fishery. It appears that both 1975 and 1977 were below average spawning years for jack mackerel.

During 1979 the annual landings continued on a downward trend. The estimated catch of 17,652 tons was the lowest since 1974. This might partially be explained by the tendency of fishermen to target on Pacific mackerel, which seemed to be more available in nearshore areas. At least partially responsible for the declining trend is the almost total lack of recruitment of both the 1975 and 1977 year classes. Length frequencies indicate that the 1976 year class was predominant in summer landings, whereas the 1978 year class made up the majority of the catch in the fall.

The price to the fishermen for both jack and Pacific mackerel rose from $130 to $150/ton during 1979.

Market Squid

California's squid fishery continues to be, in actuality, two fisheries—one centered around Monterey and the other around San Pedro.

Monterey's fishery is typically a summer fishery with good landings often occurring well into fall. The squid are caught almost exclusively by lampara net boats well within two miles of port on the "spawning grounds." During 1978, after four years of poor catches, squid appeared off Monterey as early as April, and sizeable landings continued well into November. The annual landings of 10,406 tons were caught in five months: June, July, September, October, and November. The price to the fishermen was negotiated with processors and remained at $230/ton for the length of the season. Southern California's fishery is centered at San Pedro with frequent landings at Port Hueneme. It is typically a fall-winter fishery, the season usually running from early November through February, although sizeable landings during the summer have occurred in a few years. Squid in southern California are caught by purse seines and scoop boats, which attract the fish by using powerful lights. Traditionally, the large majority of catches occur within a few miles off the seaward side of Santa Catalina Island. During 1978, 90% of the annual landings of 8,407 tons were caught in four months: January, February, November, and December.

Prices in southern California are regulated by market

conditions rather than by negotiation. They vary during the season and between processors, with market deliveries typically obtaining a higher price than cannery deliveries. During 1978, prices ranged from $60/ton in February to $140/ton in October. Markets received close to 80% of the tonnage landed.

The recovery of the Monterey fishery in 1978 together with good landings in southern California resulted in the highest annual statewide catch since 1946, when 19,000 tons were landed.

During 1979, the continued resurgence of the Monterey fishery resulted in the third straight year of increased statewide landings (Table 1), even though the southern California fishery had declined moderately the last two years.

Fishing at Monterey began in early May, and landings continued into November, although catch rates dropped off considerably after September. Peak landings occurred in June when 3,872 tons were caught. Seventy-seven percent of the annual landings of 11,598 tons were delivered from May through September. The negotiated price to the fishermen was $270/ton.

In southern California, 98% of the annual harvest of 7,356 tons was landed in January, February, November, and December. Scoop boats accounted for 81% of the catch. The price during the year continued to be regulated by market conditions and ranged between $40 and $160/ton.

Pacific Herring

During 1978, the California herring roe fishery established an annual record high for the second straight year of approximately 5,774 tons. The 1977 landings, which had previously been reported at 5,826 tons, were in actuality 4,821 tons. The previous high was recorded in 1952 when 4,748 tons were landed.

The fishery continued to be regulated by seasonal quotas by area and gear, with the season generally running from early December when spawning activity begins, to March 31, unless a quota is reached at an earlier date. Quotas during the 1977-78 season were set for five areas: San Francisco Bay, 5,025 tons; Tomales Bay, 600 tons; Bodega Bay, 575 tons; Humboldt Bay, 50 tons; and Crescent City Harbor, 30 tons.

The San Francisco Bay quotas were allocated by gear as follows: gill net, 226 permit vessels, 2,000 tons; purse seine, 30 permit vessels, 1,500 tons; and lampara net, 29 permit vessels, 1,500 tons. An additional 25 tons were allocated for fresh fish market use. In Tomales Bay gear was limited to gill nets (33 permit vessels) and beach seines (5 permits), but the quota was not allocated between gears. For the other three areas, fishing was restricted to gill net vessels only, with a total of one, four, and thirty permits issued for Crescent City, Humboldt Bay, and Bodega Bay, respectively.

Most quotas in San Francisco Bay and Tomales Bay were met by mid-January, with the lampara vessel quota being reached on February 15. Of the remaining 655 tons allocated to the other areas, only 95 tons were landed by the March 31 closure.

Age composition studies indicate that 6- through 9-year-old fish accounted for approximately 90% of fish sampled from the San Francisco gill net fishery. The round haul fishermen typically exploit 2- to 6-year-old fish.

The 1979 landings are estimated at 4,651 tons, a decline for the first time in four years, attributable to San Francisco Bay lampara and Tomales Bay-Bodega Bay gill net fishermen, who were unable to catch their quotas. The fishery continued to be managed by the California Fish and Game Commission, which establishes seasons, quotas, and gear restrictions.

Quotas during the 1978-79 season were: San Francisco Bay, 5,020 tons; Tomales Bay-Bodega Bay, 1,210 tons; Humboldt Bay, 50 tons; and Crescent City Harbor, 30 tons. The gear-allocated quotas for San Francisco Bay were 2,000 tons for 220 gill net permit vessels and 1,500 tons each for 27 purse seine and 31 lampara net permit vessels. An additional 20 tons were allocated for 10 permittees who deliver to fresh fish markets. The Tomales Bay-Bodega Bay fishery was combined for management purposes during 1979, and permittees consisted of 68 gill netters and one beach seine. Humboldt Bay and Crescent City Harbor permittees consisted of four and three gill netters, respectively. Because of congestion, San Francisco Bay and Tomales Bay-Bodega Bay gill net permittees were divided into two platoons, with each platoon fishing alternate weeks.

During the past six seasons, the California Department of Fish and Game has conducted population biomass surveys in San Francisco and Tomales Bays. During 1979, the survey was limited to San Francisco Bay where the total spawning population was estimated at 39,182 tons.

The prices paid to fishermen are based upon a negotiated sliding scale, depending on the percentage of roe recovery. At the end of 1979, a base price of $2,000/ton for 10% roe recovery was agreed upon for the upcoming 1979-80 season. For each percentage point difference from 10% recovery, $200/ton was to be added or subtracted from the price. Generally, roe recovery averages about 18-19% during a season, a yield of $3,600-$3,800/ton for the 1979-80 season. Processors sample continuously during the offloading procedure to determine the price. Gill netters have consistently received a better price, because they catch a higher percentage of females.

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ESTIMATE OF THE SPAWNING BIOMASS OF THE NORTHERN ANCHOVY CENTRAL SUBPOPULATION FOR THE 1978-79 FISHING SEASON

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ABSTRACT
The 1978 spawning biomass estimate for the central subpopulation of northern anchovies was 1,304,000 short tons. This estimate is based on the anchovy larva abundance as measured by four egg and larva surveys conducted over the period January-June 1978. Spawning biomass was estimated from larva abundance using Smith's (1972) method. Based on the Pacific Fishery Management Council's Anchovy Plan (PFMC 1978), optimum yield for the central subpopulation during the 1978-79 season was 101,333 short tons. The optimum yield in the U.S. Fishery Conservation Zone was 70,993 short tons. The 1978-79 U.S. reduction quota was 58,333 short tons.

RESUMEN
En 1978 el cálculo de la biomasa del desove para la subpoblación central de anchoveta del norte fue de 1,183,000 toneladas métricas (1,304,000 toneladas). Este cálculo se basa en la abundancia de larvas de anchoveta que se midió en cuatro cruceros de reconocimiento de huevecillos y larvas efectuados en el período enero-junio de 1978. El cálculo de la biomasa del desove se hizo de la abundancia de larvas usando el método de Smith (1972). Basado en el plan de anchoveta del Pacific Fishery Management Council (PFMC 1978), el rendimiento óptimo de la subpoblación central durante la temporada de 1978-79 due de 91,927 toneladas métricas (101,333 toneladas). El rendimiento óptimo en la zona de conservación de la pesquería de los EE.UU. fue de 64,403 toneladas métricas (70,993 toneladas). La reducción de la cuota efectuada por los EE. UU. en 1978-79 fue de 52,919 toneladas métricas (58,333 toneladas).

INTRODUCTION
The Fishery Management Plan (FMP) for the Northern Anchovy Fishery (Pacific Fishery Management Council 1978) requires that catch quotas be determined on the basis of current estimates of spawner biomass. The purpose of this paper is to document the 1978 estimate of spawning biomass of the central subpopulation of northern anchovy from which the optimum yield for the 1978-79 U.S. fishing season was established. The estimate was based on the 1978 California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larva survey for

the winter and spring quarters. This survey was conducted under the auspices of the La Jolla Laboratory, Southwest Fisheries Center, National Marine Fisheries Service. Scripps Institution of Oceanography (SIO), and Instituto Nacional de Pesca (INP), Mexico, cooperated in conducting this survey.

The procedure for estimating anchovy spawning biomass from anchovy larva abundance was based on the method given by Smith (1972), as documented in Appendix I of the FMP (PFMC 1978). In addition, the larva abundance estimate for the 1978 winter and spring quarters was expanded to an annual larva abundance based on the analysis of the historical data.

LARVA SURVEY
The data set of plankton samples for making the biomass estimate included only the four winter and spring surveys out of the eight planned for the 1978 CalCOFI triennial survey year. Only standard CalCOFI stations within the range of the central subpopulation were included even though stations were occupied as far south as CalCOFI line 137 at 25°N and approximately 400 nautical miles offshore on lines 90 and 93 (Figure 1).

Research vessels departed the weeks of 1 January 1978, 12 February 1978, 26 March 1978, and 7 May 1978. Each cruise was approximately 25 days long. The Mexican vessel, R/V Humboldt, sampled the southern waters, essentially south of the U.S.-Mexico border; the U.S. vessel, R/V Jordan, sampled the waters north of the border. Because of mechanical problems the Jordan's station pattern for the third survey was modified to include the southern stations. The outermost stations within the geographic range of the central subpopulation were dropped from the pattern.

Plankton samples were taken with a CalCOFI Bongo net, a pair of plankton nets with a combined cross-sectional area equal to a CalCOFI 1-m ring net. Plankton data and samples were brought back to the Southwest Fisheries Center (SWFC) for processing and sorting. One-hundred percent of the plankton samples were sorted if the station was beyond 200 miles or if the plankton volume was less than 26 ml; otherwise, a 25% aliquot of the sample was sorted. The only samples sorted for this estimate are from the 118 standard stations defined by Smith (1972) to be those stations routinely occupied since 1951 and within the range of the central subpopulation. These last two criteria were
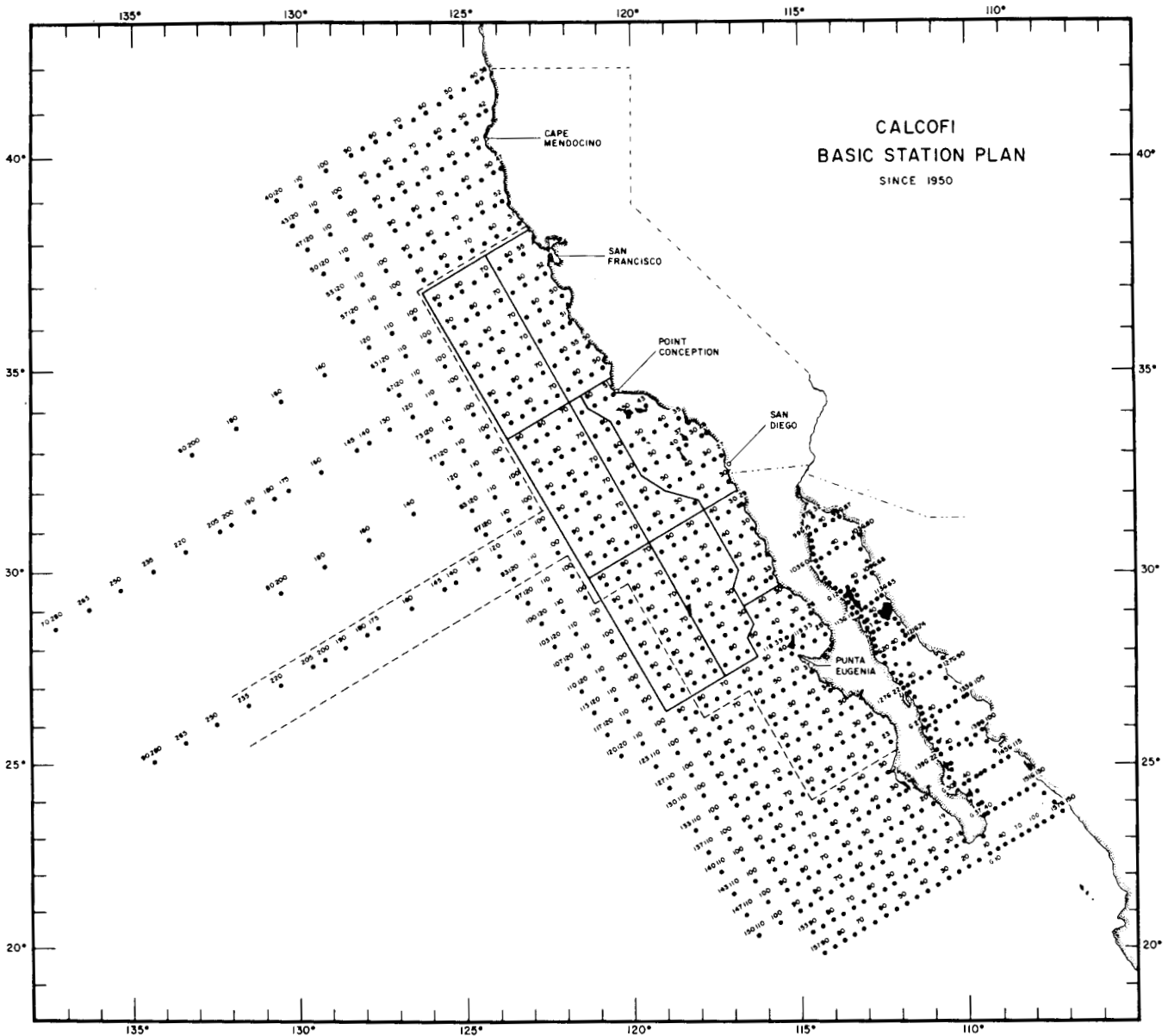
Figure 1. CalCOFI basic station plan. Solid outline is the area of the central subpopulation of northern anchovies. Dashed outline is boundary of winter and spring surveys, 1978.

necessary so that samples could be sorted by the deadline of July 1 for the biomass estimate.

SURVEY RESULTS

The distributions of larvae for the four cruises beginning with the January cruise, which form the basis for the 1978 spawning biomass estimate, are summarized in Figure 2. In general, the spawning intensity in the Southern California Bight and nearshore region was approximately the same as in earlier years, but only about ⅓ of the range of the central subpopulation contained anchovy eggs and larvae. Spawning was most intense during the March cruise. By the May cruise, spawning had fallen off

considerably. Ocean temperatures in the upper mixed layer and sea surface from mid-December to mid-April were the warmest since 1958 (J. Renner, SWFC, personal communication). The unusual weather pattern that developed in the latter half of December brought numerous Pacific storms into southern California. These events resulted in increased ocean surface temperatures along the entire U.S. west coast at a time when seasonal cooling normally takes place. The storm activity also at times inhibited the southerly flow of the California Current (Miller 1978). The February or March upwelling did not develop as usual (A. Bakun, SWFC/PEG, personal communication). These conditions may have accounted
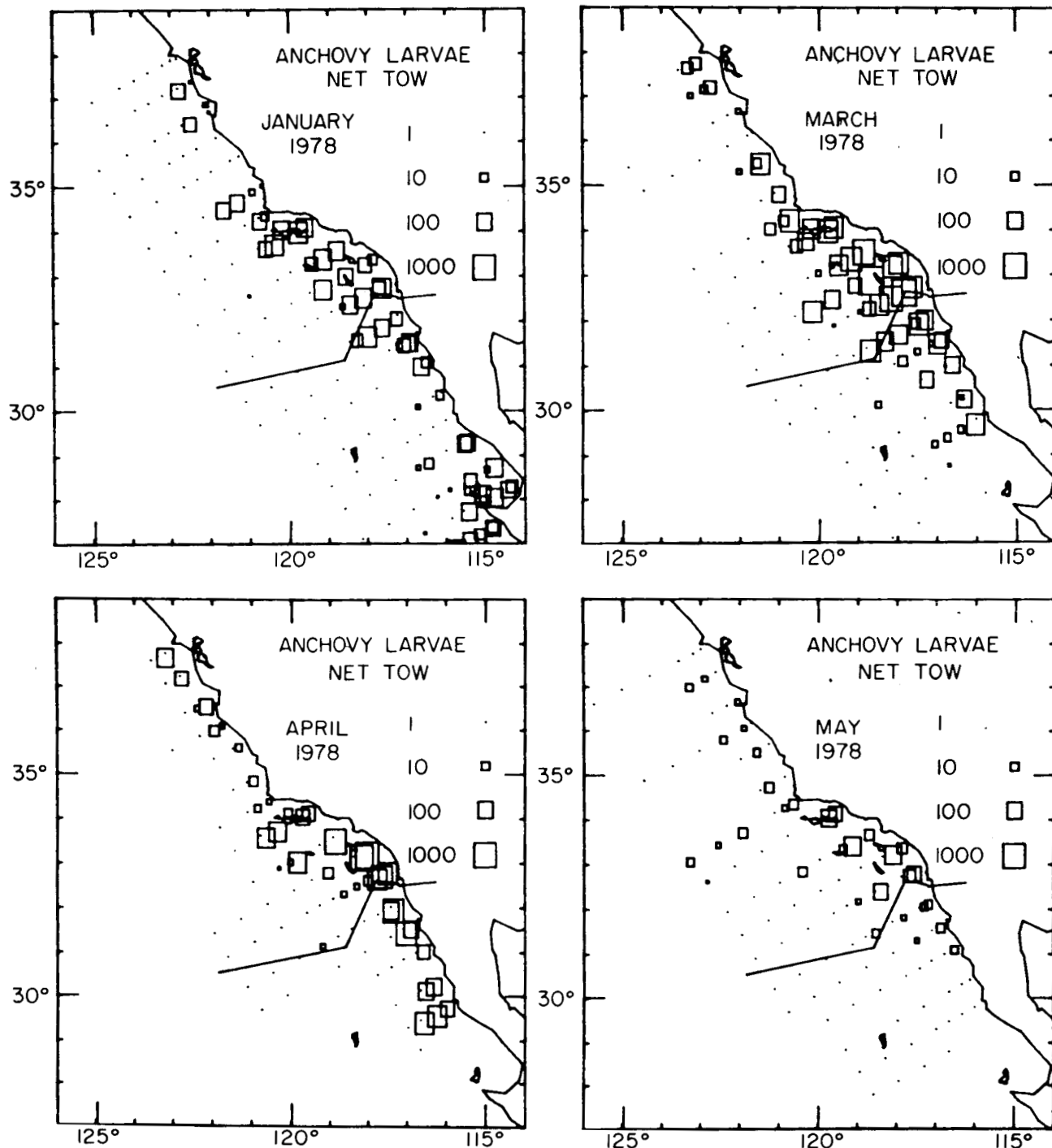
Figure 2. Geographic distribution of anchovy larvae for central subpopulation in winter and spring months of 1978 spawning season. The legend is in numbers of larvae per 10m^2 of surface area.

for the lack of offshore anchovy spawning during winter and spring months.

In the winter quarter, 240 standard stations were occupied and 98 contained anchovy larvae. In the spring, 195 stations were occupied and 64 contained larvae. The number

of occupied stations decreased in the spring quarter because the station pattern of the April *Jordan* cruise was modified mid-cruise so that priority stations south of the U.S.-Mexico border would be sampled.

The larva abundance estimates compiled by region

quarter strata after Smith (1972) are 6704.1 × 10⁹ and 4183.6 × 10⁹ larvae for the winter and spring quarters, respectively. These give a combined winter-spring larva abundance of 10,887 × 10⁹ larvae.

BIOMASS ESTIMATE

Anchovy spawning biomass estimates for previous years are based on annual larva abundance estimates. Because over 80% of the anchovy spawning takes place in the winter-spring months, the 1978 annual larva abundance $(\hat{L})$ is predicted from the sum of the winter and spring quarters larva abundance (L_{ws}) using the regression equation

$$\hat{L} = 1.062 \, L_{ws} + 1743.0 \times 10^9. \qquad (1)$$

This equation is derived from the historical time series presented in Table 2 of Appendix I in the FMP (PFMC 1978) and is repeated here in Table 1. This regression is illustrated in Figure 3. The 1978 estimate of annual larva abundance using (1) is 13,305.8 × 10⁹ larvae, where L_{ws} = 10,887.7 × 10⁹ larvae. The estimate of 1978 spawning biomass B, using Smith's (1972) method

$$B = 9.8 \times 10^{-8} \, \hat{L} \qquad (2)$$

is 1,304,000 short tons. Historical estimates of anchovy spawning biomass of the central subpopulation are shown in Figure 4.

Figure 3. Larva abundance estimates (10¹² larvae) and estimated spawner biomass in millions of tons. Plot of estimated spawner biomass and annual larva abundance versus winter plus spring larva abundance. Linear regression, Model: $Y = 1.062 \, X + 1.743 \times 10^{12}$.

TABLE 1

Estimated Larva Abundance (10¹² Larvae) and the Spawner Biomass[1] for the Central Subpopulation[2]

Year	Winter	Spring	Winter and spring	Annual	Spawner biomass in millions of short tons
1951	.298	.690	.988	1.841	.180
1952	.407	.457	.864	1.600	.156
1953	1.210	.373	1.583	5.208	.510
1954	4.469	.988	5.457	7.838	.768
1955	5.588	1.709	7.297	8.618	.845
1956	1.911	1.206	3.117	4.944	.485
1957	5.954	4.308	10.262	11.906	1.167
1958	8.114	5.236	13.350	15.087	1.479
1959	6.341	8.155	14.496	15.440	1.514
1960	7.552	7.547	15.099	15.713	1.540
1961	.992	6.714	7.706	11.827	1.159
1962	4.814	23.567	28.381	30.478	2.986
1963	17,277	24.818	42.195	43.407	4.254
1964	8.941	14.383	23.324	29.599	2.901
1965	19.155	22.690	41.845	47.540	4.650
1966	15.103	15.865	30.968	36.452	3.572
1969	19.756	6.538	26.294	30.594	2.998
1972	8.213	14.335	22.548	28.373	2.781
1975	29.754	4.071	33.825	36.768	3.603
1978	6.704	4.184	10.888	13.306	1.304

[1]in tons, calculated from annual larvae abundance ([spawner biomass = 9.8 × 10⁻⁸ × larvae abundance] from Smith 1972).

[2]taken from Appendix I, Table 2, Fishery Management Plan.

Figure 4. Estimated spawning biomass for the central subpopulation of northern anchovies, 1951-78.

OPTIMUM YIELD

As specified in the Northern Anchovy Fishery Management Plan, optimum yield for the 1978-79 season for the central subpopulation with the estimated spawning biomass of 1,304,000 short tons was 101,333 short tons. Of this amount, the optimum yield in U.S. zone was 70% or 70,933 short tons. A total of 12,600 tons was reserved for U.S. nonreduction fishing. The 1978-79 reduction quota was 58,333 short tons, of which 5,833 tons were reserved for the fishery north of Point Buchon and 52,500 short tons were available for the U.S. fishery south of Point Buchon.

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ESTIMATE OF THE SPAWNING BIOMASS OF THE NORTHERN ANCHOVY CENTRAL SUBPOPULATION FOR THE 1979-80 FISHING SEASON

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ABSTRACT

The 1979 spawning biomass estimate for the central subpopulation of northern anchovies was 1,723,000 short tons. This estimate is based on the anchovy larva abundance as measured by four egg and larva surveys conducted over the period January-May 1979. Spawning biomass was estimated from larvae abundance using Smith's (1972) method. Based on the Pacific Fishery Management Council's Anchovy Plan (PFMC 1978), optimum yield for the central subpopulation during the 1979-80 season was 241,000 short tons. The optimum yield in the U.S. Fishery Conservation Zone was 168,700 short tons. The 1979-80 U.S. reduction quota was 156,100 short tons.

RESUMEN

En 1979 el cálculo de la biomasa del desove para la subpoblación central de anchoveta del norte fue de 1,564,000 toneladas métricas (1,723,000 toneladas). Este cálculo se basa en la abundancia de larvas de anchoveta que se midió en cuatro cruceros de reconocimiento de huevecillos y larvas efectuados en el período enero-mayo de 1979. El cálculo de la biomasa del desove se hizo de la abundancia de larvas usando el método de Smith (1972). Basado en el plan de anchoveta del Pacific Fishery Management Council (PFMC 1978), el rendimiento óptimo de la subpoblación central durante la temporada de 1979-80 fue de 218,630 toneladas métricas (241,000 toneladas). El rendimiento óptimo en la zona de conservación de la pesquería de los EE.UU. fue de 153,041 toneladas métricas (168,700 toneladas). La reducción de la cuota efectuada por los EE. UU. en 1979-80 fue de 141,611 toneladas métricas (156,100 toneladas).

INTRODUCTION

The Fishery Management Plan (FMP) for the Northern Anchovy Fishery (Pacific Fishery Management Council 1978) requires that catch quotas be determined on the basis of current estimates of spawner biomass. The purpose of this paper is to document the 1979 estimate of spawning biomass of the central subpopulation of northern anchovy to establish the optimum yield for the 1979-80 season. The estimate is based on the 1979 California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larva survey for the winter and spring quarters. This cooperative survey was conducted under the auspices of the La Jolla Laboratory, Southwest Fisheries Center, National Marine Fisheries Service. Scripps Institution of Oceanography (SIO) cooperated in conducting the survey.

The procedure for estimating anchovy spawning biomass from anchovy larva abundance is based on the method given by Smith (1972), as documented in Appendix I of the FMP. In addition, the larva abundance estimate for the 1979 winter and spring quarters was expanded to an annual larva abundance based on the analysis of the historical data.

LARVA SURVEY

The geographic range of the central subpopulation is within the eight regions outlined on the CalCOFI station plan given in Figure 1. For convenience the author redefined those regions off southern California and Baja California in 1979 so that boundaries between the region group 7, 8, and 9 and the region group 11, 13, and 14 coincided with the U.S.-Mexico border. Four plankton surveys were conducted over the range of the central subpopulation during the five months, January through March 1979: 1) 7901 EB, January 12-22; 2) 7903 DS, February 25-March 13; 3) 7904 JD, March 22-April 17; 4) 7905 JD, April 30-May 21. The stations occupied by each cruise are shown in Figure 2. Unfortunately, only two of the four cruises, 7903 and 7905, received permits to conduct fishery research within Mexico's 200-mile zone.

Plankton samples on three of the four cruises were collected with a CalCOFI Bongo net, which is actually a pair of nets with a combined cross-sectional area equal to a CalCOFI 1-meter ring net. The 1-meter ring net was used on the first cruise, 7901. Station data and plankton samples were brought back to the Southwest Fisheries Center for processing and sorting. One-hundred percent of the plankton samples was sorted if the station was beyond 200 miles or if the plankton volume was less than 26 ml; otherwise, a 50% aliquot of the samples was sorted. The 1979 estimate includes station data from only the 118 standard stations defined by Smith (1972) to be those stations routinely occupied since 1951 and within the range of the central subpopulation.
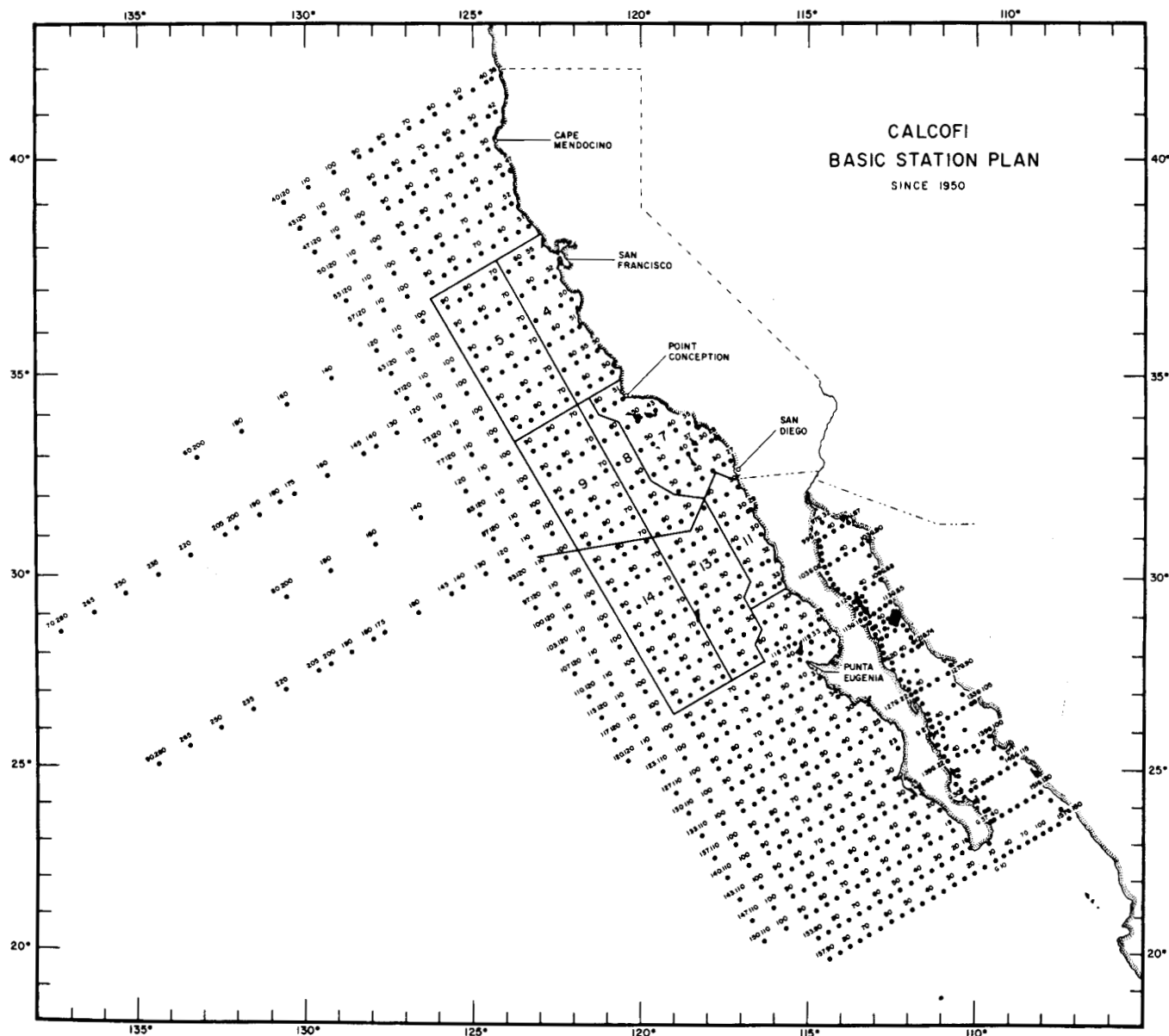
Figure 1. CalCOFI basic station plan. The geographic range of the central subpopulation of northern anchovy is within the eight numbered regions.

SURVEY RESULTS

The distribution of the number of anchovy larvae per plankton net tow for the four cruises that make up the basic data for the 1979 spawning biomass estimate is summarized in Figure 2. In general, evidence of anchovy spawning north of Point Conception in region 4 off cen-
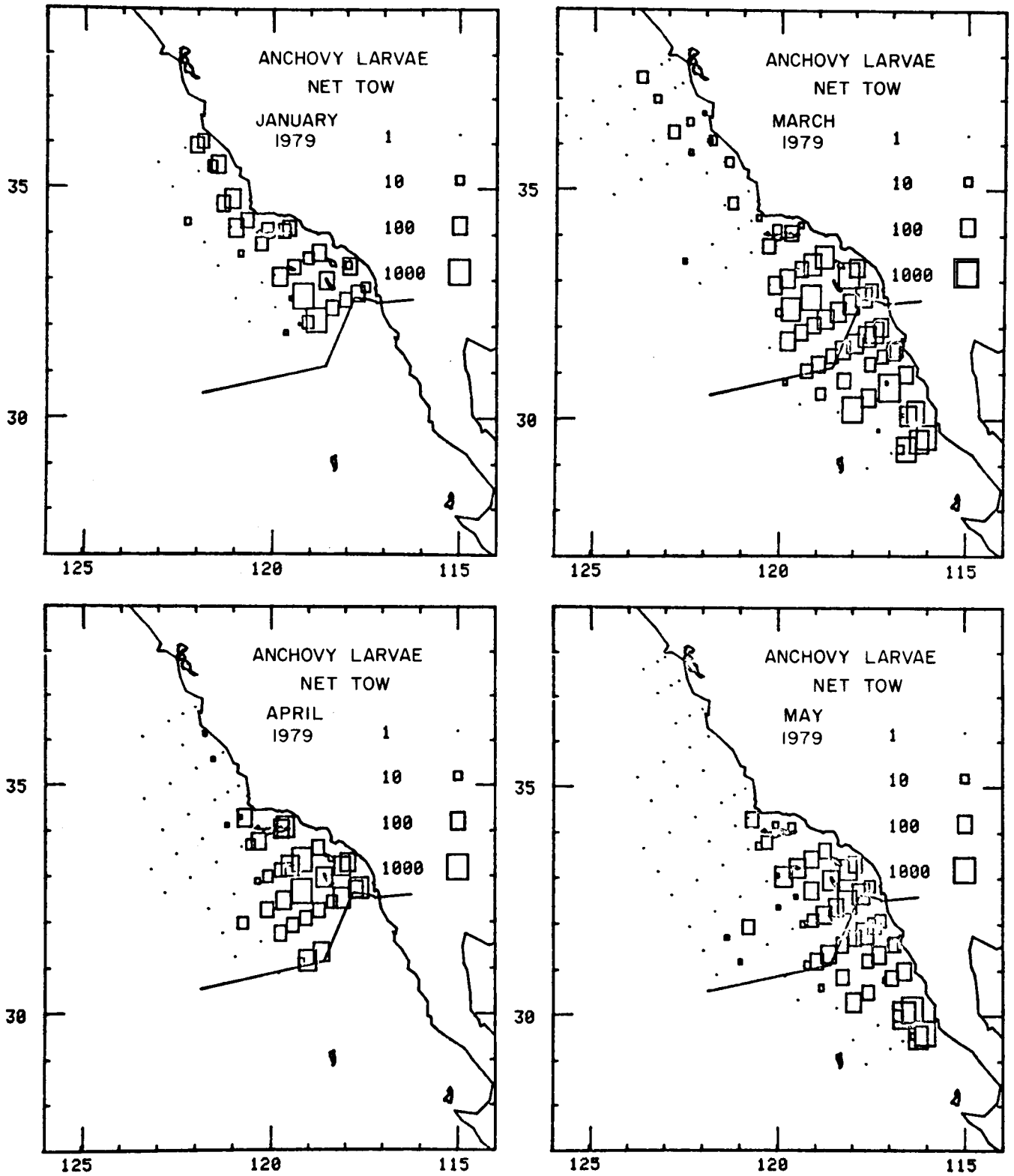
Figure 2. Pattern of occupied stations for the 1979 cruises and geographic distribution of anchovy larvae for central subpopulation in winter and spring months of 1979 spawning season. The legend is in numbers of larvae per net tow.

tral California was only found during the month of January. To the south, anchovy larvae were consistently taken on all four cruises as far out as 140 nautical miles, approximately 40 nautical miles farther than in 1978. The percent of the larvae south of the U.S.-Mexico border was 53.5% in 1979; the long-term average is 30%. Spawning persisted from January through May off southern California and Baja California.

Because the regions offshore of Baja California were only surveyed in the second half of each quarter, the quarterly larva abundance for the Baja regions 11, 13, and 14 (L_m) was estimated from a linear regression model using an adjusted larva abundance (L_a). Adjusted larva abundance is the larva abundance for the Baja regions 11, 13 and 14 based on the single cruise $(L_{m\frac{1}{2}})$ divided by the ratio of Southern California larva abundance for regions 7, 8, and 9 for the corresponding single cruise $(L_{c\frac{1}{2}})$ to the larva abundance in the same regions for the two cruises averaged together (L_c), i.e.

$$L_a = L_{m\frac{1}{2}} (L_c / L_{c\frac{1}{2}}) \text{ and}$$

$$L_m = b_0 + b_1 L_a \qquad (1)$$

This relationship for the adjusted larva abundance is based on the premise that the Baja larva abundance for the single cruise $(L_{m\frac{1}{2}})$ divided by the abundance in the same area for the two cruises averaged together (L_m) is proportional to southern California larva abundance for the corresponding single cruise $(L_{c\frac{1}{2}})$ divided by the abundance in the same area for the two cruises together (L_c), i.e.

$$L_{m\frac{1}{2}} / L_m \approx L_{c\frac{1}{2}} / L_c$$

so that

$$L_m \approx L_{m\frac{1}{2}} (L_c / L_{c\frac{1}{2}})$$

The regression model (1) was fit to the historical CalCOFI larva data for only the standard stations and with new region boundaries. The model was fit to winter quarter data from the 15 years, 1951-60, 1966, 1969, 1972, 1975, and 1978, with the following result:

$$L_m = -0.2744 \times 10^{12} + 1.0913 L_a; R^2 = 0.975 \qquad (2)$$

There were sufficient data for only 13 years, 1951-60, 1966, 1969, and 1978, to fit the model for the spring quarter. The fitted equation is

$$L_m = 0.3860 \times 10^{12} + 0.9108 L_a; R^2 = 0.627 \qquad (3)$$

The fit of equations (2) and (3) is shown in Figure 3.

For the winter quarter in 1979, L_a equals 2.882×10^{12} larvae and L_m is estimated from equation (2) to be
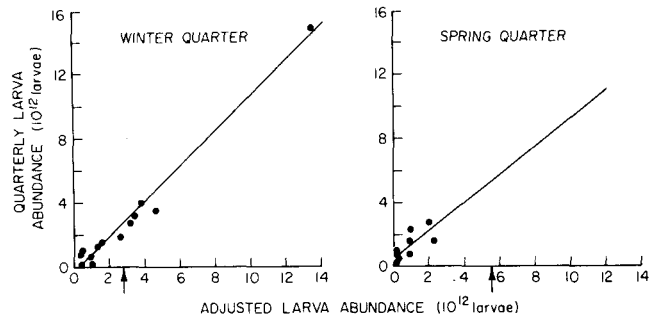
Figure 3. Regression models for estimating larva abundance in Mexico's 200-mile zone for winter and spring quarters from the adjusted larva abundance for the winter and spring quarter as defined in the text; arrows indicate 1979 values.

2.871×10^{12} larvae. This added to the larva abundance north of the U.S.-Mexico border gives a total anchovy larva abundance of 6.546×10^{12} larvae for the winter quarter. For the spring quarter, L_a equals 5.625×10^{12} larvae. The resulting L_m using equation (3) is 5.509×10^{12} larvae. Adding this amount to the northern abundance gives a spring quarter abundance of 9.124×10^{12} larvae. The sum of the two quarterly estimates give a winter-plus-spring larva abundance (L_{ws}) of 15.670×10^{12} larvae. For historical time series, the quarterly and winter-plus-spring larva abundance estimates presented in Table 2 of Appendix I in the FMP (PFMC 1978) are repeated here in Table 1, along with the 1979 values.

TABLE 1

Estimated Larva Abundance (10^{12} Larvae) and the Spawner Biomass[1] for the Central Subpopulation[2]

Year	Winter	Spring	Winter and Spring	Annual	Spawner biomass in millions of short tons
1951.....	.298	.690	.988	1.841	.180
1952.....	.407	.457	.864	1.600	.156
1953.....	1.210	.373	1.583	5.208	.510
1954.....	4.469	.988	5.457	7.838	.768
1955.....	5.588	1.709	7.297	8.618	.845
1956.....	1.911	1.206	3.117	4.944	.485
1957.....	5.954	4.308	10.262	11.906	1.167
1958.....	8.114	5.236	13.350	15.087	1.479
1959.....	6.341	8.155	14.496	15.440	1.514
1960.....	7.552	7.547	15.099	15.713	1.540
1961.....	.992	6.714	7.706	11.827	1.159
1962.....	4.814	23.567	28.381	30.478	2.986
1963.....	17.377	24.818	42.195	43.407	4.254
1964.....	8.941	14.383	23.324	29.559	2.901
1965.....	19.155	22.690	41.845	47.540	4.650
1966.....	15.103	15.865	30.968	36.452	3.572
1969.....	19.756	6.538	26.294	30.594	2.998
1972.....	8.213	14.335	22.548	28.373	2.781
1975.....	29.754	4.071	33.825	36.768	3.603
1978.....	6.704	4.184	10.888	13.306	1.304
1979.....	6.546	9.124	15.670	17.580	1.723

[1]in tons, calculated from annual larvae abundance ([spawner biomass = 9.8 $\times 10^{-8} \times$ larvae abundance] from Smith 1972).
[2]taken from Appendix I, Table 2, Fishery Management Plan.

BIOMASS ESTIMATE

Anchovy spawning biomass estimates for previous years are based on annual larva abundance estimates. For years in which surveys are conducted in only the winter and spring quarters, the annual larva abundance (L) can be predicted from the winter-plus-spring quarters larva abundance using the regression equation (see Figure 4)

$$L = 1.8233 \times 10^{12} + 1.0055\ L_{WS}\ ; R^2 = 0.990 \quad (4)$$

This equation is slightly different from the one Stauffer and Parker (1980) used for making the 1978 biomass estimate because the historical time series of L_{WS} was recalculated for the redefined regions and with data from only the standard stations. Also, equation (4) was fit to data points for only those years (1951-60, 1966, and 1969) in which surveys were conducted in each half of the winter and spring quarters (see Figure 5).

The 1979 estimate of annual larva abundance using equation (4) is 17.580×10^{12} larvae, where $L_{WS}=$

15.670×10^{12} larvae. The estimate of the 1979 spawning biomass, B, using Smith's (1972) method,

$$B = 9.8 \times 10^{-8}\ L,$$

is 1,723,000 short tons. This is a 23% increase over the 1978 biomass estimate. The historical estimates of anchovy spawning biomass of the central subpopulation are shown in Figure 5.

OPTIMUM YIELD

As specified in the Northern Anchovy FMP (PFMC 1978), optimum yield for 1979-80 season for the central subpopulation with the estimated spawning biomass of 1,723,000 short tons was 241,000 short tons. Of this amount, the optimum yield in the U.S. zone was 70% or 168,700 short tons. A total of 12,600 tons was reserved for U.S. nonreduction fishing. The 1979-80 reduction quota was 156,100 short tons, of which 10,000 tons were reserved for the fishery north of Point Buchon and 146,100 short tons were available for the U.S. fishery south of Point Buchon.
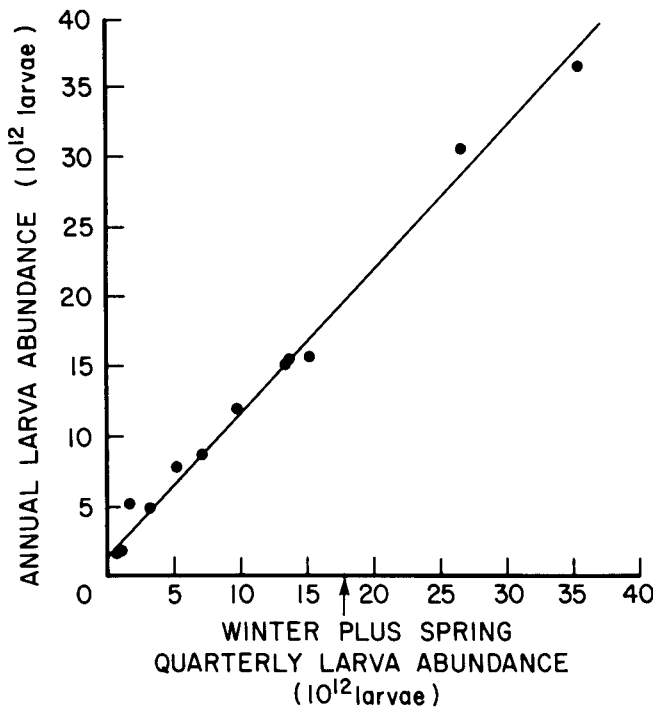
Figure 4. Regression model for estimating the annual larva abundance from winter-plus-spring quarterly larva abundance; arrow indicates 1979 value.
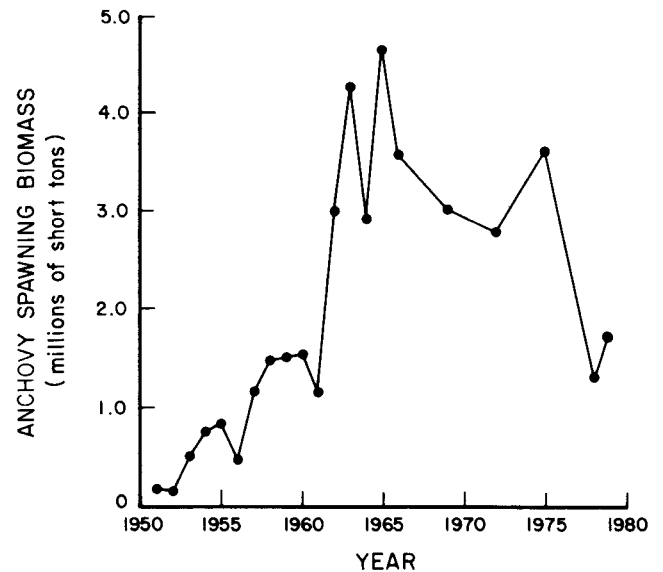
Figure 5. Estimated spawning biomass for the central subpopulation of northern anchovies, 1951-1979.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

**IDYLLWILD, CALIFORNIA
OCTOBER 31-NOVEMBER 2, 1978**

NONCONSUMABLE LIVING RESOURCES OF THE CALIFORNIA CURRENT: INTERACTIONS WITH CONSUMABLE RESOURCES AND THEIR EXPLOITATION

LARVAL FISH AND ZOOPLANKTON COMMUNITY STRUCTURE

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ABSTRACT

The macrozooplankton samples from two CalCOFI cruises have been analysed for the abundance of most of the important species of zooplankton. The data show that there are large changes in the degree of numerical dominance from place to place and that the identity of the dominant species varies strongly from sample to sample. In all of these samples larval fish were rare to very rare as compared to other species. Many of these other species must be competitors of larval fish, and some are known predators. The picture that emerges from this study is that fish larvae live in an environment dominated by many different competitors and/or predators and that this biological environment is highly variable.

RESUMEN

Las muestras de macrozooplancton de dos cruceros CalCOFI han sido analizadas para determinar la abundancia de las especies más importantes del zooplancton. Los datos indican que existen grandes cambios de un lugar a otro en cuanto al dominio numérico, y que las especies dominantes varían notablemente en las muestras. En todas estas colectas las larvas de peces eran raras en comparación con la abundancia de otras especies. Muchas de estas especies deben de competir con las larvas de peces, y algunas se sabe que son predadoras. El cuadro que surge de este estudio es que las larvas de peces viven en un ambiente dominado por una gran variedad de competidores y/o predadores, y que este medio ambiente biológico es muy variable.

INTRODUCTION

Larval fish are planktonic and are part of a much larger community of macrozooplankton. In the California Current this community consists of many species of invertebrates of sizes similar to larval fish. Although detailed studies of the feeding habits of many of these species have not been done, we do know that some of them are herbivores, some carnivores, and many seem to be omnivorous feeders on small particles. Some of the copepod, euphausiid, and chætognath species are known to be capable of feeding on larval fishes, and some copepods can eat the same size fraction of food that larval fish seem to eat (Poulet 1978). This implies that there are many species of potential competitors and predators of larval fish. Not only are there many species of competitors and predators present, but their abundance may frequently be greater than that of the fish larvae. Thus the biotic environment of larval fish is very different than that of the adult.

Since recruitment to the adult stock of many fish seems to bear little relationship to the size of the stock that spawned the recruits (Cushing 1975; Lasker and Smith 1977), there must be a large and variable mortality during the pre-recruit stage of life. Much of this happens during the egg and planktonic larval stage. For example, Isaacs (1965) and Lasker and Smith (1977) have shown large temporal variations in mortality rates for both sardine and anchovy, and the rate for anchovy is as high as 99.1% for 1.5- to 9.8-day-old larvae, with a mean of 96% for the years 1953 to 1960. Changes in the percent survival in these early stages could result in large fluctuations in subsequent adult abundance. As Larkin (1978) has pointed out, "A major question in fisheries investigations is thus: What happens to the eggs and the newly hatched larvae?" This question might be rephrased as: What are the various sources of mortality, and are some more important than others? It seems evident that in most populations of organisms there are many sources of mortality, particularly for the younger stages. For example, in terrestrial systems unusual cold snaps or wet or dry periods can kill a lot of young. But these are relatively rare events, and the effects are generally quite evident. In the ocean such abrupt and large changes in circulation or temperature are uncommon (due probably to the high heat capacity of water), and rather few mass mortalities of pelagic organisms have been associated with such temperature anomalies that do occur. More commonly it is variation in the availability of food that is hypothesized to be the critical factor in influencing the variations in larval survival (Cushing 1975; Lasker and Smith 1977). Since larval fish apparently have a threshold level of food concentration below which they do not feed "efficiently," the patchiness of their food and the factors influencing patchiness are important (Lasker and Zweifel 1978). But many invertebrate zooplankters, particularly large copepods, also have threshold levels of food density below which their feeding rate declines (Frost 1974). This phenomenon, also observed in terrestrial vertebrates, is generally referred to as the "functional response" (Holling 1966), and describes the short-term feeding behavior of individuals. However, in the case of populations, there is also a "numerical response" in which the size of the population increases and reaches a plateau with increasing

density of food. This is not an instantaneous measure but rather has a time constant dependent on the population being considered. It is obviously this numerical response that is of importance when considering survival of populations or year classes of larval fish. It is further obvious that competition can occur with other species that also have numerical responses, which co-occur with fish larvae and depend on the same food resource. The nature of the numerical response will depend then not only on the amount of food available but also on the intensity of competition for that food. A related argument may be made when larval fishes themselves are the food resource and other species having numerical responses are the predators.

Thus it seems that, on both observational and theoretical grounds, competition for a limiting resource (food) and predation rate of predators ought to be important factors influencing the survival rate of larval fish populations and the subsequent recruitment to the adult population. What do we know of the intensity of competition and predation of planktonic invertebrates with and on the young larvae of the anchovy, hake, and jack mackerel? Not much. That is, there are very few direct observations, at the population level, of these interactions. However, there are some data that bear on this question.

There are at least two CalCOFI cruises (5804 and 5810) where the species of copepods, euphausiids, thaliacians, chætognaths, pelagic molluscs, and larval fish have all been counted. From these data we can see how many of what kinds of things co-occur with larval fish, the degree to which they dominate (numerically) the fish, and the spatial constancy or coherence of the relationships. None of this information will demonstrate conclusively the importance or even the existence of competition or predation, but it can at least lead us to suspect that both could be occurring and that both could, on occasion, be quite intense.

SPECIES STRUCTURE

The number of species present and their relative abundance is what community ecologists call species structure. This may be illustrated by histograms of the rank order of species abundance. From these we can determine aspects of the position of fish larvae in the zooplankton community. Figures 1 and 2 are examples of such diagrams and are based on the zooplankton species counts from CalCOFI Cruise 5804. We selected these for presentation as rank order histograms because they represent the near- and offshore northern area, the central sector, and the near- and offshore southern sector of the system. There are several things about the ecology of larval fishes these histograms tell us. It is evident that, at the locales sampled, larval fish were *rare* species in the

zooplankton community. Further, there are usually many other species of similar sized zooplankton present, some of which are known to be small particle feeders, others are carnivores capable of eating young fish.

If we visualize a larval fish moving randomly about in its immediate environment (say the volume of water of an average CalCOFI net tow), then the probability that it will contact one of these other species will depend on the abundance of that species and its degree of aggregation. The probability that the second individual it meets will be the same species as the first depends on the relative abundance of the two, and so forth for the whole community. It is clear that at Station 60.90 the chances of a larval fish (which were so rare in this sample they do not even appear on the histogram) meeting a *Eucalanus californicus* are very high indeed (Figure 1). Its biotic habitat is strongly dominated by a single species at Station 80.60, but this time it is *Calanus helgolandicus** (Figure 2). If either of these two species is capable of eating the same food as the fish and with anywhere near the same efficiency, then these must be severely competitive environments for the fish. There are also samples where larval fish are strongly outranked by known carnivores: Station 100.40 for example, where three species of chætognaths (*Sagitta*) and the copepod *Candacia* are much more abundant than fish (Figure 2).

In all of the Cruises 5804 and 5810 samples that were analyzed, larval fish were rare species in the community. That is, their biotic habitat was strongly dominated by species of potential competitors and predators. An impression of the areal extent of these relationships may be gotten by merely examining the plots of larval fish distribution and abundance and those of species of copepods, chætognaths, euphausiids, and so forth in the CalCOFI Atlas series. It is evident that on a broad scale large numbers of these invertebrates are present where larval fish are found (Figure 3). The temporal extent may also be examined in a cruder way (i.e. above the species level) by comparing larval fish patterns with those of the taxa Copepoda, Amphipoda, Chætognatha, etc., where there are time series data available (Fleminger et al. 1974).

CONSTANCY OF STRUCTURE

The histograms show very large differences in the degree of numerical dominance of species. That is, some rank order curves are very steep; others are more flattened. This can be interpreted to mean that when a larval fish is in a locale where dominance is strong it will very frequently encounter one or a few species over its ambit, but where dominance is not strong it will encounter a wide variety of species over the same ambit. The shape of these

Calanus helgolandicus = C. pacificus in the California Current.
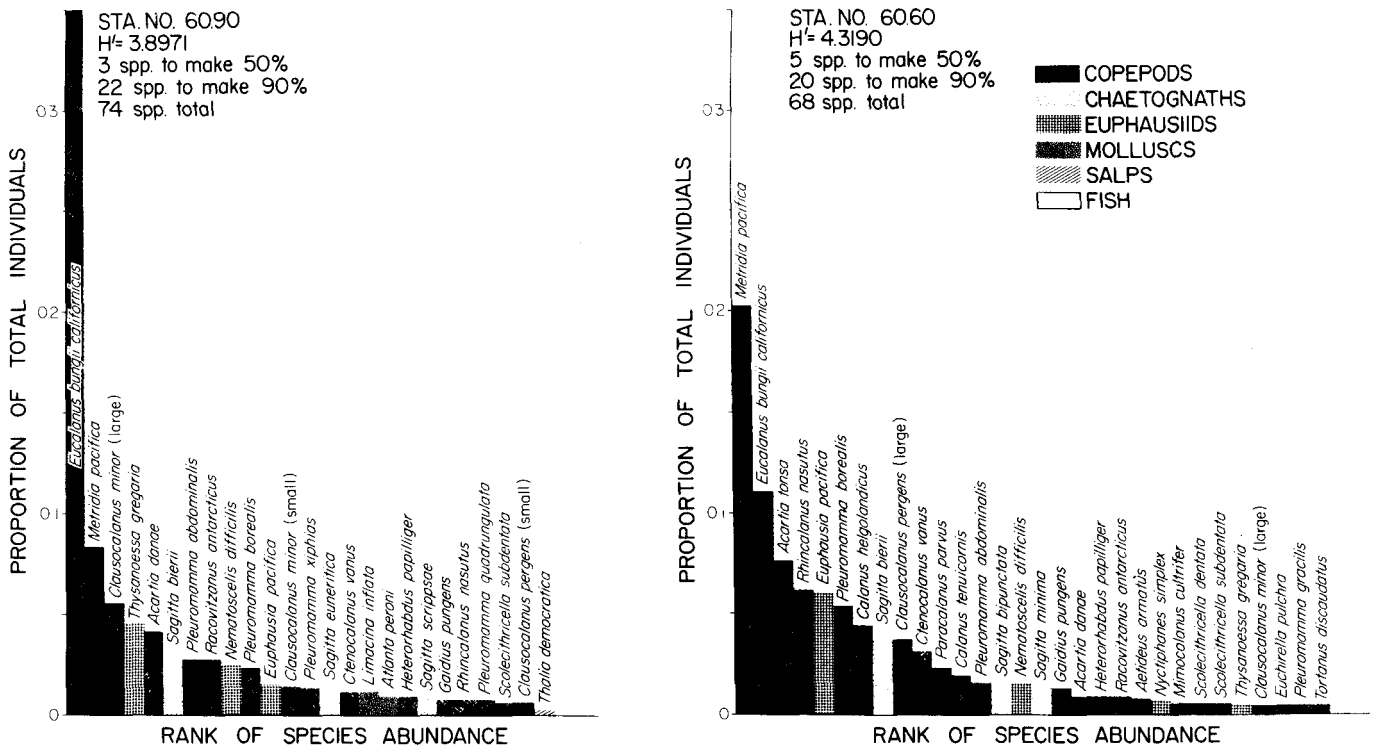
Figure 1. The rank order of abundance of zooplankton species caught by a 1-m-diameter net of 505 μm mesh size. Only the taxa shown in the key were counted to species. The category "molluscs" includes Thecosomata, Gymnosomata, Heteropoda, and larval Cephalopoda. The category "salps" includes only the orders Salpida and Doliolida. "H" is the Shannon diversity measure as defined in the text. Not all of the rare species are shown on the histograms. The stations are from line 60 off San Francisco.

curves can be quantitatively expressed by the diversity index $H' = -\sum_{i=1}^{S} p_i \log_2 p_i$ (where p_i is the proportion of the sample that belongs to the ith species). This index has an unusually large range in the California Current as compared, for example, to the North Pacific Central Gyre (Figure 5; McGowan 1977).

Another aspect of community species structure that seems highly variable in the California Current is that of constancy of rank order of macrozooplankton species. The histograms (Figures 1 and 2) show that the rank order of species changes dramatically from sample to sample. This may be expressed quantitatively by use of the Whittaker percent similarity index. This index expresses the degree to which one sample resembles another with respect to species proportions and is most strongly influenced by dominants. Figure 4 shows a series of these at two locales in the California Current and one in the Central Gyre. Again, we see that species proportions may vary widely on this scale of sampling in the California Current. Total macrozooplankton biomass and phytoplankton biomass also seem to be highly variable in both time and space as compared to the North Pacific Central Gyre (Figure 5). Thus the biotic habitat of larval fish in the California Current is much more variable than that of larvae in the Central Gyre.

DISCUSSION

The picture of the biotic habitat of California Current fish larvae that emerges from this analysis is one of extreme variability or heterogeneity. In some places, part of any one population of larvae may be heavily dominated by one or two species of potential competitors; in other places, there may be many competitors, none of which are particularly dominant. In still other places, another part of the population is experiencing a habitat where potential predators are far more abundant than are the larval fish.

This apparent heterogeneity of biotic habitat may to some degree be a product of our sampling scheme. That is, the relatively long oblique net tows may be integrating the plankton in such a way that many species which do not actually occur very close together in the ocean are caught together in the same tow. But larval fish also integrate the environment by simply swimming around in some sort of a daily ambit. Therefore, while the instantaneous habitat may not look like what is caught in a net tow, the integrated habitat over a larva's two or three day ambit may resemble what we see in a net tow quite well. There is an additional problem in interpreting these data because of the spacing of the CalCOFI tows. The average distance between stations is large (several tens of kilometers), and the community structure and its constancy

STA. NO. 80.60
H'= 2.2000
I sp. to make 50%
9 spp. to make 90%
74 spp. total

PROPORTION OF TOTAL INDIVIDUALS

RANK OF SPECIES ABUNDANCE

STA. NO. 100.60
H'= 5.0378
8 spp. to make 50%
32 spp. to make 90%
92 spp. total

PROPORTION OF TOTAL INDIVIDUALS

RANK OF SPECIES ABUNDANCE

STA. NO. 100.40
H'= 5.1298
8 spp. to make 50%
35 spp. to make 90%
80 spp. total

PROPORTION OF TOTAL INDIVIDUALS

RANK OF SPECIES ABUNDANCE
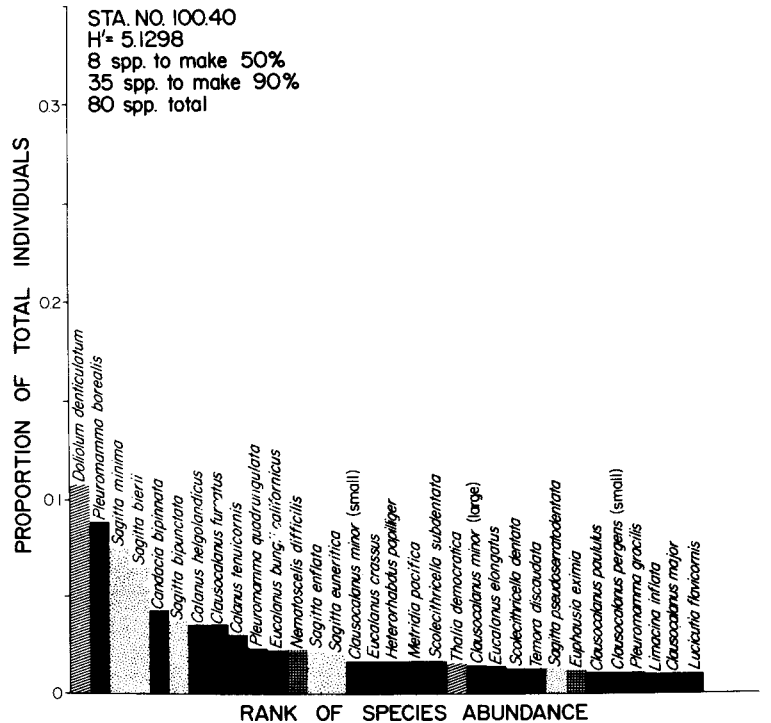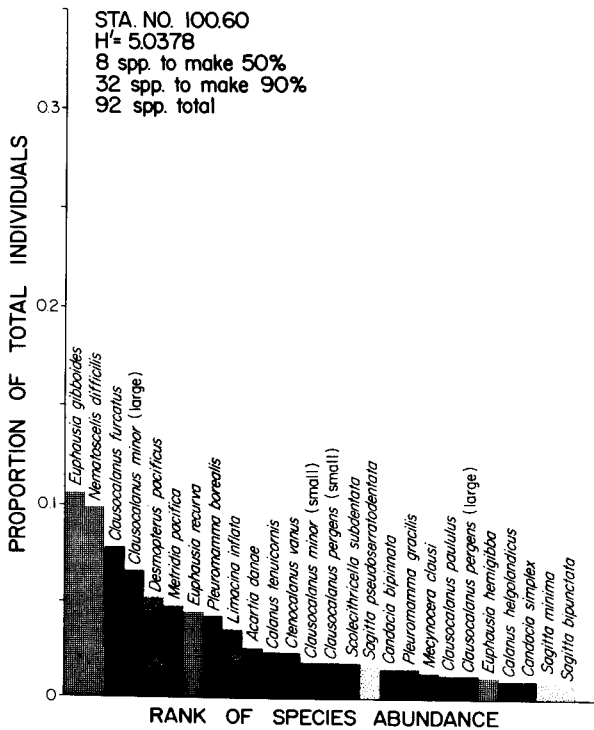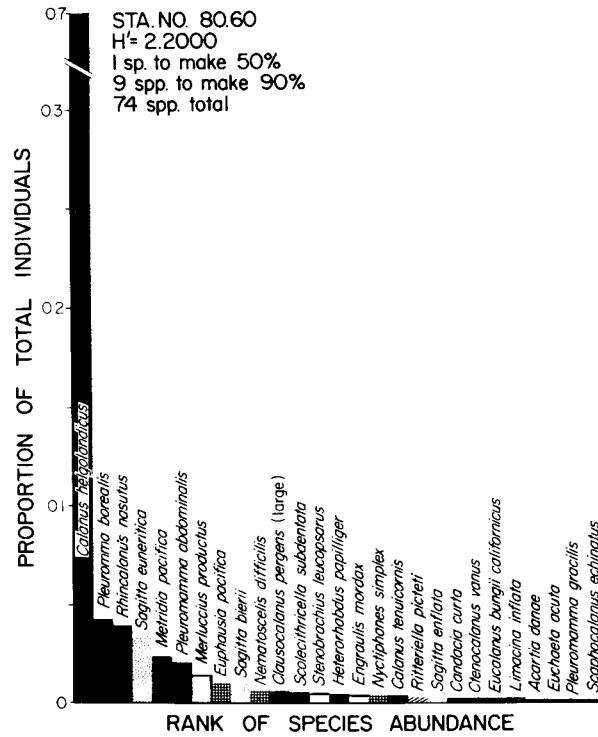
CALCOFI CRUISE 5804
30 MARCH–27 APRIL 1958

Figure 3. Contoured charts of the estimated abundance of the anchovy (*Engraulis mordax*) and three species of macrozooplankton. All estimates came from the same samples. (*Calanus helgolandicus* = *C. Pacificus*; from CalCOFI Atlases Nos. 2, 3, 5, and 9).

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PERCENT SIMILARITY

	A2 1326	A4 1230	A5 1230	A6 1230	A7 1255	A8 1305	A9 1250
A1 1425	72.80	66.81	63.18	69.47	68.69	64.42	64.98
A2 1326		71.63	67.75	71.19	75.94	64.64	68.05
A4 1230			69.00	70.52	62.81	66.46	67.82
A5 1230				71.49	68.78	66.58	64.46
A6 1230					77.94	70.68	77.13
A7 1255						72.88	75.21
A8 1305							69.78

$$\overline{X} = 69.7 \; D$$
$$\overline{X} = 70.0 \; N$$

PSI
CALIFORNIA CURRENT

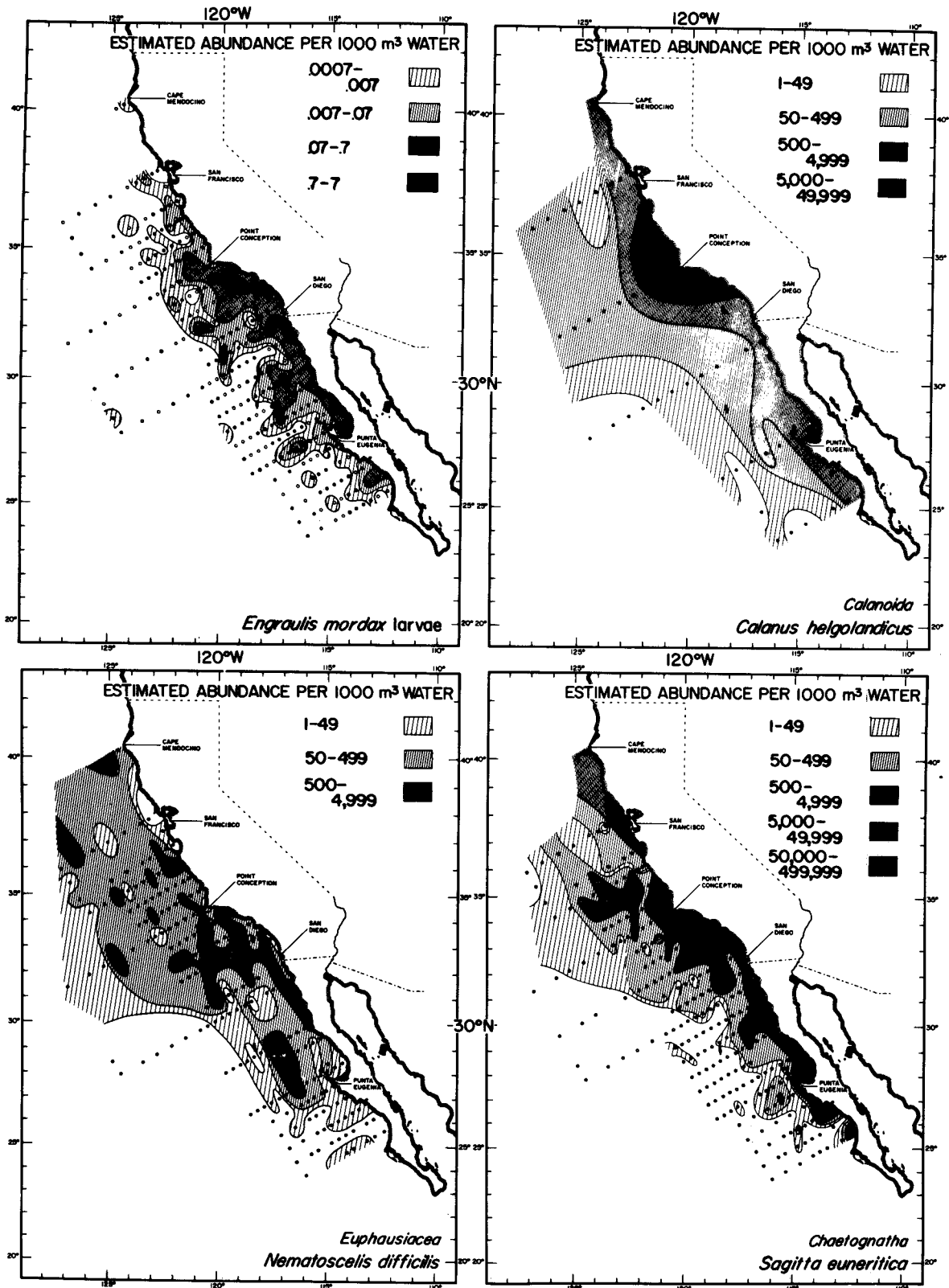|	.80	.60	.70	.80	.90	.100
80.60			79.4	39.6	19.3	14.7
.70				57.7	32.5	12.0
.80					41.9	26.8
.90						43.3
.100						

POINT CONCEPTION

$$\overline{X} = 37.2$$
$$Md = 36.0$$

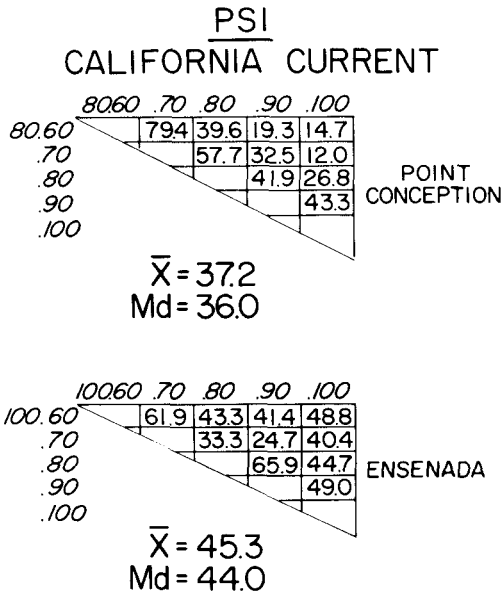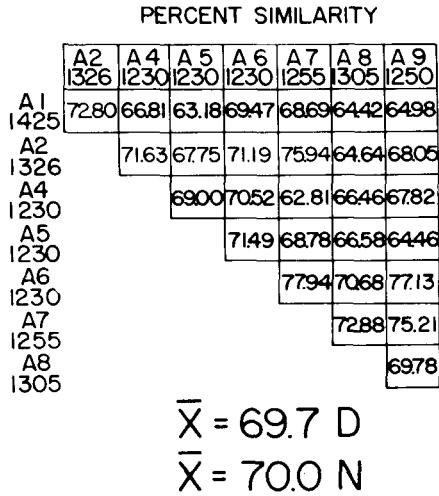|	100	60	70	80	.90	.100
100.60			61.9	43.3	41.4	48.8
.70				33.3	24.7	40.4
.80					65.9	44.7
.90						49.0
.100						

ENSENADA

$$\overline{X} = 45.3$$
$$Md = 44.0$$

Figure 4. The percent similarity index (Whittaker and Fairbanks 1958) compares the degree to which one sample resembles another with respect to species proportions. The upper matrix is from a set of stations (A1 through A9) taken in the North Pacific Central Gyre. The lower matrix is from two sets of stations taken in the California Current. The mean PSI from the Gyre is much higher than those from the California Current (from McGowan 1977).

INDEX OF DISPERSION BIOMASS

CHLOROPHYLL

		$s^2/\overline{x}$	n
CAL. CURRENT	10 m	0.3	18
	20 m	0.9	18
GYRE	25 m	0.012	18
	75 m	0.013	18

ZOOPLANKTON

CAL. CURRENT	north	1300.8	69
	central	73.3	78
	south	16.3	75
GYRE		3.6	52

DIVERSITY

GYRE	CAL. CURRENT
H': 4.5 - 4.9	H': 1.8 - 5.1

Figure 5. A comparison of the variability of phytoplankton (as estimated by chlorophyll concentration) and zooplankton biomass in the California Current and the North Pacific Central Gyre. In both cases the index of dispersion is orders of magnitude higher in the California Current. The diversity measures from copepod species counts in the Gyre show a much narrower range than do similar data from the California Current.

could be quite different on much smaller scales. But larval fish populations occur on very large scales, much larger than the station spacing, so it seems almost certain that the heterogeneity of the entire population's biotic habitat is great.

If competition for food or predation are important in larval survivorship, then this should be demonstrated directly, and such studies probably must be done on small spatial and short temporal scales. But populations grow or decline on large spatial scales. If availability of food, competition, and predation are important regulators of entire larval fish populations, then these factors must also exert their influence on large time-space scales. Somehow the results of small-scale studies must be extrapolated to the population scale. Alternatively, such studies might be done simultaneously in several locales scattered throughout the range of the larval population so that the spatial coherence of the interaction can be estimated.

It would be very useful for planning such studies if we could detect some overall trends in time and space in the co-occurrence of larval fish with dominant species of invertebrates. But relatively few zooplankton samples have been analyzed with this degree of completeness and, in view of the large variability in the community structure, it seems unlikely to be a very easy matter to detect trends or consistent patterns of co-occurrence. This carries with it the corollary that it will be very difficult to select appropriate species of zooplankters to study in terms of their competitive abilities with fish larvae. Since there seem to be many of these and the "important" ones seem to change from place to place, which one should be selected for study? The same argument may be made for predators.

There are, however, some trends that are apparent, and

these give us some additional insight on the biotic habitat of larval fish. There is an areal pattern in diversity. Figure 6 shows a contoured plot of this index and it is evident that north of Point Conception there is a large, offshore tongue of low diversity that appears to be intruding from the north. In the central sector, the Southern California Bight region, diversity is high. From Punta Eugenia to the south there is another tongue of low diversity, nearshore and apparently intruding from the south. Cruise 5810 shows a similar pattern. The "intrusions" are consistent with what we know of the gross circulation of the system. The magnitude of the diversity index, H', is sensitive to both degree of dominance and number of species present and, in our data, is very well correlated with number of species (Figure 7). From this diversity map and the two aspects of diversity (dominance and number of species), we can see that in the north, fish tend to live in a habitat with relatively few other species but where dominance by one or a few species is strong. In the central sector, the fish are exposed to a habitat where there are relatively many species present but where dominance is much less pronounced.

The data for these diversity maps came from only two

Figure 7. Diversity index (H') as a function of number of species of macrozooplankton $r_d = 0.7$ ($P < .001$).

cruises taken in a year when there was an anomalously warm California Current. Therefore, the diversity trend we see could also be anomolous and not representative of the system in general. But in addition to being consistent with the circulation, the generality of these maps is implied by long-term studies of biogeography and intuitive impressions one gains from perusal of the CalCOFI zooplankton species atlases. It would be of practical and theoretical interest to see if larval fish mortality was in any way correlated with this simple pattern.

ACKNOWLEDGMENTS

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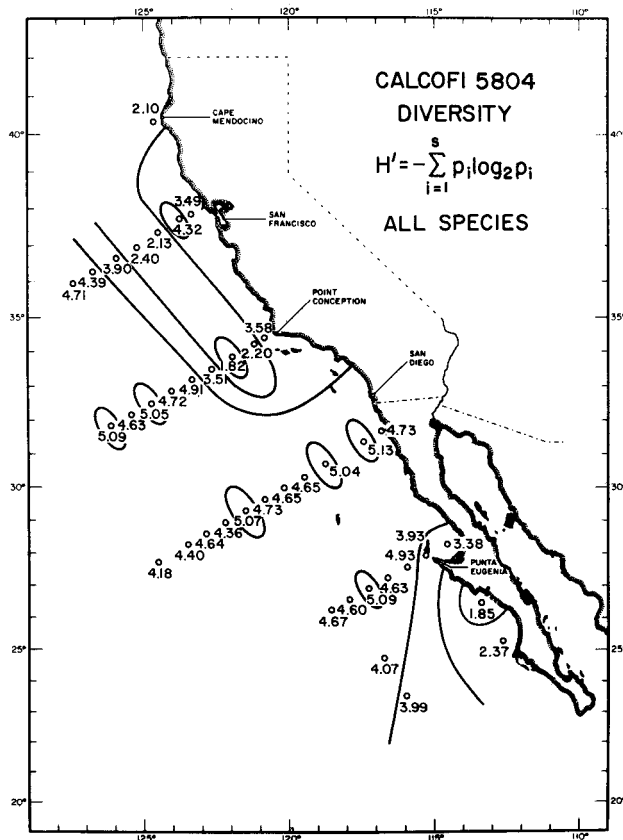
Figure 6. A contoured map of diversity measures. In the northern part of the California Current, diversity is low offshore. In the central sector, it is generally high. In the south, it is low nearshore.

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DIVERSITY AND ECOLOGICAL ROLES OF NONCOMMERCIAL FISHES IN CALIFORNIA MARINE HABITATS

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ABSTRACT

The marine fish fauna of California is highly diverse and consists of about 550 species of varied origin and complex distribution. Species richness is greatest in southern California and gradually declines northward in a pattern that is significantly correlated with increasing latitude and decreasing minimum surface temperature. Greater activity with regard to species range terminations occurs in southern California than in central and northern California and is consistent with the higher species richness in southern California waters.

Less than 3% of the species of this diverse fauna contributes significantly to the California commercial fish catch. Many noncommercial species, therefore, perform essential roles in the habitats occupied by economically important fishes. The noncommercial species may function as 1) predators or prey, thus as direct trophic links in the food chain of commercial species; 2) competitors of exploited species; or 3) fishes which otherwise, by their ecological position, affect community structure and indirectly influence economically important populations.

The fish communities and certain ecologically important species are briefly described for each of seven major habitats in California marine waters: 1) deep midwaters, 2) epipelagic zone, 3) coastal demersal region, 4) kelp beds/subtidal reefs, 5) rocky intertidal zone, 6) harbors, and 7) bays and estuaries. Bays and estuaries are emphasized in the concluding statements as important but diminished and altered habitats in need of preservation and wise management.

RESUMEN

La fauna de peces marinos de California es sumamente diversa y comprende unas 550 especies que proceden de varias regiones y que presentan una distribución compleja. La riqueza en especies es mayor en el sur de California y disminuye gradualmente hacia el norte siguiendo un patrón que se relaciona con la latitud y el descenso en la temperatura mínima de las aguas de superficie. En el sur de California se encuentran más límites de zonas de distribución de las especies que en el centro y norte de California, lo cual concuerda con el mayor número de especies que habitan las aguas del sur de California.

Menos del 3% de las especies de esta fauna diversa contribuyen a la captura comercial de los peces de California. Por lo tanto, muchas especies que carecen de valor comercial desempeñan un papel esencial en el hábitat ocupado por los peces de importancia económica. Las especies que no son comerciales pueden funcionar como 1) predadores o presas, así son eslabones tróficos directos en la cadena alimenticia de las especies comerciales; 2) competidores de las especies explotadas; ó 3) peces que, por su posición ecológica, afectan la estructura de la comunidad e influyen indirectamente en las poblaciones de importancia económica.

Se describe brevemente las comunidades de peces y ciertas especies de importancia ecológica para cada uno de los siete hábitats más importantes en las aguas oceánicas de California: 1) zona profunda mesopelágica, 2) zona epipelágica, 3) región demersal costera, 4) lechos de algas marinas/arrecifes sublitorales, 5) zona de entre mareas rocosa, 6) puertos, y 7) bahías y estuarios. En las conclusiones se señala que las bahías y estuarios son importantes, pero estos hábitats se alteran y por eso necesitan cuidados para conservarlos.

INTRODUCTION

A primary purpose of this paper is to focus attention on the diversity and complexity of the California marine fish fauna especially beyond the relatively small number of species that contribute to the commercial catch. Noncommercial forms have both direct and indirect relationships with economically important species. The "other" fishes may be predators or prey of exploited species, competitors of commercial species, or in other ways affect community structure and secondarily influence economically important populations. In this account, the fish communities are briefly described and the roles of ecologically important and interesting species emphasized in seven major marine habitats: 1) deep midwaters; 2) epipelagic zone; 3) coastal demersal region; 4) kelp beds/subtidal reefs; 5) rocky intertidal zone; 6) harbors; and 7) bays and estuaries.

DIVERSITY AND DISTRIBUTION PATTERNS OF CALIFORNIA MARINE FISHES

The fishes occurring off the coast of California comprise a rich fauna of varied origin and complex distribution. As recently shown by Horn and Allen (1978), diversity (number of species) is greatest in southern California gradually declining northward to Alaska in a pattern that is highly correlated with increasing latitude and decreasing minimum surface temperature. The steep decline in the number of California fishes occurring off Baja California and southward is apparently related (Horn and
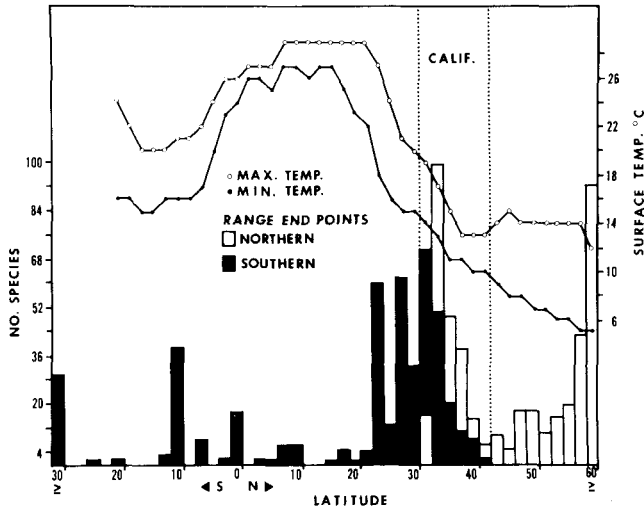
Figure 1. Frequency of northern and southern end points of geographic ranges of 499 California coastal fish species at each degree of latitude over the total distributional range (≥ 30°S to ≥ 60°N. The bars representing the number of northern and southern end points originate at the basal line. The bars for northern and southern values at 32°N are reversed in position relative to other latitudes because the open (northern) bar represents a smaller value than the black (southern) bar only at this latitude. Maximum and minimum surface temperatures are derived from monthly means for the 14-year period 1949-62. (All data from those compiled by Horn and Allen 1978.)

Allen 1978) not only to changing oceanographic conditions but to competition with the large tropical fauna south of California that is greater than that with the small boreal fauna which occurs north of California. The distribution of range end points of California fishes (Figure 1) serves to emphasize the richness and multiple affinities (especially northern and southern) of the fauna and to illustrate the relationship of diversity to surface sea temperatures. Frequency of both northern and southern terminations of species ranges are bimodal in pattern with the proximal modes of each occurring in southern California. The high concentration of range terminations in southern California is to be expected since it is the region of greatest species richness. Increased diversity in southern California is probably related (Horn 1974) to environmental heterogeneity as expressed by the expansive borderland, the insular habitats adjacent to deep basins, and the converging water masses characteristic of the region.

Species with southern affinities tend to have northern range end points off southern California, and southern end points off Baja California or much farther south off Central or South America. Fishes with northern affinities most frequently have northern range end points at high latitudes off British Columbia or Alaska and southern end points off southern California and northern Baja California. Point Conception (34.5°N), a widely recognized faunal boundary, is a more effective barrier for southern species than for northern species. Oceanographic condi-

tions, especially of temperature in the Point Conception area (Figure 1), are apparently more critical for southern species than for northern ones.

Miller and Lea (1972) listed 554 species as occurring off California. Of these, 439 are found in coastal waters (< ~ 120-m depth), 48 in meso- and bathypelagic zones (about 25% of the total midwater fauna), and 67 benthic forms found at depths greater than 120 m. Eleven families account for 256 species (46%) of Miller's and Lea's (1972) total list (Table 1). This group of families illustrates the multiple origins of the fauna since it includes families of temperate affinities (Cottidæ, Pleuronectidæ, Embiotocidæ, and Agonidæ), of tropical-subtropical relationships (Scombridæ, Carangidæ, Gobiidæ, Clinidæ, Carcharhinidæ, and of deep-water origin (Myctophidæ). Scorpænidæ is primarily a family of tropical affinity, although the subfamily Sebastinæ (containing the diverse genus *Sebastes*) has a temperate-boreal distribution.

COMPOSITION OF THE CALIFORNIA COMMERCIAL FISHERY

Only a small percentage of California species occur in the commercial catch. No more than about 120 species are among the annual landings and shipments in California (e.g. McAllister 1976). However, most of these species are rarely captured or otherwise contribute insignificantly to the total catch. The California commercial fishery is overwhelmingly dominated by pelagic wetfish (northern anchovy, *Engraulis mordax*, and jack mackerel, *Trachurus symmetricus*) and tunas (Table 2). The tunas, mainly yellowfin (*Thunnus albacares*) and skipjack (*Euthynnus pelamis*), are primarily caught in tropical waters outside of California (e.g. about 94% of the 1972 catch, Bell 1974). Trawl fisheries are relatively more important from Santa Barbara northward but con-

TABLE 1
The 11 Most Speciose Families of Fishes in California Waters.[1]

Family	Common name	Number of species
Scorpænidæ	Thornyheads, scorpionfishes, rockfishes	62
Cottidæ	Sculpins	42
Myctophidæ	Lanternfishes	32
Pleuronectidæ	Right-eye flounders	20
Embiotocidæ	Surfperches	19
Agonidæ	Poachers	17
Scombridæ	Mackerels and tunas	15
Carangidæ	Jacks and pompanos	13
Gobiidæ	Gobies	12
Clinidæ	Clinids	12
Carcharhinidæ	Requiem sharks	12
		256

[1]Based on Miller and Lea (1972).

tribute only a small percentage to the total California catch. In 1974 and 1975, only slightly more than 2% of the total fauna (about 13 species) made up 90% of all landings and shipments (Table 2). The significant point is that only a small fraction of a rich fauna contributes to the commercial fishery. This fact magnifies the importance of noncommercial species in terms of both their ecological influence on economically valuable fishes and their contribution to the structure of marine fish communities as a whole.

MAJOR MARINE HABITATS

Deep Midwaters

The midwater environment off California, especially southern California, provides a complex and heterogeneous habitat for deep-sea fishes. Three converging water masses, the California Current itself and a series of deep basins in the southern California borderland, result in a rich, dynamic midwater fauna. In general, the diversity of the mesopelagic and bathypelagic faunas increases with vertical expansion of their habitats offshore. Both resident and transient species occur and assort themselves by depth and basin.

The size of the deep-sea fauna is difficult to determine and somewhat artificial to consider because of the transitional and dynamic nature of the environment and its fish communities. According to estimates of Miller and Lea (1972), approximately 200 species comprise the fauna. Fitch and Lavenberg (1968) provided a list of 260 species, but their account included bottom-dwelling forms.

Probably well over one-half of California deep midwater species occurs off southern California.

The three numerically most abundant deep-sea pelagic fish families in southern California waters are Myctophidæ, Gonostomatidæ, and Bathylagidæ. The species most frequently encountered are two myctophids, Stenobrachius leucopsarus and Triphotorus mexicanus, (Paxton 1967; Ebeling et al. 1970) and a bathylagid, Leuroglossus stilbius (Ebeling et al. 1970). Based on larval abundance in the California Current (Table 3), these species and a fourth, the gonostomatid Vinciguerria lucetia, are the most common deepwater fishes.

The great abundance of the above three families is illustrated by their high ranking among families contributing to larval numbers in the upper 150 m of the California Current (Table 4). According to Ahlstrom et al. (1976), myctophids, on the average, make up 50% of all fish larvae in any oceanic plankton and may have the greatest

TABLE 2
Landings and Shipments of the Top 10 Commercial Fishery Species in California for 1974 and 1975.[1]

	1974			1975	
Species	Millions of lbs.	% of Total	Species	Millions of lbs.	% of Total
Yellowfin tuna	263	28.0	North anchovy	317	32.4
Skipjack tuna	230	24.5	Yellowfin tuna	262	26.7
Northern anchovy	165	17.6	Skipjack tuna	121	12.3
Albacore	89	9.5	Albacore	58	5.9
Market squid	29	3.1	Jack mackerel	37	3.8
Jack mackerel	25	2.7	Pacific bonito	32	3.3
Rockfish	21	2.3	Rockfish	24	2.4
Dover sole	19	2.0	Market squid	24	2.4
Pacific bonito	19	2.0	Dover sole	23	2.3
Bluefin tuna	13	1.4	Bluefin tuna	18	1.8
		93.1%			93.3%

1974		SUMMARY		1975
20.3%	(2 species)	Wetfish	36.2%	(2 species)
65.4%	(5 species)	Tunas	50.0%	(5 species)
2.3%	(∼5 species)	Rockfish	2.4%	(∼5 species)
2.0%	(1 species)	Flatfish	2.3%	(1 species)

∼13 species (2.3% of total fauna) comprise 90% of catch

[1]Based on McAllister (1976) and Pinkas (1977).

TABLE 3
Most Abundant Species of Larvae of the Three Principal Families of Deep-Sea Pelagic Fishes in California Current Region off California and Baja California 1955-1960.[1]

Family and species	Mean % contribution to deep-sea total
Myctophidæ	
Triphoturus mexicanus	14.5
Stenobrachius leucopsarus	10.1
Gonostomatidæ	
Vinciguerria lucetia	31.9
Bathylagidæ	
Leuroglossus stilbius	15.2

[1]Based on Ahlstrom (1969).

TABLE 4
Mean Percentage Contribution of Principal Fish Families to Larval Abundance in California Current Region off California and Baja California 1955-1960.[1]

Family	Mean % contribution
Engraulidæ	41.6
Gadidæ	12.9
Myctophidæ[2]	11.2
Gonostomatidæ[2]	10.8
Scorpænidæ	5.9
Bathylagidæ[2]	5.0
Bothidæ	3.1
Clupeidæ	2.6
Carangidæ	2.2
Scombridæ	0.4
Pleuronectidæ	0.4

[1]Based on Ahlstrom (1969).
[2]Deep-sea pelagic families.

biomass of any vertebrate family. Although such statements of the prodigious abundance of lanternfishes frequently generate ideas for harvesting these fishes, their small size and diffuse distribution tend to weaken the prospects for widespread commercial exploitation.

Lanternfishes apparently play very important ecological roles in pelagic food webs off California. The proximity of the deep-sea basins to coastal and epipelagic waters increases the probability of interaction of these abundant fishes with a variety of other organisms in the region. Ahlstron (1969) emphasized the forage role of myctophids and gonostomatids and recognized them as a vital link between the zooplankton community and the larger vertebrate predators including both economically and æsthetically important species (Figure 2). These small midwater fishes, especially the lanternfishes, appear to occupy a position in the trophic structure of offshore, basin waters similar to that of northern anchovy in more inshore, shallower waters.

Epipelagic Zone

The epipelagic fish fauna may include at any given time a mixture of species from a variety of habitats including deep midwaters, inshore bottom-associated habitats, as well as offshore surface layers. Trophic interactions in this environment are possible among a diverse array of species from dissimilar habitats. Horn (1974) provided a list of 80 species in 30 families, all of which are epipelagic to a certain degree in southern California waters. The list could be expanded since, for example, the carcharhinid sharks were not included. The present account focuses on two truly epipelagic species that occupy important but different trophic positions in California waters: 1) Pacific saury, Cololabis saira, a low-level carnivore and forage species, and 2) blue shark, Prionace glauca, a high-level carnivore.

Pacific saury is a cold temperate scomberesocid fish of the eastern North Pacific that occurs (Frey 1971) in greatest concentrations at distances of 40 to 120 miles (64 to 193 km) offshore. Although the species has been fished commercially by the Japanese in the eastern North Pacific (Frey 1971) and has been the subject of exploratory research as a potential resource (Smith and Ahlstrom 1970), its primary ecological importance lies in its utilization as forage by a variety of offshore predators (Figure 3). Immature sauries are a major food item of albacore (Frey 1971). George Hunt (personal communication, see also Hunt and Butler this volume) has noted that western gulls switch to alternate prey including Pacific saury when northern anchovy are apparently in low numbers and that as much as 50% of the diet of western gull chicks may be Pacific saury during certain years. Saury feed on large copepods, amphipods, euphausiids, and common fish larvae such as those of northern an-

chovy; thus, like the deeper living myctophids, they form a trophic link between zooplankton and higher level carnivores. Energy transfer both to and from Pacific saury includes commercially important fish species.

The blue shark is probably the most abundant of the larger noncommercial shark species in California waters. It is frequently observed at the surface and during diving activities especially around the Channel Islands. Pelagic longlining operations in the eastern North Pacific (Kato 1969; M.H. Horn unpublished data) have caught blue sharks on 30-50% of the hooks, a very high catch rate for any species with this type of gear. This shark is a voracious, primarily nocturnal, carnivore known to feed on a variety of abundant invertebrates and fishes (Figure 4). The diet includes the commercially important market squid (Loligo opalescens) and the two most important species in the pelagic wetfish industry, northern anthovy and jack mackerel. Another food item, pelagic red crab (Pleuroncodes planipes), is also significant prey of tunas off California and Baja California (e.g. Blackburn 1969; Pinkas et al. 1971). In a recent study, Tricas (1977)
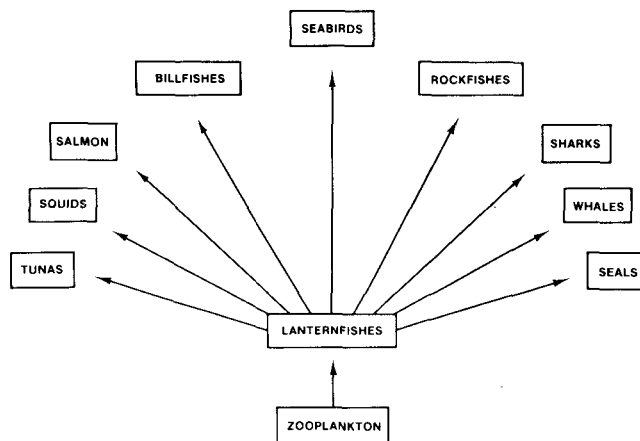
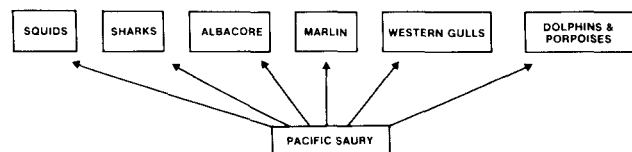Figure 2. Prey and some known predators of lanternfishes (Myctophidæ) in California waters.

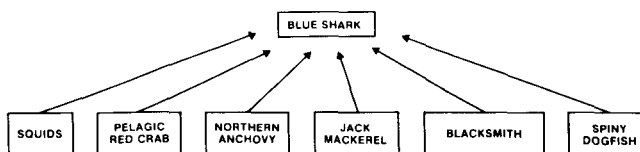Figure 3. Some known predators of Pacific saury (Cololabis saira) in California waters.

Figure 4. Some known prey of blue shark (Prionace glauca) in California waters.

found *Histioteuthis heteropsis* to be the dominant pelagic cephalopod in the diet, whereas the market squid represented the major portion of onshore squid prey, especially during winter inshore spawning of the squid. Northern anchovy was the principal fish prey item through the year of the Tricas (1977) study. Sciarrotta and Nelson (1977) suggested that evening-twilight onshore movements of blue shark in March to early June were due to nearshore abundance of squid and reduced availability of prey offshore. Conversely, the offshore pattern of late June to October may be a result of reduced squid populations nearshore and increased populations of jack mackerel and northern anchovy offshore. Blue sharks move over long distances (Tricas 1977; Sciarrotta and Nelson 1977) and do not maintain local populations (Tricas 1977).

Coastal Demersal Region

Trawl Surveys

Trawl studies conducted over the past several years, especially those by the Southern California Coastal Water Research Project (SCCWRP), of the fish populations associated with the bottom in the shelf waters of southern California have provided a variable but recurrent list of the abundant species in this habitat zone out to approximately 100-m depth. In terms of numbers of species, the list (Table 5) is dominated by flatfishes (Bothidæ, Cynoglossidæ, Pleuronectidæ) and rockfishes (Scorpænidæ). Of the 26 species that accounted for 95% of the catch in the SCCWRP trawls off Orange County (Table 5), only a few (e.g. Dover sole, English sole, northern anchovy) are of commercial importance. The ranking, therefore, identifies abundant, noncommercial species that presumably play significant roles in community structure and undoubtedly interact with economically important species.

Speckled sanddab, the most abundant fish in the Orange County surveys, is a small (< 170 mm TL) flatfish extremely numerous on sandy bottoms. Its diet includes larval and post-larval northern anchovy (Feder et al. 1974), and the fish is most likely an important forage item for larger species. Pacific sanddab, the second most abundant species in the SCCWRP trawls, is a larger (< 406 mm TL), longer lived species that is of some commercial importance in central and northern California and is also caught in the sport fishery. Because of its abundance and small size, it should, however, be considered as a significant forage species as well. According to Feder et al. (1974), the pelagic young are fed upon by tunas and other pelagic fishes and the adults by fishes from a variety of habitats. Both speckled and Pacific sanddabs occur in the diets of seabirds off California (Baltz and Morejohn 1977).

Little is known of the life history and ecology of several of the most abundant trawl-caught species. Fishes in this category include yellowchin sculpin, roughback sculpin,

Common name, scientific name	Number of individuals	% of total catch
Speckled sanddab, *Citharichthys stigmaeus* ...	19,083	16.8
Pacific sanddab, *Citharichthys sordidus*	15.418	13.5
Yellowchin sculpin, *Icelinus quadriseriatus*	12,232	10.7
Dover sole, *Microstomus pacificus*	7,361	6.5
Stripetail rockfish, *Sebastes saxicola*	6,852	6.0
White croaker, *Genyonemus lineatus*	6,090	5.3
California tonguefish, *Symphurus atricauda* ...	5,503	4.8
Plainfin midshipman, *Porichthys myriaster* ...	4,354	3.8
Calico rockfish, *Sebastes dallii*	4,028	3.5
Halfbanded rockfish, *Sebastes semicinctus* ...	4,009	3.5
Pink surfperch, *Zalembius rosaceus*	3,322	2.9
Slender sole, *Lyopsetta exilis*	2,606	2.2
English sole, *Parophrys vetulus*	2,086	1.8
Blackbelly eelpout, *Lycodopsis pacifica*	1,961	1.7
Rex sole, *Glyptocephalus zachirus*	1,605	1.4
Northern anchovy, *Engraulis mordax*	1,566	1.4
Roughback sculpin, *Chitonotus pugetensis* ...	1,562	1.4
Queenfish, *Seriphus politus*	1,545	1.4
Longspine combfish, *Zaniolepis latipinna*	1,536	1.4
Splitnose rockfish, *Sebastes diploproa*	1,491	1.3
Shiner surfperch, *Cymatogaster aggregata* ...	986	0.9
Hornyhead turbot, *Pleuronichthys verticalis* ...	846	0.7
Blacktip poacher, *Xeneretmus latifrons*	779	0.7
Shortspine combfish, *Zaniolepis frenata*	632	0.6
Bigmouth sole, *Hippoglossina stomata*	491	0.4
White surfperch, *Phanerodon furcatus*	387	0.3
	108,331	95.2

[1]Based on Mearns (1977).

shortspine combfish, longspine combfish, and calico rockfish. The last species is a small rockfish that has had high recruitment in the past four or five years, particularly in 1975 (A.J. Mearns, abstract, 1978 CalCOFI meeting). Variation in the Orange County trawl catches was shown (Mearns 1977) to be largely due to fluctuations in recruitment of juvenile rockfishes (especially calico, stripetail, half-banded, and splitnose), which, in turn, were related to changing oceanographic conditions.

Deep Demersal Habitat

The demersal fish fauna at depths greater than 200 m off California is poorly known. The information that is available has come mainly from photographs taken with deep-sea cameras and a small number of recorded trawls (Fitch 1966; Allen and Mearns 1977), all taken at depths of less than 700 m. Allen and Mearns (1977) found that, although individual fishes found at depths greater than 200 m weighed five times as much as fishes taken in shallow waters, fish abundance, biomass, and numbers of species were reduced at the greater depths. The most frequently occurring species in their deep trawls were Dover sole, sablefish (*Anoplopoma fimbria*), longspine

thornyhead (*Sebastolobus altivelis*), shortspine thorny-head (*S. alascanus*) and splitnose rockfish. Sablefish have recently become the subject of an increasingly large trap fishery in southern California, particularly off San Clemente Island. The deep bottom fauna is undoubtedly important in the vertical transfer of nutrients and energy and deserves greater attention in future studies involving offshore fish communities.

Rockfish Ecology

Members of the family Scorpaenidae form one of the most diverse groups of fishes in the eastern North Pacific. The great majority of species are in the genus *Sebastes*, which is represented by about 58 species in California waters. Rockfishes occupy a variety of habitats and depth ranges and are significant components of California sport and commercial landings. The diversity and importance of the group provided the impetus for the brief but separate account here.

Since rockfishes are ovoviviparous and produce large broods, as many as one million of more young (Moser 1967), they release enormous numbers of larvae into coastal waters. Rockfish ranked fifth in mean abundance of all fish larvae collected in the California Current for the period 1950-1975 (see Ahlstrom, Moser, and Sandknop, CalCOFI stations (shore to station 90) over the 26-year period 1950-1975 (see Ahlstrom, Moser, and Sandknop, abstract, 1978 CalCOFI meeting). These abundant young comprise a forage resource of certainly significant but as yet undetermined proportions. Rockfish larvae and juveniles are at least known to serve as prey for several fishes of high economic importance including rockfishes themselves and for a number of seabirds (Figure 5).

Although the overall abundance of rockfish larvae based on CalCOFI surveys has been increasing in recent years (Ahlstrom, Moser, and Sandknop, abstract, 1978 CalCOFI meeting), there is evidence that the rockfish resource is being overexploited or at least is under heavy fishing pressure. Although as many as 40 species are taken by the sport and commercial fisheries, a very small number of species comprise a large portion of the rockfish catch in either case. In the commercial fishery, two species, bocaccio (*Sebastes paucispinis*) and chilipepper (*S. goodei*), make up well over 50% of the catch in
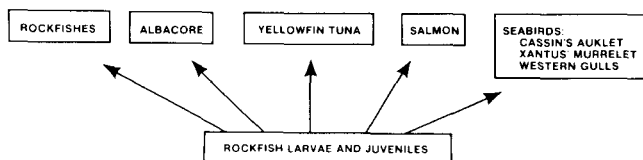
southern and central California, whereas in northern California the diversity of the catch increases with fewer chilipepper taken and the significant addition of another scorpaenid, shortspine thornyhead (H.G. Moser and W.H. Lenarz, personal communication).

In the California partyboat fishery over the period 1966-1975, the total catch remained relatively stable, but the contribution of rockfishes to this total increased from 30% to more than 70% (Figure 6). As with the commercial fishery, only a few species make up the large proportion of the catch and most of these are the same species that figure heavily in the commercial catch. In southern California, bocaccio, chilipepper, and olive rockfish (*Sebastes serranoides*) are the species of major importance, whereas in central and northern California the principal sport species are blue (*S. melanops*) and yellowtail (*S. flavidus*) rockfish (H.G. Moser and W.H. Lenarz, personal communication).

The trend toward fishing in deeper waters, especially in southern California, by both commercial fishers and partyboats, is indicative of the degree of exploitation of the shallow-water populations of the few sought-after rockfish species. Evidence exists that fishing pressure, especially by partyboats, has reduced the populations in local inshore areas of at least two species. Off Santa Barbara, adults of olive rockfish have essentially been eliminated on certain reefs (Love 1978). It has become necessary to fish for this species on the outer, deeper banks. Similarly, Miller and Geibel (1973) reported that blue rockfish have been reduced in numbers and individual fish size by partyboat and skiff fisheries within 16 km of all major ports in the Monterey area.

Rockfishes are vulnerable to overexploitation because

Figure 5. Some known predators of rockfish (Scorpænidæ) larvae and juveniles in California waters.
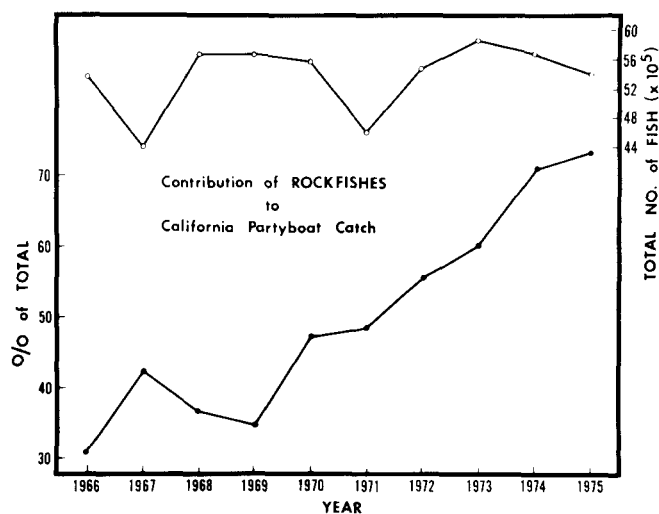
Figure 6. Percent contribution (●) of rockfishes (Scorpænidæ) to the annual partyboat catch (O) in California for the years 1966 to 1975 (based on Pinkas 1977).

they grow rather slowly (bocaccio is an exception), mature only after several years of age, and often have limited movements. If the species are schooling or aggregating forms over reefs and kelp beds, they are especially subject to excess fishing pressure by the sport fishery.

These and other considerations have led Miller and Geibel (1973) to recommend the establishment of subtidal reef preserves to allow proper management of rockfish and other reef-dwelling populations. These areas would be closed to sport and commercial fishing and would provide source regions from which recruits could repopulate adjacent exploited areas. Bag limits are of questionable value, because once caught the species may not be recognized or it may die even if released due to injury on ascent. Closed seasons likewise do not provide the full answer since under intense fishing pressure mature adults of low vagility would be removed during open season and therefore unavailable to spawn during closed season. I concur with Miller and Geibel's (1973) recommendation of the designation of subtidal preserves as perhaps one of the few effective procedures available for managing vulnerable reef species.

The potential of rockfishes as a resource of increased importance in the future is apparently not great. Many of the species not presently utilized are either too small in size or too deep living for efficient exploitation. A few species currently being studied, however, do seem to have the appropriate population characteristics to withstand greater exploitation. These include blackgill rockfish (*Sebastes melanostomus*; Moser and Ahlstrom 1978), calico rockfish (previously mentioned as having high recruitment in recent years) and, in central and northern California, stripetail rockfish and shortbelly rockfish (*S. jordani*). This last species is a midwater schooling fish found to be of high abundance in the San Francisco Bay region (W.H. Lenarz, personal communication).

In summary, rockfishes are a diverse group of particular ecological and economic importance. Much more research is needed on their life history and population biology so that the population sizes of individual species can be accurately estimated and predicted.

Kelp Beds/Subtidal Reefs

The above discussion of rockfishes associated with rocky substrates leads to this account of kelp beds and subtidal reefs which occur as distinct habitats in California coastal waters. Kelp stands and adjacent rocky outcrops provide a heterogeneous environment that serves as a source of food, shelter, and attraction for fishes (Quast 1968a). A total of 57 species were listed by Quast (1968a) as being associated with kelp beds in southern California; kelp bass (*Paralabrax clathratus*), California sheephead (*Pimelometopon pulchrum*), and blacksmith (*Chromis punctipinnis*) were the most frequently en-

countered species. Even larger numbers of species have been recorded in other studies. Miller and Geibel (1973) identified 67 species over a five-year period in kelp beds from San Simeon to Monterey in central California, and Feder et al. (1974) listed 111 species that were observed by diving in kelp bed-rocky bottom habitats in southern California.

Quast (1968b) determined that the mean standing crop of resident kelp bed fishes was 313 pounds/acre (351 kg/ha), an estimate close to median values for lakes and coral reefs. Miller and Geibel (1973) obtained higher estimates (706-1120 kg/ha) for fishes of central California kelp beds using techniques difficult to compare with those of Quast (1968b). Increased standardization of sampling procedures are required to obtain comparable values.

In terms of habitat complexity and species richness, kelp beds and associated areas form the temperate counterpart of coral reefs in the tropics, although overall diversity is greater in the latter environment. The diel behavior of kelp bed fishes follows the same basic patterns as tropical reef species but the kelp bed community appears (Ebeling and Bray 1976) to be more loosely programmed in terms of specialized day-night activities. Less large-scale replacement of fishes between discrete areas or vertical zones occurs at dusk, even though Hobson and Chess (1976) have shown that there are generalized planktivores feeding at night in open shallow waters seaward of kelp beds off Santa Catalina Island.

Interestingly, Ebeling and Bray (1976) have observed that kelp bed fishes belonging to primarily tropical families, especially Labridæ and Pomacentridæ, tend to show the same specialized pattern of nocturnal shelter-seeking as do their close tropical relatives. Perhaps this behavoir stems from the historic threat of crepuscular/nocturnal predation in tropical regions (Hobson 1972). Alternatively, Ebeling and Bray (1976) suggested that crepuscular and nocturnal predation by, for example, Pacific electric ray (*Torpedo californica*), is important in kelp beds but that the fishes derived from tropical families compete more successfully against temperate species for shelter.

The predatory role of the Pacific electric ray, a unique species associated with kelp beds, has not been fully appreciated. According to recent observations off Santa Barbara by Bray and Hixon (1978), this species is an important nocturnal predator of temperate reef fishes. The ray apparently forages exclusively on fishes and uses powerful electric discharges to immobilize a variety of prey species (Figure 7). Off Santa Barbara, the primary dietary item was northern anchovy (thus a direct link with this predator and an important commercial species), although kelp bass and demersal fishes of the sand-mud community were also taken. Bray and Hixon (1978) concluded that Pacific electric ray may be a major preda-

tor of temperate reef fishes that descend from the water column at night and become quiescent within about 1 m above the bottom.

Rocky Intertidal Zone

An important landward extension of subtidal reefs is the rocky intertidal zone, a productive and heterogeneous habitat that is particularly well developed on the California coast and offshore islands. A wide variety of fishes occupy the intertidal environment either on a permanent or a periodic basis. Rocky shores with associated tidepools are generally considered to be important habitats for the juveniles of a number of commercial and noncommercial species. Reduced predation in these habitats, as compared to subtidal areas, is frequently cited (e.g. Barton in press) as a major factor in the occupation of the intertidal zone by young fishes; however, solid support of this hypothesis is yet to be obtained.

Although the eastern North Pacific including California has one of the most highly diverse intertidal fish faunas in the world, relatively little research has been conducted on community structure and composition. It is possible, however, to identify the fish families that contribute the greatest number of species to the zone. The results of a two-year survey of intertidal fishes at Diablo Cove, 35.2°N (Burge and Schultz 1973) is indicative of species composition for central California shores. In this study 54 species were encountered in the intertidal zone, with Cottidæ (10 species), Scorpænidæ (8 species), Embiotocidæ (8 species), and Stichæidæ (6 species) being the principal families in terms of richness of species. Intertidal habitats are particularly important for the juveniles of scorpænids and embiotocids, whereas many of the cottids and stichæids occur as adults and spawn in the intertidal zone.

Rocky intertidal habitats offer a number of interesting and important problems for ichthyological research. Among these are the following: 1) Several species (>5) of cottids co-occur in tidepools in central California. Increased knowledge of their life histories and mechanisms of coexistence would be a significant contribution to the understanding of community structure, resilience, and recruitment of tidepool fishes. Yoshiyama (1977) recently completed a study of competition in rocky intertidal fishes, especially cottids, on the central California coast and proposed that exploitative competition was a major factor responsible

for the vertical stratification of species in the intertidal zone. 2) A wide range of color patterns exist within individual species of several families (e.g. Clinidæ, Cottidæ, Pholidæ). Burgess (1978) proposed that for the rockweed gunnel (Philidæ: *Xererpes fucorum*) multiple color phases allow expanded utilization of available resources within the intertidal zone. Ecological significance of color variations in other species awaits clarification. 3) Among the best examples of temperate herbivorous fishes are certain stichæids which occur in the intertidal zone. These fishes become progressively dependent upon a plant diet with age (Montgomery 1977; Horn et al., in preparation). 4) Plainfin midshipman (*Porichthys notatus*), one of the most abundant demersal fishes in trawl surveys off southern California (Table 5), spawns, among other sites, in the intertidal zone of central and northern California. This species is an example of a California marine fish of high abundance and broad habitat whose ecological role, although probably significant, has not been elucidated. According to Fitch and Lavenberg (1971), plainfin midshipman eat primarily small shrimp-like crustaceans and fishes (mostly northern anchovies) and are in turn fed upon by numerous large predators including rockfishes, lingcod (*Ophidion elongatus*), and sea lions. Attention to certain morphological and physiological attributes (e.g. luminescence, sound production) has overshadowed study of the ecological importance of this species and its shallower water congener, specklefin midshipman (*P. myriaster*).

Harbors

Harbors are artificial habitats formed by breakwaters that slow the movement of water and affect other changes making them in some ways similar to natural semi-enclosed bays and estuaries. These habitats are frequently characterized by calm, nutrient-rich waters and a variety of substrates. The protected rocky environment on the leeward side of a breakwater becomes an important and distinct habitat for shallow, subtidal fishes. King Harbor and Los Angeles/Long Beach Harbor are two such habitats that in recent years have been shown to support diverse and abundant fish faunas.

The number of fish species known to inhabit or visit Los Angeles/Long Beach Harbor has been more than doubled by recent investigations. Chamberlain (1974) compiled a list of 126 species in 48 families for this harbor complex. Based on trawl samples, Stephens et al. (1974) found that the fish density (one fish/8.9 m²) in Los Angeles/Long Beach Harbor was the highest recorded for local waters and that diversity and richness approximated values recorded for similar depths outside the harbor (i.e. San Pedro Bay). The ten most abundant species in the trawls were 1) white croaker, 2) northern anchovy, 3) California tonguefish, 4) speckled sanddab, 5) queenfish,
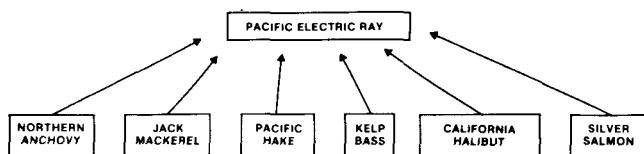
Figure 7. Some known prey of Pacific electric eel (*Torpedo californica*) in California waters.

6) shiner surfperch, 7) white surfperch, 8) specklefin midshipman (*Porichthys myriaster*), 9) bay goby (*Lepidogobius lepidus*), and 10) vermilion rockfish (*Sebastes miniatus*). White croaker, especially juveniles, and northern anchovy made up 69% of the catch. The abundance of these two species probably reflects a nutrient enrichment in the harbor. Stephens et al. (1974) were able to recognize three areas of distribution within the harbor: 1) an area rich in flatfishes, 2) one of high white croaker abundance, and 3) an area identified by the presence of rockfishes.

The King Harbor fish fauna has been shown (Stephens 1978) to be extremely diverse and abundant, especially in the vicinity of the breakwater. More than 90 species have been recorded in this harbor. Based on diver surveys, considerable seasonal variation existed in both abundance and species richness, but in general the community was dominated by speckled sanddab, shiner surfperch, and white surfperch. Two species abundant in Los Angeles/Long Beach Harbor but absent in the King Harbor surveys were white croaker and California tonguefish. The former species is known to avoid divers, and the latter has never been recorded in King Harbor. Stephens (1978) attributed much of the faunal richness in King Harbor to the thermal diversity and substrate heterogeneity characterizing the harbor.

Stephens (1978) stated that because of the limited amount of natural bay-estuarine habitat, especially in southern Califoria, the numerous harbors of the region supplement or replace the few estuaries as nursery areas for juvenile fishes. Although a large percentage (perhaps 75%) of the coastal wetlands and estuarine habitats in southern California have been obliterated as a result of human activities, the remaining bay-estuarine areas provide the principal habitat for several fish species and the setting for a unique fish community (see below).

Bays and Estuaries

According to data compiled by Horn and Allen (1976), almost one-half (224 species) of the California coastal fish fauna has been recorded from the major bays and estuaries in California. Horn and Allen (1976) showed that the number of species in each of these habitats was positively correlated with area and mouth width of the bay or estuary. This finding becomes important with the realization that these habitats are being continually altered including reduced in size by human activity.

Natural bays and estuaries in California do function in the classic sense of serving as spawning and nursery areas for coastal fishes, including those of economic importance such as northern anchovy and California halibut (*Paralichthys californicus*) (e.g. Allen 1976; White 1977—Newport Bay). A frequently overlooked characteristic of bays and estuaries, however, is that they support unique fish assemblages. Thus, to obliterate an estuary eliminates a unique community of fishes in a given area. In addition to seasonally occuring coastal species, the bay-estuarine community is primarily composed of a set of abundant, low trophic-level fishes that together form a distinct assemblage of species. Based on larval surveys, the principal species, other than gobies, in northern California are members of the Clupeidæ, Cottidæ, and Osmeridæ, whereas in southern California the main species, other than gobies, are representatives of the Engraulidæ, Blenniidæ, and Atherinidæ (White 1977; White and Horn in preparation). Various species of surfperches (Embiotocidæ) are also important members of bay-estuarine communities. Gobies (Gobiidæ) are among the most abundant bay-estuarine fishes and are well represented in all such California habitats. The focus below is on the abundant members of the Gobiidæ and their apparent ecological importance in bays and estuaries.

The most important goby species in California bays and estuaries are 1) arrow goby (*Clevelandia ios*), 2) longjaw mudsucker (*Gillichthys mirabilis*), 3) cheekspot goby (*Ilypnus gilberti*), 4) shadow goby (*Quietula ycauda*), and 5) bay goby (*Lepidogobius lepidus*). The larvae of one or more of these species are the most consistently abundant of all California fishes in bay-estuarine ichthyoplankton samples (White and Horn in preparation). The adults also appear to be highly abundant (Brothers 1975; MacDonald 1975), but the difficulty of adequately sampling them (Horn and Allen, in press) has resulted in an underestimation of their numbers and their role in the structure of bay-estuarine communities. A primary indication of their ecological importance, however, has come from the occurrence of these species in the diets of predatory fishes and birds.

MacDonald (1975) listed 12 species of fishes as predators of arrow goby, the most abundant and widespread bay-estuarine goby, in Anaheim Bay. These predators included California halibut, walleye surfperch (*Hyperprosopon argenteum*), California corbina (*Menticirrhus undulatus*), white croaker, staghorn sculpin (*Leptocottus armatus*), specklefin midshipman, and round stingray (*Urolophus halleri*). For some of these and other species identified, arrow goby was probably only an incidental prey item. Haaker (1975), however, showed that gobies were the most frequently occurring item in stomachs of California halibut in Anaheim Bay. Thus, gobies serve as forage for a fish of sport and commercial importance when the fish, especially in the juvenile stage, enters bays and estuaries.

Brothers (1975) commonly observed shorebirds probing invertebrate burrows in Mission Bay, possibly to feed on arrow gobies, and found that several species of shorebirds readily ate anesthetized gobies left on mud and sand flats. Other, primarily anecdotal, evidence (Brothers
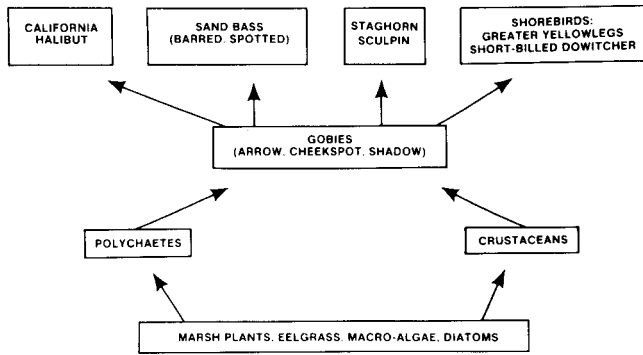
Figure 8. Trophic interactions involving gobies (Gobiidæ) in California estuarine habitats.

1975) indicates that gobies are important food for shorebirds.

Although little quantitative data are available to establish the importance of gobies in the bay-estuarine trophic structure, Brothers (1975) was sufficiently impressed with goby abundance to postulate a significant position in the food web for them. These fishes make available the high production of eelgrass (*Zostera marina*), green algae (e.g. *Ulva* sp.), diatoms, and marsh plants to higher level carnivores (Figure 8). By consuming large numbers of small crustaceans and worms that directly or indirectly feed on plants or plant detritus, gobies serve to channel substantial amounts of energy to the large predators in the ecosystem. Goby larvae may be equally important in the planktonic segment of the bay-estuarine food web.

Bays and estuaries serve as breeding and nursery areas for a wide array of coastal fishes, provide habitat for unique assemblages of fishes, and support large populations of small fishes that are important forage for high-level consumers in the ecosystem. For these ecological reasons, which directly relate to fishery considerations, natural bays and estuaries are worthy of preservation and wise management. The steps taken by the State of California to establish Upper Newport Bay as an ecological reserve should be repeated for other such habitats in California.

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BIRDS AS MARINE ORGANISMS: A REVIEW

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ABSTRACT

Only 9 of 156 avian families are specialized as sea-birds. These birds are involved in marine energy cycles during all aspects of their lives except for the 10% of time they spend in some nesting activities. As marine organisms their occurrence and distribution are directly affected by properties of their oceanic habitat, such as water temperature, salinity, and turbidity. In their trophic relationships, almost all are secondary or tertiary carnivores. As a group within specific ecosystems, estimates of their feeding rates range between 20 and 35% of annual prey production. Their usual prey are abundant, schooling organisms such as euphausiids and squid (invertebrates) and clupeids, engraulids, and exocœtids (fish). Their high rates of feeding and metabolism, and the large amounts of nutrients they return to the marine environment, indicate that seabirds are probably important components in pelagic ecosystems. As such they have been strongly affected by human fisheries; for example, decline in the size of Peruvian anchovy and South African sardine populations have led to tremendous reductions in associated bird numbers. Evidence indicates that seabirds could provide an understanding of fish stock dynamics prior to overexploitation by man.

RESUMEN

De 156 familias avícolas solamente 9 incluyen aves marinas. Estas aves están involucradas en los ciclos de la vida marina durante todos los aspectos de su vida excepto en el 10% del tiempo que pasan en los nidos. La distribución de estos organismos marinos está directamente afectado por las características del hábitat oceánico, tales como la temperatura del agua, salinidad, y turbulencia. En sus relaciones tróficas casi todas son carnívoras secundarias o terciarias. Como un grupo dentro de ecosistemas específicos, el cálculo de su porcentaje de alimentación fluctúa entre el 20 y 35% de la producción anual de presas. Sus presas comunes son bancos abundantes de organismos, tales como eufáusidos y calamares (invertebrados), y clupéidos, engráulidos y exocétidos (peces). Sus índices elevados de alimentación y metabolismo, y las grandes cantidades de nutrientes que retornan al ambiente marino, indican que las aves marinas son probablemente componentes importantes de los ecosistemas pelágicos. Así, han sido muy afectadas por el incremento de las pesquerías; por ejemplo, la reducción en el tamaño de las poblaciones de anchoveta peruana y de sardina surafricana ha contribuido a tremendas reducciones en el número de las aves asociadas con esos peces. Se indica que el estudio de las aves marinas podría contribuir a comprender mejor la dinámica de las poblaciones de peces anterior a la sobre-explotación por el hombre.

BIRDS AS MARINE ORGANISMS: A REVIEW

As pointed out by Sanger(1972) and Ainley and Sanger (1979), otherwise comprehensive reviews of biological oceanography have said little or nothing about seabirds in spite of the fact that they are the most visible part of the marine biota. The reasons for this oversight are no doubt complex, but there are perhaps two major ones. First, because seabirds have not been commercially harvested to any significant degree, fisheries research, which supplies most of our knowledge about marine ecosystems, has ignored them. Second, because ornithologists have mostly studied seabird breeding behavior and biology, they, too, have discovered little about avian roles in marine ecosystems. The purpose of this paper, then, is to establish seabirds as bona fide marine organisms, review some of what we know about their marine biology, and encourage the idea that a more complete understanding of marine ecosystems will be attained by including studies of marine birds. In that my own research has been directed toward these goals, I will take this opportunity to summarize that work.

WHAT ARE SEABIRDS?

Avian taxonomists currently recognize about 156 existing families of birds, and only 9 of these are rather specialized as seabirds: the Speniscidæ (penquins), Diomedeidæ (albatrosses), Procellariidæ (petrels), Hydrobatidæ (storm-petrels), Pelecanoididæ (diving petrels), Phæthontidæ (tropicbirds), Sulidæ (Boobies), Fregatidæ (frigatebirds), Alcidæ (auks), and a few species (terns) of Laridæ (gulls and terns). Members of these families share the following characteristics: they derive all their food from the sea, they void virtually all their feces into the sea, and when individuals die they do so at sea. They are full-time participants of marine energy cycles. Because of these characteristics, and in spite of the fact that most birds can travel above the sea's surface instead of being confined to the water (as are fish or marine mammals) or that they have to spend some time on land to raise young, these birds should be recognized as true marine organisms. The time that they do spend away from the sea is in fact minimal. Using the Adélie Penguin

(*Pygoscelis adeliae*) as an example, and the data in Ainley (1978) and Ainley and DeMaster (in press), it can be calculated that a typical seabird spends about 85% of its time annually at sea during its breeding years; over its entire lifetime, it spends 90% of its time at sea. This assumes 6 years of breeding and a life span of 10 years. All of the time on land is devoted to breeding activities, mainly the incubation of eggs, and during these activities, seabirds rely entirely on fat reserves built up at sea. Some species that live much longer than Adélie Penguins and that breed every other year, for instance some albatrosses, probably spend even less time on land over the duration of their lives.

Oftentimes avian species that undertake even a small part of their life cycle at sea are also considered to be "seabirds." Included are species from 15 other families, principally the Gaviidæ (loons), Podicipedidæ (grebes), Pelecanidæ (pelicans), Phalacrocoracidæ (cormorants), Anatidæ (ducks and geese), Scolopacidæ (shorebirds), Stercorariidæ (skuas), Rynchopidæ (skimmers), and the majority of the Laridæ. It is from these groups that the general but rather misleading conception of a seabird is derived, the one shared by most people. The "sea gull" is the typical example. Such birds, like man, are based on land and from there undertake trips to sea or to terrestrial and freshwater habitats for food. They are involved only part time in marine energy cycles; and because they spend a third or more of their time on land, they remove energy from marine ecosystems that is not returned.

THE MARINE DISTRIBUTION OF SEABIRDS

Much has been written about the distribution of seabirds at sea, but the factors that affect occurrence are not well understood. Murphy (1936) was among the earliest writers to point out that around South America (since proved to be true elsewhere) some species were confined to the "blue" oceanic waters offshore whereas others occurred in more turbid coastal waters. From there, through the work of many authors (for example Wynne-Edwards 1935; Jehl 1973) the idea has arisen that seabirds occur in concentric zones spaced outward from continents and islands. This view explains the occurrence of some species, especially the coastal ones, most of which are only part-time marine organisms, but it is biased towards the land orientation of man and the sea gull type of seabird. It is further biased to the breeding season (10% of a seabird's life) when birds must return repeatedly to their nests.

We are beginning to understand that the distribution of seabirds is affected by some of the same oceanographic factors that affect the distributions of what are thought of as typical marine organisms, such as fish. One such factor is water temperature. For instance, when the California Current weakens, as it periodically does (Sette and Isaacs

1960), California waters become warmer and species of warmwater birds move farther north than they normally occur in the eastern North Pacific (Ainley and Lewis 1974; Ainley 1976). Since the California Current moves parallel to the coast and displaces warmer waters westward, warmwater bird species also move closer to shore in such circumstances. This concept that birds live where their preferred water occurs is complicated by their abilities to fly over, but still technically occur in, unsuitable waters. For instance, Leach's Storm-Petrels (*Oceanodroma leucorhoa*) prefer warm oceanic waters, but because the only suitable West Coast breeding sites in the Pacific are coastal islands they must cross cold waters of the California Current as they fly between feeding and breeding areas (Ainley et al. 1975; Wiens and Scott 1975; Ainley 1976).

It is rather amazing, in light of the present land-oriented zonal conception of seabird distribution, that on two cruises from North America to the New Zealand sector of Antarctica, during which seabirds and sea temperatures were monitored continuously, with a temperature range of 28° to 0°C, 1-2°C changes brought about a consistent turnover of 30-70% ($\bar{x}$ about 45%) of bird species (Ainley and co-workers, work in progress). Some species were very precisely related to certain temperature ranges, i.e. stenothermal, whereas others occurred over larger ranges, i.e. eurythermal. This same pattern is evident in other groups of marine organisms.

Brown et al. (1975) recently tried to correlate seabird occurrence in Chilean fjords with not just temperature but also salinity profiles. Pocklington (1979) attempted the same for seabirds in the Indian Ocean. They found several good correlations. It is rather easy to understand how seabirds might sense temperature changes, but it is not easy to visualize how they might sense changes in salinity, even though they do drink seawater. It is just that, as far as we know, they do not fly about continuously sampling salinity as they would be able to "monitor" temperature. Brown et al. and Pocklington tried to explain the correlation as an indirect one involving the temperature/salinity profiles of the preferred prey of different bird species. The opportunistic and unspecialized feeding habits of most seabirds, as reviewed below, would also argue against this for all but exceptional species.

Other physical oceanographic factors can also affect seabird occurrence. For instance, some species that employ certain methods of food capture live only where conditions favor those methods. The prime example is given by birds that plunge for food (Ashmole 1971), principally the boobies and tropicbirds. Spotting prey as deep as 10 m or more below the surface while flying 15 m or more above it, and thereafter using only momentum from a "fall" to reach the prey, requires water of high clarity. For this reason deep plungers occur only in tropical/sub-

tropical waters where low phytoplankton standing stocks (compared to those in cooler waters) result in very clear water (Ainley 1977). Supporting this is the fact that deep-plunging species occur most consistently off California during the later summer and fall when the annual marine cycle is in its oceanic period (Ainley 1976). At that time water temperatures reach the subtropical range and phytoplankton standing stocks are lowest for the year (Bolin and Abbott 1963).

TROPHIC RELATIONSHIPS

Marine biologists, in their discussions of food webs, rarely make specific mention of marine birds, but the latter are part of what they refer to as "primary," "secondary," and "tertiary carnivores" or, in other words, the "third trophic level" (see Steele 1974), or "other carnivores" (Cushing 1975), or "nekton" (Sverdrup et al. 1942). In their review of trophic relations among marine birds of five oceanographic domains in the North Pacific, Ainley and Sanger (1979) found that 77% of seabird species were predators at the secondary and tertiary carnivore levels. Most of the remainder (21%) were scavengers, which still put them in the third trophic level. Only 2%, in that they feed principally on other species of seabirds, were in the fourth trophic level. Seabirds thus by and large occupy the same position in marine food webs as do the larger fish, mammals, and man.

The crux of the matter is how important are marine birds as predators relative to other occupants of the third trophic level in marine food webs. Quite a bit is known about the species of prey eaten by seabirds (e.g. review by Ainley and Sanger 1979), but little is known about their food consumption rates to compare with other upper trophic level predators. Some estimates though have been attempted. Wiens and Scott (1975), by computer simulation, estimated that Common Murres (*Uria aalge*) consumed 11% of pelagic fishes produced annually in Oregon's neritic zone. They also estimated that four seabird species off Oregon alone consumed annually about four times the tonnage of anchovies (*Engraulis mordax*) caught commercially each year in the northern permit area (Point Conception to Oregon) during the years 1966 to 1971. They also figured that 22% of the annual pelagic fish production off Oregon was eaten by seabirds. Furness (1978), using a different computer simulation, estimated that within 45 km of breeding colonies in the Shetland Islands, seabirds consumed between 20 and 35% of annual food-fish production. It has been calculated that off Peru during the height of the commercial anchovy (*Engraulis ringens*) harvest in the late 1960's, birds consumed 2.5 × 10⁶ metric tons of the fish or as much as a quarter of what was harvested commercially (Idyll 1973). That commercial harvest, of course, was by far the larg-

est in the world. Laws (1977) estimated that in the Antarctic pelagic ecosystems birds and seals equal each other in biomass, an amount for each that is about half that of whales. Prévost (1976) figured that all three groups consumed about equal amounts of euphausiids, about 30-40 × 10⁶ tons each. Both authors agreed, however, that more information was needed. More data are also needed elsewhere, but with seabird food consumption estimates of such high magnitudes, it is surprising that fishery and marine biologists, and ornithologists, have not paid more attention to the seemingly significant impact that marine birds may have in pelagic ecosystems.

High rates of food consumption and very high metabolic rates in turn mean that seabirds, through production of excrement, may also play a significant role in the recycling of nutrients and energy in pelagic ecosystems. This, as pointed out by Wiens and Scott (1975), may be especially true in areas where upwelling is not strong but where some species of seabirds are abundant. There is, in fact, compared to knowledge on food consumption, even less known about the role seabirds play in nutrient recycling. Sanger (1972) estimated that seabirds in the Central Subarctic Domain (see Dodimead et al. 1963) consumed 278 × 10³ tons of food and voided up to 74 × 10³ tons of feces per year. Wiens and Scott (1975) estimated that off Oregon four seabird species, with numbers fluctuating seasonally from about 1.2 × 10⁵ to 4.4 × 10⁶ birds, consumed about 62,500 metric tons of fish, or 7.56 × 10¹⁰ kcal of food, and returned 2.32 × 10¹⁰ kcal to the system each year in their feces. They were not able to equate kcal of guano to nutrients. On an artificial platform in South Africa, less than 240,000 seabirds produced, at a minimum, an average (1941-1965) 777 metric tons of guano per year, the composition of which included 16% nitrates, 9% phosphates, and 4% potash (Rand 1963; Berry 1975).

In the types of prey they feed on, most seabirds do not appear to specialize. In the review by Ainley and Sanger (1979), it was evident that certain prey over and over again predominated in the diets of different marine birds of the eastern North Pacific. These prey included species of *Euphausia, Loligo, Clupea, Engraulis,* and *Sebastes.* As specific examples, 43% of prey eaten by four Oregon seabirds (Wiens and Scott 1975) and 80 to 95% of prey eaten by three Peruvian "guano birds" was *Engraulis* (Idyll 1973); 23% of prey eaten by seven seabirds in the central tropical Pacific was exocoetids (Ashmole and Ashmole 1967); somewhat more than 50% and often more than 75% of prey eaten by six species nesting at the Farallon Islands was *Sebastes* (Ainley unpublished); 26 to 85% of prey eaten by nine species in the Farne Islands was *Ammodytes* (Pearson 1968); 19 to 85% of prey eaten by three South African "guano birds" was *Sardinops* (Crawford and Shelton 1978); and 50 to 90% of prey

eaten by most Antarctic penquins and petrels was *Euphausia* (Emison 1968; Mougin 1975). There is thus great overlap in what they eat, and it seems that whatever prey species is most readily available predominates in seabird diets. "Readily available" prey, it would seem, are those species that tend to occur in dense concentrations and within 70 m of the surface. The latter seems to be a typical maximum feeding depth for diving seabirds (Kooyman 1974). Offsetting the lack of specialization, seabird species differ in their feeding by the size of their prey, which relates to predator bill size (Ashmole and Ashmole 1967; Bedard 1969), and by the habitat and method of food capture (Ashmole 1971; Ainley 1977, unpublished).

SEABIRDS AND FISHERIES

The prey that seabirds prefer, largely because of availability, are often sought in pelagic fisheries for the same reason, or they are also the prey of pelagic predatory fish that in turn are fished for by man. Since the time that man first established pelagic fisheries, he often looked for feeding flocks of birds to tell where the sought-after fish were located. Direct or indirect "competition" for fish between birds and man is thus theoretically possible, and the fact that both birds and man are capable of tremendous fish harvest makes an interrelationship likely. Whether or not the fish harvest by birds can affect or has affected that by man, or vice versa, must be considered on a case-by-case basis.

There is little doubt that the crash of Peruvian anchovy populations resulted in the crash of seabird populations from 30 to 1 million individuals. As summarized by Idyll (1973), overfishing in conjunction with natural environmental stress was probably responsible for the reduction in fish. It is also fairly evident that in the several years before the ultimate crash, intense fishing pressure resulted in depressed bird populations, or at least prevented recovery of bird numbers from an earlier natural reduction.

The story of the Peruvian anchovy remains the outstanding, relatively unequivocal example of a human fishery out-competing birds for fish. Few other examples are as conclusive. Another example though is given by Crawford and Shelton (1978), who equated seabird numbers, guano production, fish availablity, and fishery catches of pelagic species (mainly *Sardinops*) off South Africa from 1940 to the present. Beginning about 1965 the fishery began a sharp decline from which it has not recovered, and with it the bird populations declined as well. The authors concluded that the fishery was ultimately responsible for the decline in bird numbers. In a less conclusive example, Ainley and Lewis (1974) hypothesized that the disappearance of Pacific sardines (*Sardinops coerulea*) prevented recovery in several California populations of seabirds previously reduced by unrelated factors. In this case, one major question involved the extent to which overfishing played a role in the disappearance of these fish (Cushing 1975). Other instances of fishing impact on seabird prey, and ultimately on the seabirds themselves, are in the realm of discussions over the potential for such interaction. For example, Furness (1978) and Bailey and Hislop (1978) recently presented arguments, pro and con, over whether fisheries in the northeastern Atlantic could have depressing effects on seabird populations. The only clear conclusion from this particular instance was that more information was needed, particularly on seabirds.

There is also controversy over whether fishery harvest of predatory fish, by reducing species that naturally compete with seabirds for food, would result in increased availability of prey for birds and other predators. Few unequivocal examples are available. Furness (1978) and Bailey and Hislop (1978) presented arguments on the potential for this situation in the North Atlantic, and they concluded that such an interrelationship is theoretically possible. On the other hand, several authors (e.g. Sladen 1964; Conroy 1975; Laws 1977) have proposed that increases in southern fur seals (*Arctocephalus gazella*) and Adélie and Chinstrap Penguins (*P. adelie* and *P. antarctica*) in the Scotia Sea area are the result of overfishing on baleen whales, which formerly "competed" with seals and birds for Antarctic krill (*Euphausia superba*). The reduction in whales, in fact, has led some fisheries experts (e.g. Gulland 1970) to propose that a large "surplus" krill stock now exists and should be harvested.

There are also potential interrelationships between fisheries and seabirds that are even more indirect. A dramatic decline of Thick-Billed Murres (*Uria lomvia*) in West Greenland waters has been attributed in large part to heavy mortality due to drowning in drift nets set for salmon (*Salmo salar*; Evans and Waterston 1978). Ripley (1976) indicated the potential for such an interaction in the North Pacific as well. An increase in Northern Fulmar populations (*Fulmarus glacialis*) in the North Atlantic during this century has been attribued to an increase in fish offal resulting from fisheries, largely on demersal species (Fisher 1952, 1966). Others (e.g. Brown 1970; Bailey and Hislop 1978) argue against such an explanation for the increase. As in other controversies, it is clear that information on seabird trophic and energetic relationships in marine ecosystems is inadequate.

SUMMARY AND CONCLUDING REMARKS

Established in this review are the facts that seabirds are marine organisms and that they can be important predators on marine vertebrate and invertebrate prey species. Potentially, they may play another important role in pelagic ecosystems, that role being in the recycling of

nutrients. In light of these real and potential impacts, the fact that marine ecologists generally overlook seabirds is surprising. Because birds are so visible, they should be of use in helping us to understand marine ecosystem interactions. Indeed, and rather surprisingly, a marine biologist, Green (1971), on the basis of a computer simulation, recently suggested that the study of seabirds may provide a sensitive and relatively inexpensive means to monitor ecosystem state in the Antarctic. Using much more complete data, and an interaction less extensive than an entire ecosystem, Crawford and Shelton (1978), fisheries research biologists, proposed that seabirds "have value in providing an understanding of fish stocks prior to exploitation and as indicators of the current state of the resources."

It was pointed out in this review that overharvest of a fish stock can depress seabird populations. It would be unusual if other predator populations were not affected. The recent history of the Peruvian anchovy made this clear, at least regarding birds, and the potential exists or has existed for similar interrelationships elsewhere. There are certain species of marine fish and invertebrates that, because of their abundance, availability, and suitability as food, are important prey for many predators. Of these predators, only man has the power to "manage" the resource. Especially in the cases of "universal prey" species, management from an ecosystem perspective, rather than that of the single stock sustainable yield approach, would seem to be the wisest course of action. In that way the impact of the fishery elsewhere in the food web may be lessened before it is too late to do so.

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BROWN PELICANS AS ANCHOVY STOCK INDICATORS AND THEIR RELATIONSHIPS
TO COMMERCIAL FISHING

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ABSTRACT

Seabirds as offshore wildlife resources have largely been unstudied by wildlife managers until recently. Brown pelicans (*Pelecanus occidentalis californicus*) in Southern California Bight (SCB) have received special attention in the past under the Endangered Species Act of 1973 (ESA). Special consideration is given to species with endangered status in commercial fishery management plans mandated by the Fisheries Conservation and Management Act of 1976, but such plans also attempt to deal positively with all species of seabirds and marine wildlife as society's values change more positively toward such offshore wildlife resources.

Brown pelican breeding status is heavily dependent on abundance and/or availablility of anchovies during the prebreeding and breeding periods. This is likely due to the dominance of northern anchovy (*Engraulis mordax*) biomass in surface schooling fishery stocks in the SCB. The predator-prey relationship that involves brown pelicans and anchovies in the SCB is a tenuous one due to 1) the strong dependence almost solely on anchovies evidenced over the last nine years of study and 2) potential increases of commercial harvest of anchovies since 1979 under some options of the Anchovy Management Plan provided by the Pacific Fishery Management Council. There are also two elements of this interaction that complicate straightforward management of pelicans: a) implementation of a liberal harvest option under the Anchovy Management Plan rather than a more conservative one and b) increasing anchovy harvests in Mexico. Unless anchovies are replaced by another prey, breeding pelicans may ultimately require a larger forage reserve of anchovies, offshore refuges (critical habitat under the ESA), and possibly more conservative quotas in the anchovy reduction fishery. A management plan for brown pelicans and other seabirds in the SCB has not yet been developed by the appropriate agencies.

Past anchovy harvests (pre-1979) probably did not detectably disrupt the pelican/anchovy relationship, although at the higher observed levels of pelican reproduction (coincident with higher levels of anchovy biomass and catch), pelican reproductive rate was not maximal. This is more likely because pollution may still be chronically affecting pelican reproduction. Anchovy harvests under an optimum yield scheme will be monitored closely for possible effects on pelican reproduction. Although more detailed studies are needed, we provide some initial suggestions based on brown pelican requirements.

RESUMEN

El estudio de las aves marinas como recursos faunísticos en las zonas lejos de la costa ha sido bastante desatenido hasta fecha reciente por los organismos encargados de la fauna silvestre. Los pelícanos gris (*Pelecanus occidentalis californicus*) de la Bahía del Sur de California han recibido atención especial con el Endangered Species Act (ESA) de 1973. En los planes de administración de la pesquería comercial incluidos en el Fisheries Conservation and Management Act de 1976, se ha prestado atención especial a especies en peligro de desaparición, pero esos planes también intentan abarcar todas las especies de aves marinas y de vida marina a medida que cambian más los valores que la sociedad atribuye a esos recursos de los animales salvajes oceánicos.

El pelícano gris depende básicamente de la abundancia y/o disponibilidad de anchoveta durante los períodos de precrianza y crianza. Probablemente ésto se debe a que la biomasa de anchoveta del norte (*Engraulis mordax*) es dominante en los cardúmenes de la Bahía del Sur de California. La relación predador-presa entre el pelícano gris y la anchoveta en la Bahía del Sur de California es débil a causa de 1) su casi exclusiva dependencia sobre la anchoveta, según se evidencia en los últimos nueve años de estudio, y 2) incrementos en la captura comercial de anchovetas desde 1979 bajo algunas opciones del Anchovy Management Plan según las provisiones del Pacific Fishery Management Council. En esta interacción hay también dos elementos que complican la administración directa de pelícanos: a) la implantación de una opción de pesca amplia bajo el plan de administración de la pesquería de anchovetas, en lugar de una más conservadora, y b) el incremento de pesca de anchoveta en México. A menos que se reemplacen las anchovetas con otra presa, los pelícanos en estado de crianza podrían requerir una reserva más grande de alimento de anchovetas, refugios fuera de la costa (hábitat crítico bajo el ESA), y posiblemente cuotas más conservadoras reduciendo la pesquería de anchoveta. Las agencias responsables no han desarrollado todavía un plan para la conservación de los pelícanos gris y otras aves de la Bahía del Sur de California.

La pesquería de anchoveta anterior a 1979 probablemente no afectó notablemente la relación pelícano/anchoveta, aunque se ha observado que a niveles elevados de reproducción del pelícano (que coinciden con niveles más

elevados de captura y biomasa de anchoveta), el índice reproductor del pelícano no alcanzó un máximo. Probablemente se debe a que la contaminación puede estar aún afectando crónicamente la reproducción del pelícano. La pesca de anchoveta bajo un esquema de rendimiento óptimo será cuidadosamente inspeccionada para determinar posibles efectos sobre la reproducción del pelícano. Aunque se necesitan estudios más detallados, proveemos algunas sugerencias iniciales basadas en los requisitos del pelícano gris.

INTRODUCTION

As wildlife values change in our society, the chances for socioeconomic conflict increase. This will be especially true where commercially harvested resources might relate in some way to æsthetic or noncommerial ones, especially through conflicts in different value systems (see Langford and Cocheba 1978; Bart et al. 1979; and others). In the past, seabirds and other marine wildlife were viewed as undesirable competitors. Marine birds, a "neglected" resource in North America until recently (Bartonek and Sowl 1974), are often dependent on commercially utilized resources, and only recently are they being viewed by wildlife managers as valuable, conservable, and manageable resources in themselves (see Cline et al. 1979; Nisbet 1979; and this symposium). The alternative approach of using seabird population parameters as indices to aid the monitoring of commercially valuable fishery stocks is a technique with much potential in providing added, independent input for fishery managers.

Some seabirds such as the California brown pelican (*Pelecanus occidentalis californicus*), and its habitat, are given special protection under the Endangered Species Act of 1973 (ESA); this act enables the various management agencies to cooperate on the management of offshore ecosystems.

The collapse of the anchoveta (*Engraulis ringens*) fishery in Peru (Clark 1977) and associated detrimental effects on seabirds, both before the collapse (intentional and predicted population reductions of seabirds due to heavy fishing activities; Schaefer 1970; Paulik 1971) and after the collapse (Idyll 1973), are well-known. Related events occurred in the South African pilchard (*Sardinops ocellata*) fishery (Cram 1977), with well-demonstrated negative interactions between intensive commercial fishing activities and seabird populations (Frost et al. 1976; Crawford and Shelton 1978; Cooper 1978). There is also concern that increased krill (*Euphausia superba*) harvests will detrimentally affect marine wildlife in Antarctica (Beddington and Lawton 1978; May et al. 1979).

Fortunately in the Southern California Bight (SCB), through the Fishery Conservation and Management Act of 1976, there is an optimum yield management plan (Pacific Fishery Management Council [PFMC] 1978;

see Radovich 1979, Radovich and MacCall 1979, MacCall 1980 for further details and discussion) that will ideally insure that northern anchovies (*Engraulis mordax*) will not be overfished. Several potential problems exist, however, off southern California that might affect anchovy predators, in this case namely the brown pelican: 1) increasing Mexican harvests of anchovies (Chavez et al. 1977) and 2) increased harvests off southern California under a liberal option provided in the Anchovy Management plan (PFMC 1978; McCall 1980).

Values of offshore wildlife and the needs of those resources further complicate a management situation in the SCB that May et al. (1979) have summarized as such: "This is a particularly clear example of a complex situation where biology, economics, and politics roil together, and it is doubtful whether any 'scientific' principles of management are particularly relevant." We are not so sure that the situation here is as hopeless as might be implied; and in fact, we believe that the potential for interdisciplinary and interagency collaboration in the SCB area is great. Here we intend to approach this situation from the viewpoint of one local population of seabird: brown pelicans nesting on islands off southern California.

PELICAN DEPENDENCE ON AND RELATIONSHIPS TO ANCHOVIES

Keeping in mind that we are here referring to breeding populations and productivity of SCB brown pelicans only (not migrants), previous research (Anderson et al. in preparation, Gress et al. in preparation) has established that:

1) There are only two major brown pelican nesting colonies in the SCB, Anacapa Island (and associated Scorpion Rock) and Isla Coronado Norte just across the Mexican border. On occasion, pelicans have also nested on such islands as Santa Barbara, Prince, and others (Gress 1970).

2) Pelican breeding effort at both colonies (numbers of pairs that attempt to breed each year) is probably dependent largely on regional levels of anchovy abundance, but this relationship is difficult to document without total population censuses of pelicans.

3) Pelican reproductive rate (fledging success = F) depends largely on levels of anchovy abundance and availability. The diet of breeding pelicans from 1972-79 was comprised of 92% anchovies ($N = 2195$; Gress et al. in preparation). At Anacapa Island, breeding pelicans feed mostly in the Santa Barbara Channel later in the breeding season, but their feeding areas are variable due to mobility of their prey, anchovies (Gress et al. in preparation). Less is known of pelicans nesting at Coronado Norte, but a similar situation involving feeding areas is likely.

4) Anchovy availability in the local situation is

usually, but not always, related to overall abundance in the SCB.

5) Past complications from pollution in the SCB disrupted the above pelican/anchovy relationships until about 1972. Therefore, the situation as we know it today is recent. The major source of DDT in pelicans was contaminated anchovies, but both pelicans and anchovies have shown significant declines in DDT-related pollutants since 1972. Present pelican recruitment is still bolstered by young pelicans produced at colonies in southern Baja California or the Gulf of California. Productivity in the SCB is still most likely depressed due to residual pollutants (Anderson et al. 1975, 1977), but this is difficult to evaluate in comparison to the acute problems observed earlier.

6) Past Pelican breeding populations in the SCB probably had a larger prey base than they do today, perhaps also importantly involving Pacific sardines (*Sardinops caerulea*) and Pacific mackerel (*Scomber japonicus*; see Anderson and Anderson 1976). Pacific mackerel populations in the SCB have recovered considerably since 1978 (J. Radovich, personal communication), but this formerly abundant fish species was not a significant prey item of breeding brown pelicans in 1978 and 1979 (Gress et al. in preparation). Preliminary results of recent pelican food habit studies suggest, however, that Pacific mackerel was a more common forage item in 1980.

The "simplified" situation makes pelicans (and other predators dependent on anchovies) all the more sensitive to changes in these fish due a) to environmental stochasticity and its associated variation in anchovy carrying capacity (MacCall 1980) and b) to reduced carrying capacity for pelicans through increased anchovy harvests. Of course, the only variable that managers can manipulate or control is b).

We envision the prey (anchovy) situation as varying from widespread abundance and availability to only local availability (see PFMC 1978). In both situations pelicans can reproduce above the long-term mean if availability occurs near the breeding colonies long enough to sustain a complete reproductive season; but they do best when total anchovy biomass is high over the entire SCB. For pelicans, a complete reproductive season amounts to about 4½ months (Anderson et al. in preparation; Schreiber 1980). Pelicans are also restricted to a timely breeding season, especially in the later phases, partly due to the energetic and nutritional constraints of molt (D.W. Anderson unpublished).

For the purposes of our discussions here, we will emphasize one very important pelican/anchovy relationship: mean SCB anchovy biomass and mean pelican reproductive rate in the SCB (Figure 1). We cannot review all pelican reproductive parameters that are respon-

sive to anchovy abundance (total biomass of nonlarval fish in the SCB) or availability (total biomass of catchable fish). In fact, our field studies are just beginning to yield fruitful insights from our long-term data base; and they continue, especially now that harvests of anchovies are likely to change. Productivity ($= F =$ fledging rate $=$ number of young produced to flying age per nest attempt) is one of the most sensitive reproductive parameters of brown pelicans as an index to anchovy availability (Anderson et al. in preparation). Therefore, we will stress F in this discussion. Actually, F is probably a better index of local food supplies, but because of the usual relationship to regional abundance and the large cruising range of feeding pelicans (D.W. Anderson unpublished data), it provides a valuable starting point.

One thing is certain: SCB's brown pelicans definitely reproduce best during periods of high anchovy abundance (Figure 1), or in rarer cases, as in 1979 at Anacapa Island[1], when anchovies were locally abundant (Gress et al. in preparation). It is interesting that also during another period of high anchovy abundance, the mid-1960's (see Stauffer 1980), brown pelican population indices were also high (see Anderson and Anderson 1976).

The year of greatest disparity, 1973, needs to be mentioned at this point. The data from 1973 should be excluded from our calculations (Figures 1 and 3) because of unusually large numbers of migrant pelicans in the SCB during the resident breeding season that probably interfered with the resident breeding effort that year (Anderson et al. in preparation for detailed discussion). Therefore, normal predator/prey relationships were perhaps clouded by unusual behavioral phenomena.

But for the skeptic, we here present data both with 1973 (w/73) and without it (w/o 73). Exclusion of 1973 does not change our conclusions, but it gives more precise data fits for our predictions. Ignoring the behavioral phenomenon of 1973, or accepting it as one element of stochasticity in a more idealized relationship, we have then examined one important pelican reproductive parameter against an index of SCB anchovy biomass. It is important to do so because management for the central stock of anchovies is put on a similar large-scale geographical basis (PFMC 1978; Radovich and MacCall 1979; MacCall 1980).

We hope to illustrate how brown pelicans might act as useful indicator species to provide fishery managers an added basis for estimating "forage reserve" (PFMC 1978) for pelagic consumers. Hopefully, our long-term

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[1]The brown pelican breeding effort on Anacapa Island in 1979 was unusual in that the period of egg-laying extended over a six-month period (from 1970 to 1978 the range was 2.0 to 3.75 months). Moreover, the number of nesting attempts ($n = 1,258$) and number of young fledged ($n = 980$; 0.78 young fledged/nest attempt) from the Anacapa Island colony was greater than in any year since continuous studies began in 1969 (Gress et al. in preparation). Although overall anchovy biomass was low in the SCB in 1979, a local abundance comprised primarily of juveniles was concentrated in the Santa Barbara Channel just north of Anacapa and Santa Cruz Islands (Mais 1979). These anchovies were for the most part too small to harvest but were apparently of sufficient abundance to support a greatly expanded pelican breeding effort.
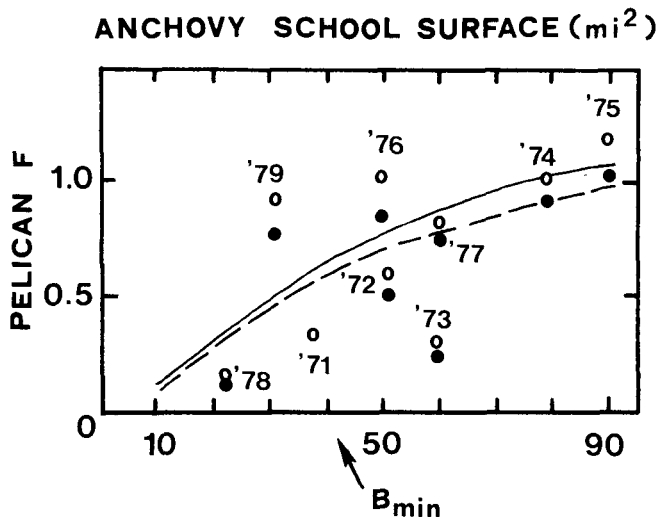
ANCHOVY SCHOOL SURFACE (mi^2)

Figure 1. Relationships between brown pelican fledging rates (F = young fledged per nest attempt) at Anacapa Island (closed circles) and Isla Coronado Norte (open circles) and indices of general anchovy abundance (B) in the Southern California Bight. The dashed line is the regression with the 1973 data included, and the solid line is with 1973 data excluded (see text for explanation). Anacapa Island for 1971 is not plotted because severe DDT effects were still evident there (see Anderson et al. 1977). B_{min} represents minimum anchovy biomass for effective pelican reproduction under average conditions. The 1979 anchovy school surface area indices were projected from biomass estimates of Stauffer and Parker (1980) and Stauffer (1980) because budgetary restrictions prevented comparative data via the acoustic surveys (Mais 1974, manuscript).

data represent optimum parameters under the current set of SCB conditions, although we know that local SCB pelican reproduction is still too low for population stability (Anderson et al 1975, 1977, in preparation).

An index to anchovy abundance (B) is expressed in one way by Mais (1974) as mi^2 of anchovy schools in a constant sample zone of the SCB. We have related this index to pelican reproduction. The best fit for the F versus B relationship is found to be in the form of the logarithmic curve, $F = a + b\ln B$ (Figure 1):

(w/73); $n = 17, r = 0.62, F = -1.2 + 0.48 \ln B$,

(w/o 73); $n = 15, r = 0.80, F = -1.4 + 0.55 \ln B$,

where n equals the number of data points and r equals the correlation coefficient.

It appears that the curve breaks at about $B = 40 mi^2$ (denoted as B_{min} on Figure 1). This break is defined on the basis of the long-term mean pelican fledging rate (F) of about 0.6; however, this is probably not sufficient for population maintenance in the SCB. But it represents an estimate of the present situation in the SCB as complicated still by pollution. First, we are assuming that B_{min} represents, under SCB conditions, minimum levels of anchovy abundance for effective pelican reproduction. The zero deviation level from the long-term mean of F represents B_{min}, as well. That level of food in terms of anchovies is as follows (where Dev. B is the deviation from its long-term mean):

(w/73); $r = 0.62$, Dev. $F = 1.1 + 0.71 \ln$ Dev. B, and

(w/o 73); $r = 0.75$, Dev. $F = 1.2 + 0.82 \ln$ Dev. B;

(w/73); 0 deviation (pelicans) = 41 mi^2,

(w/o 73); 0 deviation (pelicans) = 46 mi^2.

Therefore, it appears (Figure 1) that a total biomass level of roughly 43 mi^2 (by acoustical survey, or = about 2.15×10^6 short tons using an extension based on 1978 comparative data from Stauffer and Parker (1980) might represent a level in the SCB below which pelican reproduction is very poor. This forage reserve estimate of 2.15 million short tons represents about 78% of the long-term mean of 2.75 million short tons of biomass estimated for the central stock of anchovies (MacCall 1980). That spawning biomass might be a minimum goal for wildlife needs, assuming that the brown pelican is a suitable and representative indicator species. Our estimate is, however, almost twice the forage reserve recommended in the Anchovy Management Plan (PFMC 1978), but at this point must also be regarded as an estimate. Certainly we need a more accurate measurement of pelican (wildlife) needs relative to anchovy biomass, availability, and behavior of prey and a better estimate as to how such relationships between pelicans and anchovies are applicable to other wildlife species.

PELICANS AND COMMERCIAL ANCHOVY FISHERIES

Catch statistics represent a confusing mixture of biological, political, and regulatory phenomena. Here we use catch data only for the period when pelicans would be expected to be breeding to enable further comparisons that might shed some light on the seabird/fisherman interaction. A good argument might be made for the premise that commercial anchovy catches of the past had little or no effect on pelicans for the period where data on pelicans are available (1972-78; Figure 2). MacCall (1980) has suggested that the existing, small fishery of the SCB apparently did not affect the large variance in anchovy biomass previous to 1979. A logical extension of this would be that both pelicans and fishermen responded to variations in anchovy biomass for both consumers without mutual intereference (Figure 2). Because of this, one could argue that, although perhaps arbitrary (PFMC 1978; probably because CDFG was responding to political pressures from sportsmen; see Kaneen 1977, May et al. 1979), the previous establishment of quotas and the resulting catches were somewhat in pace with anchovy stocks and pelicans.

When plotted with an equation of the same logarithmic form as above, it appears that the old fishery outpaced pelicans in response at the higher levels of anchovy abundance (Figure 3). Such a relationship can be interpreted
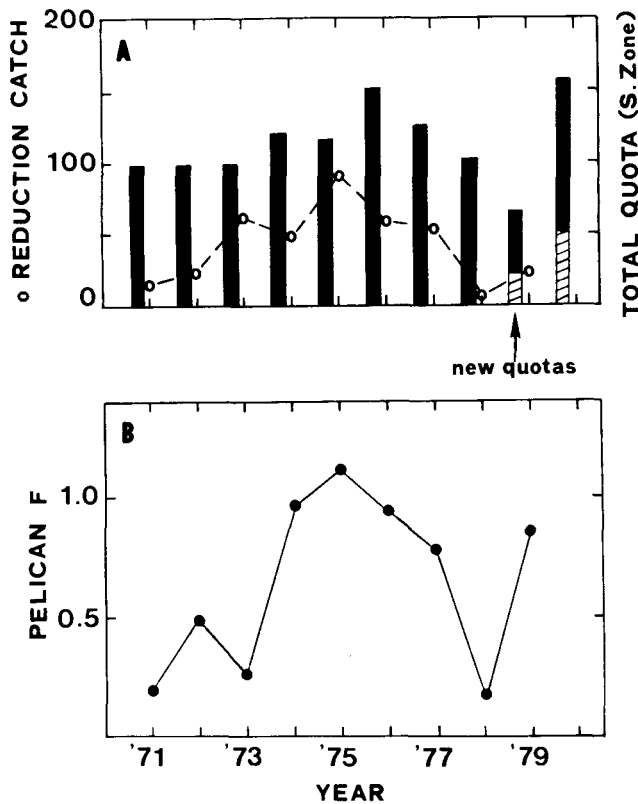
Figure 2. A. Anchovy catches (open circles) during the pelican breeding seasons (February through May only) superimposed on the various anchovy catch quotas (bar graphs) from 1971 through 1979. This does not represent the entire catch (see PFMC 1978 for those data). Catch and quota data are expressed as tons $\times$ 10³. B. Pelican reproductive rates (=F= young fledged per nest attempt) at Anacapa and Coronado Norte Islands combined (closed circles). The 1979 bar graph represents the start of a new quota system for the harvest of anchovies, and the hatched portions of the 1979 and 1980 quotas represent a more conservative option for harvest under the same Anchovy Management Plan (PFMC 1978; Radovich and MacCall 1979; MacCall 1980). The 1979 increase in pelican productivity was due to locally abundant concentrations of 1978 year-class anchovies near the breeding colonies (Gress et al. in preparation). Southern zone (SCB) quota data are from Kaneen (1977), PFMC (1978), Stauffer and Parker (1980), and Stauffer (1980). Under the new system, only U.S. quotas are shown, and they comprise about 70% of calculated optimum yield (Stauffer 1980). A fall catch for 1979 of 5,810 tons was the lowest in recent years (K.F.M.)

Figure 3. Anchovy reduction catch (fishing activities) versus pelican productivity (fledging rate) in the Southern California Bight from 1971 through 1979. See text and Anderson et al. (in preparation) for explanation of anomalous conditions in 1973 (1972-73 breeding season).

in several ways:

1) Both predators (man and birds) are limited by their own asymptotic rates, but the birds approach it somewhat sooner. Reproductive output in pelicans undoubtedly has an upper psysiological limit in this K-selected species due to the constraints of genetically-fixed upper clutch size (which is in turn determined largely by the number of young the parents can effectively feed; Lack 1954). Maximum clutch size in pelicans is very close to three (Anderson and Hickey 1970) but almost never exceeds three.

2) The two predators respond to aspects of fish behavior which differentially change with fish abundance. Density-dependent behavioral changes might occur in the prey: a) At very high densities, schools of

anchovies may become larger and proportionately more resistant to predation by brown pelicans and other natural predators (review by Radovich 1979). Conversely, at very high densities, anchovies may be more vunerable to purse-seining. b) At the higher biomasses in the SCB, fish may disperse into areas where they are less likely to be found when at lower biomasses. Local carrying capacity (K) for pelican food may be at a maximum, although total biomass may increase. In either case, prey would continue to be vulnerable to fishing by man, but vulnerability to natural predation may decrease (Clark 1974).

3) There may be direct competition between boats and birds, with boats being the controlling or more effective competitor. There might actually be a biomass or availability decline at the higher fishing levels that interferes with further increases in K for pelicans, i.e. fishing becomes more competitive with natural predators. This would be likely in the heavy fishing regime such as the Peruvian example cited previously. Because pelican F versus biomass from SCB's previous fishery takes the same form (Figure 1 versus Figure 3), this is the least likely explanation in our example.

4) A.D. MacCall (personal communications) has proposed a fourth hypothesis: There may be less of a differential response than is apparent from the available data. Fishermen may have varied fishing effort according to its profitability. Fish prices increased in the mid-1970's due to the collapse of the Peruvian fishery (Clark 1977), but fuel costs increased in the late-1970's. This aspect deserves study.

All of the above might operate, or various combina-

tions of them. At this point, we cannot say what has actually happened. It should prove very interesting to monitor this relationship under the increased quotas of the new Anchovy Management Plan.

PELICAN FEEDING ZONES

Anacapa Island is the only regular brown pelican breeding colony in U.S. waters of the SCB, and our most intensive research has been conducted there. At Anacapa, pelicans feed mostly in the Santa Barbara Channel during the later phases of the breeding season but in essence wherever the fish are earlier (Gress et al. in preparation). Important anchovy catches could also come from those areas (PFMC 1978; see also Chavez et al. 1977). Such areas (and equivalent areas also at Coronado Norte as yet undefined) are perhaps where the most significant pelican/fisherman overlap might occur. But, because of the unpredictable nature of the prey, these areas may not be definable from season to season or even within seasons. When plotted by California Department of Fish and Game statistical blocks, it does not appear that anchovy harvests near Anacapa have contributed a major portion of the total catch (Figure 4). Equivalent data are not available for Los Coronados. Loss of the area near Anacapa to fishing would amount to a loss of about 15 to 20% of California's SCB anchovy fishing waters. Since brown pelicans, like other seabirds, are most sensitive to local food supplies during the breeding period involving the raising of young (Ashmole 1971), the establishment of local feeding areas may be one important management strategy, particularly until better quantitative data are available. Such zones are in need of more accurate definition, but the studies of Briggs et al. (1980) suggest that near-colony refuge areas might encompass waters of 40 fathoms or less.
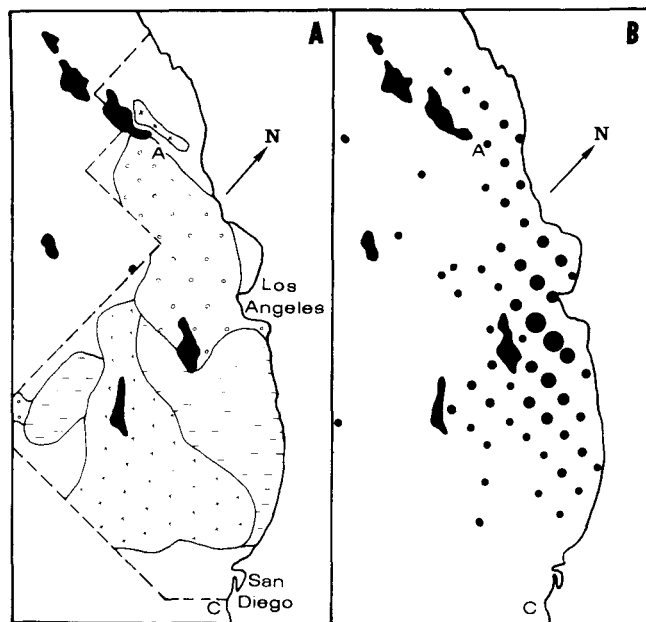

Figure 4. A. Anchovy biomass distribution from cruise 77-A-3 (K.F.M.), roughly showing typical relative densities of anchovies during the pelican breeding season. Abundance in this case was low compared to previous years. This figure was selected from a larger series of recent surveys as representative of one of many variable anchovy distribution patterns. The x's represent high relative densities, open circles moderate, dashes low, and blank spaces very low or negligible values. The letter "A" shows the location of Anacapa Island (including Scorpion Rock) and the letter "C," Islas Coronados. Major offshore islands are shown in black. B. Total anchovy reduction catches by California Department of Fish and Game block for 1972 through 1977 (catch in 1978 was nearly nil) in the Southern California Bight during the brown pelican breeding period (February through May). Increasing sizes (5 sizes) of circles indicate increased catches in the 10-minute blocks as follows (lbs $\times$ 10^6): <1,000, 1-5,000, 5-25,000, 25-75,000, and >75,000. In August 1973 and 1974, there were also 2,672 $\times$ 10^6 and 221 lbs $\times$ 10^6 of anchovies taken, respectively, very near Anacapa Island. Due to a consistent, but unavoidable, failure of three boats operating near Anacapa Island to report exact areas of catch by block, the catches for all those blocks surrounding Anacapa should be increased by about 20% to more accurately reflect effort there (K.F.M.).

GENERAL DISCUSSION AND CONCLUSIONS

We believe that potential interaction between brown pelicans and newly adopted commercial fishing quotas for anchovies represents a challenge for wildlife and fisheries managers alike. Of course we can only predict what might happen and can never know for sure until pelicans have been monitored for many years under such a regime. MacCall (1974), Radovich (1979), and others have urged careful expansion of the southern California anchovy fishery in light of multiple uses of this resource. We think the management and conservation needs of offshore wildlife such as brown pelicans add a new dimension to the goals of management of commercially valuable resources such as anchovies. The PFMC Anchovy Management Plan already provides viable harvest options that can be altered or chosen to best fit the needs of multiple use.

The dependency of brown pelicans on anchovies under present conditions is well demonstrated, but more quantitative data are needed for recommendations on management specifics. Tentatively, it appears that a larger forage reserve is needed. Regarding production of brown pelicans, and likely other avian piscivores in the SCB, it seems that the most effective management will occur when anchovy populations are maintained above B_{min}.

Even from the limited data presented here, it is suggested that some brown pelican feeding zones (critical habitat by the ESA) need to be defined soon. Refuges and closed areas should be established by the management agencies to minimize adverse wildlife and commercial fishery interactions.

A crude estimate of forage requirements (even assuming total anchovy diet) indicates that pelicans, as only one of many potential predators, consume negligible proportions of total anchovy biomass. Assuming a mean resident

pelican population of 6,000 SCB birds (see Briggs et al. 1980), a food requirement of about 2 lbs/day (Anderson unpublished data), 2,000 breeders producing 900 young each year at 150 lbs/young (see Schreiber 1976), only 0.08% of the mean SCB anchovy biomass of 2.75 million short tons (MacCall 1980), or about 2,260 short tons/year (including 67.5 short to produce young) is required. With migrant pelicans added in the fall period (Anderson and Anderson 1976) and assumed to be about 75,000 birds for a mean period of three months (Briggs et al. 1980), this requirement increases to only 0.33%, or about 9,000 short tons. However, the conditions of the food-base resource would seem to strongly dictate the status of pelican populations, for the birds require a much larger population size to produce availability levels such that this ration can actually consumed.

Several fishing management promoters may therefore need reexamination as seen by the brown pelican; and in the least, we hope that we have stimulated enough interest to further necessary studies, and with more species of seabirds. Seabirds represent a potential tool to fishery managers besides being valuable resources in themselves. Fishery managers in the SCB have requested that wildlife managers provide them added input, and we hope that a start has been made here, although perhaps meagre.

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REPRODUCTIVE ECOLOGY OF WESTERN GULLS AND XANTUS' MURRELETS WITH RESPECT TO FOOD RESOURCES IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Western Gull (*Larus occidentalis*) and Xantus' Murrelet (*Endomychura hypoleuca*) reproduction on Santa Barbara Island, California, showed considerable sensitivity to changes in pelagic fish populations in the Southern California Bight. Western Gulls responded to decreases in the availability of schooling fish by failing to breed or by switching to alternate foods. The use of alternate foods may result in lower growth rates and chick survival. Timing of breeding was not significantly changed. Xantus' Murrelets foraged on larval fish, particularly larval northern anchovies (*Engraulis mordax*). Murrelets responded to the unavailability of larval anchovies either by failing to breed or by delaying breeding until larval anchovies became available. Our results demonstrate not only the sensitivity of marine bird reproduction as an indicator of the availability of their food resources, but also how specific differences in reproductive biology influence the flexibility of response to environmental change.

RESUMEN

La reproducción de la gaviota del oeste (*Larus occidentalis*) y el arán de Xantus (*Endomuchura hypoleuca*) en la Isla de Santa Bárbara, California, presentaron gran sensibilidad a los cambios en las poblaciones de peces pelágicos en la Bahía del Sur de California. Las gaviotas no criaron o variaron su régimen alimenticio cuando se produjo un descenso en la abundancia de peces en los cardúmenes. Al utilizar otros alimentos se puede producir una disminución en el índice de crecimiento y en la supervivencia de los polluelos. El tiempo de crianza no cambió significativamente. El arán de Xantus se alimentaba de larvas de peces, particularmente de anchoveta del norte (*Engraulis mordax*). Cuando hubo una escasez de larvas de anchoveta, el arán no lograba criar o retrazaba la época de cría hasta que las larvas de anchoveta eran abundantes. Nuestros resultados muestran no sólo la sensibilidad de la reproducción de aves marinas como un indicador de la disponibilidad de sus recursos de comida, sino también muestran cómo las diferencias específicas en la biología de reproducción influyen en la flexibilidad de respuestas a cambios en el medio ambiente.

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INTRODUCTION

Ashmole (1963) hypothesized that "... short term and even slight fluctuations in the availability of food . . ." would have " . . . a profound effect on the breeding success in a particular season . . ." for tropical seabirds. He documented a number of cases in which reproductive success was diminished by chick mortality due to starvation. Harris (1978) also discussed the impact of food availability on temperate-breeding Common Puffins (*Fratercula arctica*). He found that supplemental feedings allowed chicks to grow faster and attain a heavier weight, and he suggested that these extra reserves of fat could be of survival value in brief episodes of food shortage.

Other workers have found that changes in food availability may affect not only reproductive success but also the number of birds attempting to breed. In both the guano industries of South Africa and of Peru, declines in fish abundance have been reflected by declines in the number of adult birds attempting to breed (Crawford and Shelton 1978; Jordan 1967; Murphy 1973). Ainley and Lewis (1974) also suggest that certain bird populations on the Farallon Islands, California, have been reduced due to the demise of the Pacific sardine (*Sardinops caerulea*), but their evidence is mostly circumstantial.

Evidence that fluctuations in the availability of a single food species might have a significant impact on the reproductive biology of a presumably generalized forager was presented by Hunt and Hunt (1976b). They found in Western Gulls (*Larus occidentalis*) nesting on Santa Barbara Island, California, a strong inverse correlation between the percent of chicks found empty and the percent of chicks containing anchovies in any one day's sampling. Gull chick survival is linked to food not only through starvation, but more importantly through behavioral differences in satiated and hungry chicks (Hunt and McLoon 1975; Hunt and Hunt 1976a).

We here examine the foraging preferences of two species of seabirds, the Western Gull and the Xantus' Murrelet and the effect of changes in northern anchovy availability on their reproduction at Santa Barbara Island. In particular, we show that as the availability of anchovies fluctuates, Western Gulls on Santa Barbara Island have different responses to these changes than Xantus' Murrelets nesting on the same island.

METHODS

To measure the impact of changes in prey availability on seabird reproductive ecology, it is necessary to determine prey availability or abundance, the number of birds attempting to breed, and their reproductive performance. Three measures of reproductive are phenology, chick growth rates, and the number of chicks surviving to some age or weight criterion.

The number of Western Gulls attempting to nest on Santa Barbara Island was determined by direct counts of incubating and territorial gulls. Counts were made during the incubation period from a series of vantage points that allowed us to enumerate all nesting birds. Counts were repeated as often as once per week in some years to insure accuracy. Xantus' Murrelet numbers were not censused with sufficient accuracy to allow a quantitative assessment of their numbers. However, qualitative assessments of changes in abundance were made by individuals studying murrelet biology around the periphery of Santa Barbara Island.

The reproductive phenology of Western Gulls was measured on the major portion of Western Gull population in 1972 and 1974, and in 1975-77 in five 100 x 100-m grids on the west side of the Island. By concentrating our efforts consistently in these five grids, we avoided the potential problems of variability in the age or experience of the gulls biasing our year-to-year comparisons. Although formal study quadrants were not set up for Xantus' Murrelets, the same areas were used for study each year. Breeding phenology of Western Gulls and Xantus' Murrelets was determined by checking staked nests at least once every four days. In some years checks were made more frequently.

Growth rates of gull chicks were calculated using the slope of the linear portion of the growth curve (Spaans 1971; Hunt 1972; Hunt and Hunt 1975, 1976a) that occurs when Western Gull chicks weigh between 125 and 600 g. Weights were checked approximately once every four days. Xantus' Murrelet chicks are not fed in the short interval between hatching and their departure to sea, so growth rates could not be obtained for this species.

Gull chicks were recorded as surviving when they attained a weight of 500 g. Xantus' Murrelet chick survival is not relevant to the present study, as the major source of their mortality is predation by mice (Hunt et al. 1979).

Samples of food used by Western Gulls were obtained from chicks when they voluntarily regurgitated material during handling for banding or weighing. Occasionally samples were extracted by inserting an index finger down a chick's throat and withdrawing the contents of the proventriculus (Hunt 1972). Samples were obtained from chicks of all sizes and throughout the period when chicks were present on the Island. Most samples were obtained

before 1000 or after 1600 in order to avoid subjecting chicks to heat stress during midday. Except for 1972, when samples were identified in the field (Hunt and Hunt 1976b), food samples were preserved and subsequently identified in the laboratory. Since anchovies appear to be a preferred food in the diet of Western Gulls at Santa Barbara Island, the percent weight or percent occurrence of anchovies in the diet of chicks is assumed to be a measure of their availability to foraging Western Gulls.

A second method for estimating changes in the abundance, and presumably the availability of anchovies, was to compare the year-to-year changes in the tonnage of anchovies reported by commercial fish spotters (Squire 1972). An index of northern anchovy abundance was calculated on the estimated total tons of anchovies reported by commercial spotters for daytime flights during the first and second quarters of each year, divided by the number of times pilots flew through the foraging areas used by Western Gulls nesting on Santa Barbara Island. The foraging area was determined from studies of radio-tagged and color-banded gulls reported in Hunt et al. (1979).

RESULTS

Adult Western Gulls feed their chicks by regurgitating food to them at the nesting territory. Western Gulls in the Southern California Bight use a wide variety of foods (Table 1). Foods used varied from colony to colony, presumably depending upon what was consistently most readily available near the colony. Likewise for a given colony, the types of foods used varied from year to year, again presumably reflecting changes in availability (Tables 2-4).

On Santa Barbara Island, not only do we have a longer time period over which sampling has been done, but also we have obtained considerable independent data on anchovy availability and reproductive success. From Table 4 it is clear that Santa Barbara Island Western Gulls depend primarily on fish, and to a lesser extent on the market squid, *Loligo opalescens*. These gulls did not make extensive use of intertidal organisms, and in only one year, 1976, did sea lion (*Zalophus californicus*) placentae or garbage and offal constitute a significant portion of their diet.

The species of fish taken by the Western Gulls on Santa Barbara Island have varied from one year to another. Most striking is the marked decline in the use of northern anchovies from a high of 42% of the diet in 1972 to a low of 18% in 1977. Alternative species taken have included Pacific saury, *Cololabis saira*, and the market squid. Only in 1976, when apparently there were no alternative marine species available, did gulls resort to using sea lion placentae and garbage, the availability of which is unlikely to change from one year to the next.

Over the course of the study, not only has the per-

centage of anchovies fed to gull chicks declined, but also the number of pairs laying eggs at Santa Barbara Island has decreased (Figure 1). This drop in the number of nesting birds has paralleled a decline in the amount of anchovies seen during daytime surveys in the first quarter of the year by commercial spotter pilots (Anchovy Stock Index; Figure 1). The correlation between numbers of breeding gulls and the Anchovy Stock Index is statistically significant ($r = 0.97$, $N = 4$). Given the relative importance of anchovies to the reproductive biology of this population of Western Gulls, it is reasonable to assume that changes in the yearly availability of anchovies influence the number of gulls attempting to breed.

The amount of anchovies fed to chicks also correlates with the abundance of anchovies (Figure 2), although in an unanticipated way. There is a very strong correlation ($r = 1.00$, $N = 4$) between the percentage of anchovies in the chick diets and the log of the Anchovy Stock Index for the first quarter of the year, during which gulls are preparing to nest. There is no statistically significant correlation between the Anchovy Stock Index during the second quarter when nesting and chick growth is occuring and the percentage of anchovies in the diets of chicks ($r = 0.33$, $N = 4$).

Gull chick survival has been correlated with growth rates in this study (Figure 3; $r = 0.99$, $N = 4$) and other

TABLE 1

Foods Commonly Fed to Western Gull Chicks, 1975-77

	Percent by occurrence			
Island	Prince	San Nicolas	Santa Barbara	Anacapa
N	87	76	250	36
Food type				
Euphausiacea	0	7	4	0
Loligo opalescens	21	15	4	3
other Cephalopods	7	1	2	8
other mollusks	0	9	1	0
Engraulis mordax	5	14	24	11
Porichthys notatus	2	4	1	3
Merluccius productus	5	1	3	3
Cololabis saira	1	1	30	8
Atherinops affinis				
Sebastes sp.	14	9	6	17
Perciformes	1	5	2	25
unidentified and				
other fish	45	29	15	31
all fish	68	63	81	98
sea lion placenta	3	18	4	0
garbage and offal	7	3	6	14

TABLE 2

Food Commonly Fed to Western Gull Chicks, Prince Island

	Percent by weight		
Year	1975	1976	1977
N	26	27	34
Food type			
Euphausiacea	1	0	0
Loligo opalescens	58	7	28
other Cephalopods	0	1	4
other mollusks	0	0	0
Engraulis mordax	0	21	0
Porichthys notatus	0	16	0
Merluccius productus	0	3	19
Cololabis saira	0	2	0
Atherinops affinis	0	0	0
Sebastes sp.	0	13	8
Perciformes	0	5	2
unidentified and			
other fish	30	22	17
all fish	30	82	46
sea lion placenta	3	3	0
garbage and offal	8	7	25
other	0	1	0

TABLE 3

Foods Commonly Fed to Western Gull Chicks, San Nicolas Island

	Percent by weight		
Year	1975	1976	1977
N	21	39	15
Food type			
Euphausiacea	0	6	0
Loligo opalescens	9	18	26
other Cephalopods	0	6	3
other mollusks	0	6	0
Engraulis mordax	16	22	0
Porichthys notatus	0	6	4
Merluccius productus	0	0	14
Cololabis saira	0	0	0
Atherinops affinis	0	13	6
Sebastes sp.	0	3	3
Perciformes	0	3	0
unidentified and			
other fish	59	2	13
all fish	75	49	40
sea lion placenta	14	16	10
garbage and offal	0	0	13
other	0	1	8

TABLE 4

Foods Commonly Fed to Western Gull Chicks, Santa Barbara Island

|	Percent by weight			
	1972	1975	1976	1977
N	157	18	79	153
Food type				
Euphausiacea	0	0	0	0
Loligo opalescens	12	8	4	3
other Cephalopods	0	0	2	1
other mollusks	0	2	0	0
Engraulis mordax	45	32	28	18
Porichthys notatus	2		0	4
Merluccius productus			2	2
Cololabis saira	3	4	7	53
Atherinops affinis			6	0
Sebastes sp.			13	3
Perciformes			2	2
unidentified and				
other fish	30	46	9	7
all fish	80	82	65	89
sea lion placenta	0	4	15	1
garbage and offal	7		13	3
other	0	5	0	2
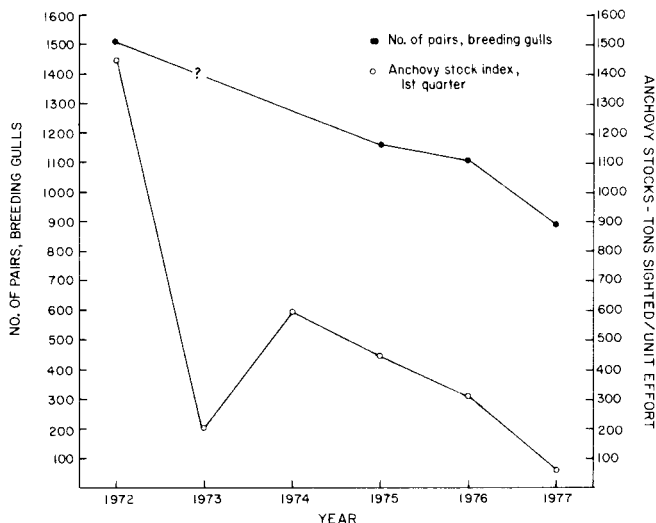
Figure 1. Recent changes in the number of Western Gulls breeding on Santa Barbara Island showing similar changes in the abundance of northern anchovies (see text for an explanation of the Anchovy Stock Index).

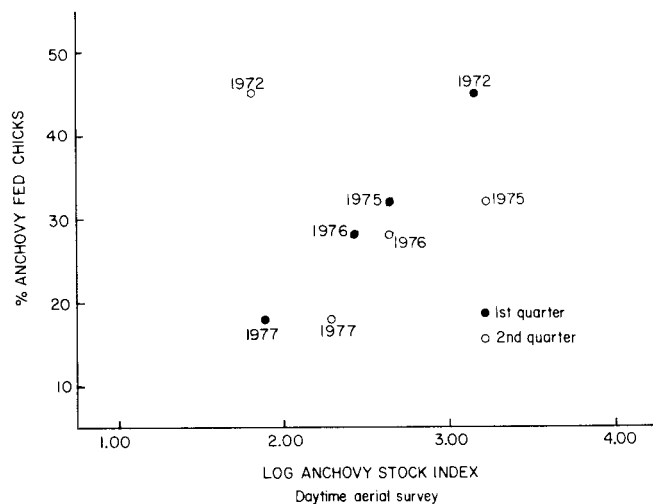Figure 3. Relationship of Western Gull chick survival to their growth rates on Santa Barbara Island.

Figure 2. Relationship between the Anchovy Stock Index in the first quarter (January-March) and the second quarter (April-June) and the percent anchovies in the diets of Western Gull chicks.
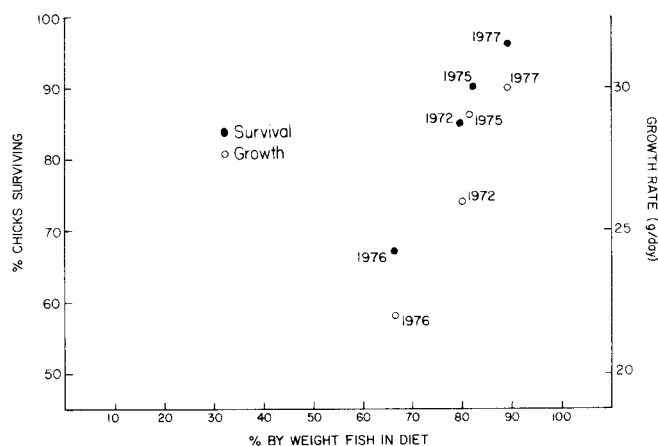
Figure 4. Relationship between the amount of fish in the diet fed young Western Gulls by adults and the growth and survival of gull chicks on Santa Barbara Island.

studies (Hunt and Hunt 1975, 1976a). Growth rates in turn were influenced by the amount of fish in the diets of chicks (Figure 4; $r = 0.98, N = 4$), but they were not significantly correlated with the percent of anchovies in the diet ($r = 0.30, N = 4$). In 1977 growth rates were high, despite the reduced use of anchovies. The use of sauries clearly made up for the lack of anchovies in 1977.

The timing of egg laying by Western Gulls might have also been expected to be sensitive to food availability (Hunt and Hunt 1976a). However, on Santa Barbara Island there was virtually no difference in the mean date of egg laying for any of the four years studied (Figure 5).

In contrast, Xantus' Murrelet clutch initiation varied in 1976, 1977, and 1978 (Figure 6). In 1978, murrelet egg laying was delayed by five to six weeks. When laying

did begin, the number of birds nesting appeared reduced. Additionally, the interval between laying of eggs and the period of time between exchange of incubating adults was increased (Hunt et al. 1979).

Murrelets eat larval fish, particularly larval anchovies (Hunt et al. 1979). According to Lasker (1979), in 1978 larval anchovies failed to survive the stage of first feeding until after March. Thus, the late-larvae of the anchovies, upon which these birds appear to be specialized foragers, would not have been available until late April or early May, instead of in late February or early March as is more usual.

DISCUSSION

This study shows that Western Gulls feed their chicks a wide variety of foods, most of which are pelagic in origin

Figure 5. Clutch initiation in Western Gulls, Santa Barbara Island.

Figure 6. Clutch initiation in Xantus' Murrelets, Santa Barbara Island.

distant, less nutritious (Hunt 1972) garbage (Table 4, 1976), growth rates and reproductive success declined.

As additional data on anchovy abundance become available, it will be interesting to see if the number of gulls attempting to breed at Santa Barbara continues to track changes in anchovy populations. There appears to be uncertainty about the true size and health of the central stock of northern anchovies in the California Current. The numbers of breeding gulls at Santa Barbara Island may provide an index of their prey populations, much as have the guanay birds in Peru and southern Africa (Crawford and Shelton 1978; Murphy 1973; Jordan 1967).

The contrast between the reaction of the gull population and the murrelet population to food shortage is remarkable. In particular, the murrelets apparently delay reproduction while food is scarce. The Xantus' Murrelet has one of the largest eggs and clutches in relation to adul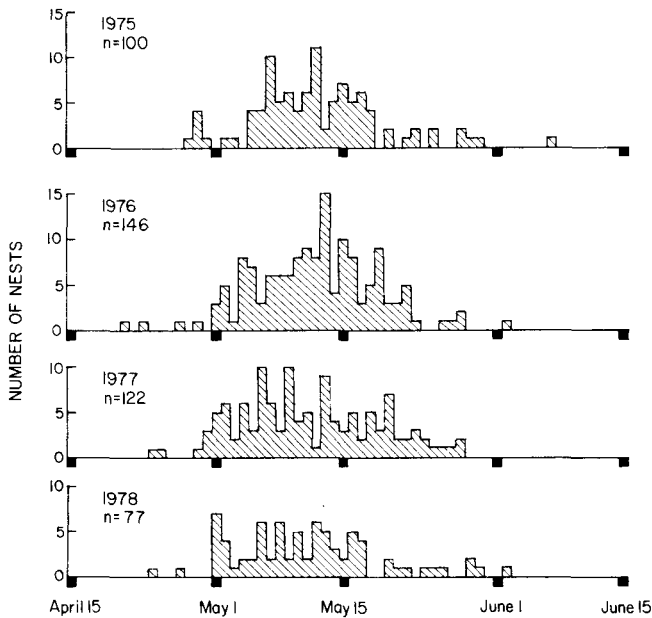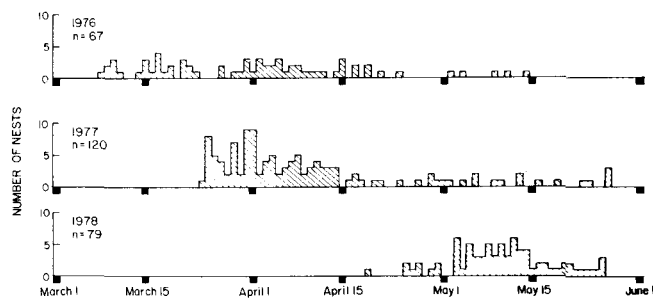t body weight of any seabird (Sealy 1975). This species may have a very precarious energy balance when it comes to egg production and may have no option but to delay egg-laying if its preferred foods are scarce. The delay in breeding in 1978, coupled with the greater interval between laying of eggs and incubation exchange, supports this hypothesis.

In contrast, the Western Gull showed no striking changes in the date of egg laying. For this species the ratio of egg weight or clutch weight to female body size is relatively small, and with the addition of courtship feeding by the male (Hunt in press), the female may not be under particularly strong energetic constraints. However, because Western Gulls nest in the open, unlike murrelets which nest in caves or under bushes, and because chicks are sensitive to thermal stress (Hunt et al. 1979; Bennett, unpublished field notes; Sayce, unpublished field notes) delay of gull reproduction may increase exposure of chicks to lethal thermal stress. Thus, Western Gulls that are unable to procure sufficient energy for egg production at the appropriate season may forego reproductive effort entirely for that season. The low chance for survival of chicks hatched late in the season would not compensate for the effort and risk expended in attempting to reproduce. Rather, these birds stay in the vicinity of the colony, but do not attempt to hold territory or lay eggs.

These differences in the reaction of two species of seabirds to apparent shortage of food provide a means of determining more precisely changes taking place in forage fish populations. Since the birds depend upon different life-history stages of the fish, changes in bird reproduction can be related to specific aspects of the fish populations and can be separated from effects due to weather, disturbance, etc. Thus, these seabirds provide a powerful, alternative tool for monitoring marine populations.

and few of which can be considered offal. Each colony tends to differ from other colonies in the kinds of foods taken, and these variations are believed to reflect relative availability of foods.

Hunt and Hunt (1975) concluded that the reproductive success of this population of Western Gulls was clearly related to the availability of anchovies. Daily fluctuations in the delivery of food to the chicks in 1972 were correlated with the percent of anchovies brought to Western Gull chicks. The present study also suggests the importance of anchovies to the Western Gulls of Santa Barbara Island. However, we now find that Western Gulls can make use of alternative foods and have nearly as good reproductive success. Early in the breeding season, anchovy availability may determine the number of gulls attempting to breed. Later, during the chick phase, the presence of abundant, nutritious pelagic forage fish, regardless of species, appears critical. When gulls turned to

ACKNOWLEDGMENTS

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THE PINNIPEDS OF THE CALIFORNIA CURRENT

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ABSTRACT

There are six species of pinnipeds—California sea lion, *Zalophus californianus*; northern sea lion, *Eumetopias jubatus*; northern fur seal, *Callorhinus ursinus*; Guadalupe fur seal, *Arctocephalus townsendi*; harbor seal, *Phoca vitulina richardsi*; and northern elephant seal, *Mirounga angustirostris*—that inhabit the study area of the California Cooperative Oceanic Fisheries Investigations (CalCOFI).

The numbers of animals in each population are given; the size, distribution, and seasonal movements are described. The known prey species of the pinnipeds are listed for each species. The otariids, with certain exceptions, consume the same kinds of prey, although in slightly different amounts. In general they feed most commonly on the smaller schooling fishes and squids of the epipelagic zone, and the two sea lion species enter nearshore and estuarine waters to prey on small schooling and anadromous fish. The two phocids, again with certain exceptions, prey on different species. The elephant seal apparently feeds in deeper water than the harbor seal on benthic and demersal species and the harbor seal on nearshore demersal and neritic species, occasionally entering estuarine and river waters to prey on anadromous fish and such small schooling fishes that regularly enter these waters.

RESUMEN

Existen seis especies de pinípedos — el lobo marino de California, *Zalophus californianus*; el lobo marino del norte, *Eumetopias jubatus*; el oso marino austral del norte, *Callorhinus ursinus*; el oso marino austral de Guadalupe, *Arctocephalus townsendi*; la foca peluda, *Phoca vitulina richardsi*; y el elefante marino del norte, *Mirounga angustirostris* — los cuales habitan el área de estudio de California Cooperative Oceanic Fisheries Investigations (CalCOFI).

Se da el número de animales de cada población; se describe el tamaño, la distribución, y sus desplazamientos con la estación. Se ha hecho una lista de las especies que se consideran son presas de cada especie de pinípedo. Los otariídos, con ciertas excepciones, consumen los mismos tipos de presas, aunque en cantidades ligeramente diferentes. En general se alimentan de los peces más pequeños en los cardúmenes y de calamares de la zona epipelágica, y las dos especies de lobo marino entran en la zona cerca de la costa y las aguas estuarinas y engullen los pequeños peces en los cardúmenes y peces anadromos. Los dos fócidos, otra vez con ciertas excepciones, predan especies diferentes. Aparentemente, el elefante marino se alimenta en aguas más profundas que la foca peluda, alimentándose de especies demersales y bénticas, y la foca peluda se alimenta de especies demersales costeras y neríticas, entrando ocasionalmente en ríos y aguas estuarinas haciendo presa de los peces anadromos y otros pequeños peces que entran regularmente en estas aguas.

INTRODUCTION

The California Current, its components, and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) station plan have been described many times in the past and are well known (Kramer et al. 1972). Some portions of this area are inhabited by six species of pinnipeds—the California sea lion, *Zalophus californianus*; the northern sea lion, *Eumetopias jubatus*; the northern fur seal, *Callorhinus ursinus*; and the Guadalupe fur seal, *Arctocephalus townsendi*—and two phocids (earless seals)—the harbor seal, *Phoca vitulina richardsi*; and the northern elephant seal, *Mirounga angustirostris*. These six species are year-round residents, although the northern fur seal is present in large numbers only from January to April, and several others make seasonal migrations throughout the region.

In this paper we present both published and unpublished information on population size, on sightings at sea, and on food and feeding habits of each pinniped species found in the CalCOFI area. Their feeding activities are compared, and predation on commercially valuable fish species is discussed.

SPECIES ACCOUNTS

California Sea Lion, *Zalophus californianus*

Physical Description

The California sea lion is the most commonly observed pinniped in the CalCOFI study area. The species is characterized by relatively short hind flippers and by foreflippers that are haired on the dorsal surface from the insertion of the limb down to the first or second digit. Adult males weigh about 380 kg and measure about 2.2 m in length; their pelage is mostly dark brown with a light (almost white) sagittal crest. Adult females are consider-

ably smaller, weighing about 100 kg and reaching 1.8 m in length; their pelage varies from light brown to straw color. At sea both males and females usually appear dark chocolate-brown to gray. Newborn pups are dark brown, weigh about 9 kg, and measure 65 cm in length.

Distribution and Migration

The California sea lion ranges along the west coast of Mexico from about Latitude 19°N northward to southern British Columbia, Latitude 50°N; its breeding range extends from several Gulf of California islands north to San Miguel Island, California. Some pupping has been reported north to the Farallon Islands, but the overall effect of pupping north of San Miguel on the population is minimal (Ainley 1977; Braham 1974).

During the breeding season (May-July), almost the entire population of 80,000 to 125,000 animals is found south of 34°N Latitude (National Marine Fisheries Service 1978; Le Bouef et al. 1976). Beginning in mid-July, a portion of the male population migrates northward, some reaching waters off Vancouver Island, British Columbia. Mate (1975) estimated that 4,000 males may be found north of California from early fall (September) until spring (May) and the rest of the population remains in California and Mexican waters.

Le Bouef et al. (1976) carried out surface and aerial surveys of the Southern California Bight in 1975-76 from about Point Conception (34°30'N, 121°10'W) south to 32°20'N. This area included the California Channel Islands and most major banks and ridges. The Southern California Bight includes northern breeding islands that support a population of about 40,000 during the breeding season. Le Bouef concluded that California sea lions are mainly coastal animals that rarely venture more than 50 km from their hauling grounds. In 1965-66, Marine Mammal Division personnel of the NMFS Northwest and Alaska Fisheries Center (hereinafter referred to as MMD) carried out a series of surface transects starting from about 8 to 16 km offshore and extending for 185 to 200 km at intervals of 20' of latitude from 32°N to 38°N. The objective of the survey was to determine the winter distribution of the northern fur seal; however, records were kept of all marine mammals sighted (Fiscus and Kajimura 1967, 1969). In 1976 Le Bouef and his colleagues observed California sea lions along similar transects. The reports from both of these surveys confirmed that this species is a coastal animal rarely venturing seaward off the continental slope. Out of 278 sightings, MMD personnel reported a few sightings of single or, in one instance, two animals sighted over deep water, well offshore: 1) 16 April 1965, one adult male sighted at 37°58'N, 125°25'W, 122 km west of Point Reyes, California; 2) 3 February 1966, one adult male sighted at 33°20'N, 121°33'W, 126 km southwest of San Miguel

Island, California; 3) 4 February 1966, a pair and one adult sighted at 34°00'N, 122°14'W, 161 km west of San Miguel Island, California.

Food and Feeding Habits

Known prey species consumed by the California sea lion include: Pacific lamprey, *Entosphenus tridentatus*; Pacific herring, *Clupea harengus pallasi*; northern anchovy, *Engraulis mordax*; salmon, *Oncorhynchus* sp.; plainfin midshipman, *Porichthys notatus*; Pacific hake, *Merluccius productus*; Pacific tomcod, *Microgadus proximus*; jacksmelt, *Atherinopsis californiensis*; white croaker, *Genyonemus lineatus*; jack mackerel, *Trachurus symmetricus*; rockfish, *Sebastes* sp.; rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; English sole, *Parophrys vetulus*; and squid, *Loligo opalescens* (Ainley et al. 1977; Best 1963; Briggs and Davis 1972; Fiscus and Baines 1966; Jameson and Kenyon 1977).

Sea lion spewings were examined at Southeast Farallon Island throughout the year when animals were present (Ainley et al. 1977). Investigators discovered Pacific hake to be an important food item, being found almost exclusively in the spewings when the population peaked on its southbound migration in April and May, at the time when hake are beginning to appear on the continental shelf in that vicinity. Sea lion numbers during this peak period in 1974-75 were slightly under 1,400 animals and in 1976 slightly under 1,200.

One of the authors (G.A.A.) collected 50 California sea lion scats from haul sites and rookeries on San Miguel Island in August 1978. Otoliths and cephalopod beaks found in the scat samples were identified by John E. Fitch (California Department of Fish and Game, Terminal Island) and by Clifford H. Fiscus, respectively. Pacific hake (mostly juvenile) occurred in 24 samples; rockfish (mostly juvenile) in 20; northern anchovy in 3; California lanternfish, *Symbolophorus californiensis*, in 1; queenfish, *Seriphus politus*, in 2; pink seaperch, *Zalembius rosaceus*, in 1; Pacific pompano, *Peprilus simillimus*, in 1; *Loligo opalescens* in 30, *Onychoteuthis borealijaponicus* in 6; Gonatidæ in 3; *Histioteuthis* sp. in 1; and Octopoda (mostly very small) in 7.

Fiscus has seen sea lions leave the rookeries and haul sites, form into large groups, and presumably leave for the feeding areas. Large groups of sea lions have been observed feeding in relatively small areas where prey items are highly concentrated; however, the number of sea lions gradually decreases as prey becomes less abundant. The seasonal abundance of schooling fishes such as the northern anchovy, Pacific hake, and the squid, *Loligo opalescens*, in the vicinity of rookeries of the California Channel Islands provides an abundant food supply for this species. California sea lions appear to feed opportunistically on a variety of prey; however, seasonally abun-

dant small schooling fish and squid are common prey species.

Northern Sea Lion, *Eumetopias jubatus*

Physical Description

The northern sea lion is easily distinguished from the California sea lion by its larger size; members of this species are also recognized by their relatively short rear flippers and by a lack of hair on the dorsal surface of the foreflippers below the wrist.

Adult males weigh from 700 to 1,000 kg and reach 3.0 m in length; females weigh from 275 to 450 kg and reach 2.0 m in length (Bonnot 1951; Kenyon and Scheffer 1953). The pelage color in both sexes is blond dorsally and brown ventrally; adult males have a mane of longer hair on neck and shoulders. At sea they appear to be gray or light colored as compared to the darker California sea lion. Newborn pups weigh about 20 kg and are about 1 m in length.

Distribution and Migration

The species range extends around the North Pacific Ocean rim from off southern California, to the Bering Sea, to the Kurile Islands and the Okhotsk Sea. The southern limit of the northern sea lions' breeding range in the eastern North Pacific is presently located at San Miguel Island at about Latitude 34°N. In 1977, the breeding population on San Miguel and adjacent Castle Rock was comprised of four adult females, two large males, and three pups born during the season. The breeding colony at Año Nuevo Island at about 37°N numbered about 1,200 animals (Robert Gisiner, University of California Santa Cruz, personal communication), a decline of about 33% from the population described in 1968-69 (Mate 1977; Gentry 1970). The breeding colony at Southeast Farallon Island, at about 38°N Latitude, contains less than 200 animals. Ainley et al. (1977) reported a breeding population there of about 130 animals in 1976. The northern sea lion population on these three breeding areas has declined in numbers since the 1920's and 1930's, as indicated in available census data. The northern sea lion population off California north of 38°N Latitude in July numbers about 800 to 900 animals (Mate 1977); thus the California breeding season population numbers from 2,200 to 2,300 animals.

Most northern sea lions are on or near their breeding islands during May and June. After the breeding season, a general northward movement of male northern sea lions, similar to that which occurs in California sea lions, was proposed by Bonnot (1951) and by Bartholomew and Boolootian (1960). Adult females and young animals apparently stay in the general area of the southern rookeries year-round (Bonnot 1951; Orr and Poulter 1965; Spalding 1964; Le Bouef et al. 1976).

In 1958-61 and 1964-66, MMD personnel recorded 120 northern sea lions at sea. These animals were commonly seen in the nutrient rich waters of the continental shelf and slope in 50 to 200 m of water. There were a few occasions, however, when northern sea lions were observed in water deeper than 200 m.

Single northern sea lions were most commonly observed at sea, although small groups of two to four were occasionally seen. The largest group seen off California (37°09'N, 122°45'W) numbered 20 individuals.

Food and Feeding Habits

Prey species consumed by the northern sea lion in this region include rockfish; sanddab, *Citharichthys* sp.; and turbot, *Pleuronichthys* sp. (Fiscus and Baines 1966). In waters north of the CalCOFI area, prey species include Pacific lamprey: Pacific herring; salmon; smelt, Osmeridæ; Pacific hake; walleye pollock, *Theragra chalcograma*; greenling, Hexagrammidæ; sculpin, Cottidæ, Pacific sandlance, *Ammodytes hexapterus*; arrowtooth flounder, *Atherestes stomias*; flatfish, Pleuronectidæ; ratfish; *Hydrolagus colliei*; spiney dog fish, *Squalus acanthias*; squid; octopus; shellfish; and shrimp (Spalding 1964; Fiscus and Baines 1966).

The food and foraging habits of the northern sea lion are highly variable. Mathisen et al. (1962) and Spalding (1964) have shown that the food of this species varies with season, location, age class, and sex of the animals. In another food study, Fiscus and Baines (1966) suggested that northern sea lions feed in waters of less than 180-m depth. There are, however, offshore sightings of this species in water deeper than 200 m, which suggest that these animals are also epipelagic and mesopelagic feeders.

Northern sea lions presumably feed both nocturnally and diurnally. Several authors (Spalding 1964; Gentry 1970) reported evidence of nocturnal feeding during certain times of the year. Diurnal feeding was reported by Fiscus and Baines (1966).

Northern sea lions usually consume whole small fish and cephalopods below the surface. Larger prey are consumed at the surface, where the prey is torn to pieces by a violent shaking motion of the sea lion's head.

Northern Fur Seal, *Callorhinus ursinus*

Physical Description

The northern fur seal is easily distinguished from other otariids by its longer hind flippers, which are about twice the length of sea lion flippers, and by the hair line on the foreflipper which stops abruptly at the wrist line. Adult males weigh from 227 to 318 kg and may reach a length of 2 m, whereas females weigh from 36 to 59 kg and may reach 1.2 m in length (National Marine Fisheries Service 1978). Adult male pelage varies in color from dark brown to dark gray, with a mane of longer hair on the neck

and shoulder areas. Adult female pelage varies from dark brown to light gray brown and is usually lighter ventrally. At sea, fur seals appear black with a lighter muzzle and if startled, they often rear out of the water exposing lighter colored or gray throats. Pups weigh approximately 5.3 kg and measure about 50 cm in length at birth. The black birth coat is retained until fall, when at first molt the pup acquires a silver gray pelage.

Distribution and Migration

The northern fur seal ranges across subarctic waters of the North Pacific Ocean and portions of the Bering and Okhotsk Seas and the Sea of Japan. Its breeding grounds are located in the Pribilof and Commander Islands in the Bering Sea, Robben Island in the Okhotsk Sea, on several of the Kurile Islands in the western Pacific, and on San Miguel Island and adjacent Castle Rock off California in the eastern North Pacific Ocean. A maximum count of 2,388 fur seals was obtained for San Miguel Island and Castle Rock during the 1977 breeding season. Current population estimates of the more northern breeding locations are Pribilof Islands, 1,300,000; Commander Islands, 265,000; Robben Island, 165,000; Kurile Islands, 33,000.

Most fur seals are on or near their breeding islands from July to October. Southbound movements into wintering areas of the North Pacific Ocean and Sea of Japan begin in late October.

About 1,000,000 fur seals winter in the eastern North Pacific, from the Aleutian Islands eastward and south to about 32°N Latitude (Fiscus et al. 1977). In the offshore waters of California, the first seals begin to arrive in late November, generally moving south over waters of the continental shelf and slope with maximum numbers occurring from January to March from about 34°N to 42°N Latitudes. The northward migration begins in March and most seals have left the offshore area by early June with the exception of the San Miguel-Castle Rock population.

The fur seal wintering range extends south to about 32°N, although there have been verified sightings farther south. Most fur seals wintering in California waters are females of all age classes and young males 2-4 years old.

Fur seals seldom approach land during the winter months although there are a few exceptions. In 1965-66 off California, transects were run from near shore over the continental shelf and slope seaward over deep water. Seals were seldom seen within 18 to 28 km of shore, being most numerous along the continental slope and those areas where bottom topography caused upwellings of nutrient rich water (Fiscus and Kajimura 1967, 1969).

Fur seals are usually alone at sea, although pairs and groups of three are fairly common. The largest group seen during 15 years of ocean research numbered about 100 animals, its members feeding on a large school of an-

chovies off the Farallon Islands, California. Fur seal densities are quite variable, ranging from 0 to 20 per km².

Food and Feeding Habits

Fur seals congregate in areas of abundant food supply, even though they usually remain in small separate groups of two to three animals. On occasion larger groups of seals are formed but these probably disperse after the prey schools have broken up. Most feeding is done at night, although daytime feeding may occur when schools of prey are located near the surface. Fur seals are able to swallow whole fish or squid up to 25 cm in length but usually surface and break up larger prey there before eating it.

During pelagic studies of the northern fur seal off California from 1958 to 1966, 3,595 seals were taken, of which the stomachs of 2,516 contained food. Among the prey items identified were 26 species of fish and 9 cephalopods. Species of prey that formed a major portion of the fur seals' diet off California are listed in Table 1.

TABLE 1
Principal Prey from the Stomachs of Northern Fur Seals Collected off California[1].

| Species | Year and Month of Collection | | | | | |
	1958 Feb. Mar. Apr.	1959 Jan. Feb. Mar. Apr.	1960 Dec. Jan. Feb. Mar. Apr.	1964 Apr. May	1965 Apr.May June	1966 Jan. Feb. Mar.
	Percentage of Volume					
Engraulis mordax	14.3	58.9	29.7	2.1	15.0	74.4
Merluccius productus	17.0	24.4	7.1	73.8	36.7	19.8
Cololabis saira	20.7	3.5	13.4	0.4	3.0	2.8
Onychoteuthis borealijaponicus	.6	.6	27.2	2.4	2.6	1.0
Loligo opalescens	7.9	2.0	11.4	12.9	24.0	.5
Sebastes sp.	—	—	—	—	11.6	—
Trachurus symmetricus	5.1	2.4	—	—	3.3	—
Anoplopoma fimbria	—	—	—	7.5	—	—
Number of stomachs with food	323	893	565	228	226	331

[1]Data from North Pacific Fur Seal Commission 1965, 1969.
Note: Does not include all food items listed.

Guadalupe Fur Seal, *Arctocephalus townsendi*

Physical Description

The Guadalupe fur seal can be distinguished from the other otariids by the distinctive feature of having hair on the dorsum of the foreflipper that extends past the wrist line. Their rear flippers are relatively small and similar to those of the sea lions. Adult males grow to a weight of

about 170 kg and may reach 2.0 m in length. Females weigh over 50 kg and may reach 1.7 m in length. Their general overall color is dark brown with lighter shading on the chest. In addition to the obvious size difference, males have a mane of longer hair which also distinguishes them from females. At sea, both sexes appear black under most conditions. Newborn pups are probably about the same size and color as northern fur seal pups.

Distribution and Migration

The former range of the Guadalupe fur seal may have extended from about 18°N, Isla Socorro, northward to the Santa Barbara, California, Channel Islands to about 34°N, and there is some evidence from the bones of Guadalupe fur seals found in Indian kitchen middens that breeding colonies existed as far north as these islands (Repenning et al. 1971).

The Guadalupe fur seal breeds only on Guadalupe Island. Once thought extinct, an adult male was seen on San Nicolas Island in 1947, and breeding animals were rediscovered on Guadalupe Island in November of 1954 by Dr. Carl L. Hubbs (1956). Hubbs returned in June 1955 and counted more than 30 seals. Since 1955, counts of this species have been made periodically, and increasing numbers of animals have been found. The most recent counts were made in July and July 1977 by Fleischer (1978), who counted a total of 1,073 animals. Fleischer calculated that the population ashore in 1977 was made up of 30% mature males, 38% mature females, 19% pups, 7% juveniles, 2% subadults, and 4% uncategorized seals.

Recently, individual animals have been seen at Isla Cedros, Baja California (National Marine Fisheries Service 1978), and on San Clemente Island (Le Bouef et al. 1976). Robert DeLong and one of us (G.A.A.) both of the Marine Mammal Division, have observed one or more subadult or adult males at San Miguel Island each year since 1968. DeLong, Fiscus, and Karl Kenyon observed a juvenile female on San Miguel Island in 1971. On 25 April 1977, a young Guadalupe fur seal was found on a beach in Monterey Bay, California (M. Webber, personal communication).

The appearance of this species on islands in its former range, the midden records, Webber's record from Monterey Bay, and one sighting of a seal at sea in the Southern California Bight (Le Bouef et al. 1976) may indicate a breeding season movement of a few subadult and adult males and a northward post-breeding season movement of juveniles. Best and Shaughnessy (1975), in describing pup behavior of the Cape fur seal, Arctocephalus pusillus pusillus, report that pups begin to enter the water at about 4 and 5 months after birth; by 7 months of age they may stay away from land for 2 to 3 days at a time; and after that some may go to sea at age 7 months and by the 10th

month the seaward dispersal is quite evident. Should a similar pattern occur in the Guadalupe fur seal, most pups could be expected to be at sea from about February to April/May. The southern species of this genus does not migrate great distances from the rookery islands and spends more time on land or in the sea relatively near its regular haul sites. This same behavioral trait may also occur in the Guadalupe Fur Seal.

Food and Feeding Habits

We have no information on the prey species or feeding habits of the species. Shaughnessy (1976a) records the food of the Cape fur seal as 50% fish, 37% cephalopods, and 13% crustaceans. Of the fish, pilchards, anchovy, and hake were identified. Shaughnessy (1976b) listed fish, cephalopods, and euphausiids as prey of the Amsterdam Island fur seal, Arctocephalus tropicalis. Raul Vas-Ferreira (1976) recorded fish, cephalopods, and crustaceans as food of the South American fur seal, Arctocephalus australis, and Bonner (1976) listed krill, Euphausia sp., as the principal food of the Antarctic fur seal, Arctocephalus gazella.

Nurtient-rich waters surrounding Guadalupe Island support an abundant supply of small schooling fishes belonging to the same families as those utilized by their southern counterparts; squids of several species are plentiful in the area, and we can probably assume that anchovy, Pacific hake, jack mackerel, and other small schooling fishes and squid form a large portion of the Guadalupe fur seal's diet. Only one of the southern species existed principally on crustaceans; therefore, it is possible that if present in sufficient numbers, crustaceans may be utilized by the Guadalupe fur seal.

Harbor Seal, Phoca vitulina richardsi

Physical Description

The harbor seal is the smallest pinniped found in the CalCOFI study area. All flippers are relatively small and completely haired. Adults of both sexes generally weigh from 65 to 105 kg and reach from 1.2 to 1.8 m in length. Females usually weigh only about three-fourths the weight of males (Sheffer and Slipp 1944). The pelage of both sexes is spotted or mottled, and their general overall color ranges from silver gray to dark brown or black. At sea, they usually appear dark gray-brown or black with lighter mottling or spots. Most often, only the head is visible. The pelage of newborn pups is similar to that of the adults; however, there are rare occasions in California when they are born with a white lanugo coat (usually shed in utero). At birth, the pups weigh about 11 kg and measure 75 cm in length.

Distribution and Migration

Five subspecies of harbor seals are distributed along the coastline and offshore islands of the North Pacific Ocean, the North Atlantic Ocean, and contiguous seas. *Phoca vitulina richardsi* is the subspecies that inhabits the CalCOFI area (Shaughnessy and Fay 1977). It ranges from about 65°N Latitude southward along the coasts of Alaska, Canada, Washington, Oregon, California, and Baja California to Isla San Martin, 30°29′N, 116°07′W (Shaughnessy and Fay 1977; Scheffer 1974).

Harbor seals usually haul out on secluded beaches, rocky intertidal areas, or mud flats in bays and estuaries. There is no obvious segregation by sex or age class in these areas, although it is believed that some beaches are preferred for pupping (Houck 1975, personal communi-cattion; Le Bouef et al. 1976). Both Houck and Le Bouef report that in the spring, when the breeding season begins, the numbers of adults and newborn pups increase steadily. The population then reaches an annual high in early sum-mer, then again declining to the lowest numbers ashore in mid-winter.

In 1976 Mate (1976) conducted an aerial census from British Columbia southward to the Gulf of California between 17 June and 1 July. He reported a harbor seal count of 7,517 for Washington, Oregon, California, and Mexico, including a CalCOFI area count of 3,127 animals.

There is little evidence of seasonal migrations in har-bor seals, although seasonal changes in numbers in Hum-boldt Bay (Houck 1975, personal communication) and in the Southern California Bight (Le Bouef et al. 1976) suggest that some form of predictable haulout pattern may exist. It is not known if the smaller population ob-served during the non-breeding season represents a change in haulout behavior, or increased time spent at sea. There is evidence that harbor seals in the northeastern North Pacific Ocean are more pelagic during their foraging activities than previously suspected (Pitcher and Calkins 1978). In California waters, harbor seals have seldom been reported from water deeper than 90 m.

Food and Feeding Habits

Little is known about the food consumed by the harbor seals off California and Baja California. In one study, two harbor seals were collected by Bob DeLong at San Mi-guel Island on 2 June 1971. One harbor seal stomach contained otoliths from plainfin midshipman and pile-perch, *Rhacochilus (Damalilicthys) vacca*, whereas the other contained pileperch and an unidentified species of octopus. There are, however, several other studies of harbor seals in more northern waters that can also be used to generally describe harbor seal feeding habits. This spe-cies is believed to be an opportunistic feeder, preying on seasonally abundant species (Scheffer and Sperry 1931;

Scheffer and Slipp 1944; Spalding 1964; Calambokidis et al. 1978). All of these authors reported a wide variety of food items including Pacific hake; plainfin midship-man; walleye pollock; Pacific tomcod; Pacific staghorn sculpin, *Leptocottus armatus*; starry flounder, *Platich-thys stellatus*; Pacific herring; rockfish; salmon; and a few species of squid, octopus, crustacea, and bivalve mollusc.

Harbor seals are believed to be late afternoon feeders (Spalding 1964), although movement to the water is also related to tidal changes and changes in the diel photo-period (Woodhouse personal communication; Kenyon 1965; Spalding 1964). Typically, large prey are con-sumed at the surface, whereas smaller prey are eaten underwater. Bivalve molluscs are brought to the surface, crushed, and opened in the mouth before consumption (personal observation G.A.A.).

Northern Elephant Seal, *Mirounga angustirostris*

Physical Description

The northern elephant seal is the largest pinniped found in the CalCOFI study area. All flippers are relative-ly small and completely haired. Adult males grow to a weight of about 2,700 kg and a length of 5.0 m. They can be easily distinguished from females by their long pro-boscis and thickly wrinkled neck shields. Adult females may weigh 900 kg and reach a length of about 3.4 m. The color of the pelage of both sexes ranges from silver-gray to light brown. At sea their pelage varies in color from gray-black to black. Newborn pups have a black pelage and may weigh 35 kg and reach about 1.0 m in length.

Distribution and Migration

The population has recovered from an estimated low of 100 in 1890 to its present high of about 60,000 (Le Bouef and Bonnell in press). This species ranges along the west coast of Baja California northward into the Gulf of Alas-ka and breeds from Isla Natividad, Mexico, north to the Farallon Islands, California. Breeding rookeries are lo-cated on Isla Natividad, Isla Cedros, Islas San Benito, Isla Guadalupe, Isla San Martin, and Islas Los Coro-nados in Mexico, San Miguel Island, Año Nuevo Island, Point Año Nuevo, and Southeast Farallon Island off California (National Marine Fisheries Service 1978; Le Bouef and Panken 1977; Le Bouef and Mate 1978). There are three records of elephant seals from the east-ern Aleutian Islands in 1977-78 (David Withrow, per-sonal communication) and two records from Midway Atoll, northwestern Hawaiian Islands in 1978 (John Naughton, personal communication).

The portions of the elephant seal population at sea varies according to season. Le Bouef et al. (1976) de-scribe the periods ashore for the islands of the Southern California Bight. During the breeding season (from about

December to 15 March), breeding-age males, adult females, and newborn pups are ashore; during the spring season (from about mid-March to early June), adult females and juveniles molt and the pups begin to go out to sea; during the summer (from early June through August), subadult and adult males are molting; during the fall (from September through November), yearlings and juveniles 2 to 5 years haul out. Thus the entire population is not at sea at any given time as is the case of the northern fur seal. During fur seal research cruises off California between 1958 and 1966 (388 sea days), MMD personnel sighted 51 elephant seals, all solitary animals. During the period 9 May 1975 to 15 March 1976, Le Bouef et al. (1976) sighted 28 animals in the Southern California Bight, most of which were individual animals. Our sightings were made over the continental shelf and slope. Scheffer (1964) records the taking of three young elephant seals from a depth of 180 m (100 fathoms) on longline gear set for sablefish, *Anoplopoma fimbria*, about 26 August 1963 off Florence, Oregon. The largest animal, estimated to be 2-3 years old, from cranial characters and teeth, was dead; the two smaller seals were still alive and were released by the fisherman. This report is our only record of three seals being in the same area at the same time at sea and represents the only depth of dive records. The MMD has several reports of this species from seaward of the continental shelf over deep water from fishermen and from recent Alaskan and Midway Atoll sightings which indicate that some offshore movements must occur.

Food and Feeding Habits

Information on the food and feeding habits of the northern elephant seal are scanty. Anthony (1925) mentions that of the seals (seven) taken in 1892 on Isla Guadalupe, the stomach of one contained a fish, *Sebastes* sp., and a few fragments of kelp, and the other stomachs were found to be empty. Townsend (1912) mentioned that Harris found small sardines, not more than 2 inches long, in the stomach of an elephant seal he took in 1907. Huey (1930) reports that the stomach of the large adult male taken about 40 miles (74 km) off Point Loma, California, on 20 September 1929, contained seven ratfish; one spiney dogfish; one swell shark, *Cephaloscyllium ventriosum*; three skate, *Raja* sp.; and four squid, *Loligo opalescens*. Cowan and Guiguet (1965) wrote that the stomach of a seal taken at Ucluelet, British Columbia, contained only eggs of Pacific hagfish, *Eptatretus stouti*, and a vertebral column, also possibly from a hagfish.

Brown and Norris (1956) reported seeing adult elephant seals on three occasions with groups of Pacific whiteside dolphin, *Lagenorhynchus obliquidens*, and California sea lions, all apparently feeding on the same northern anchovy school. Morejohn and Baltz (1970) examined the stomach contents of a subadult male found dead on a Monterey Bay beach on 20 December 1968 and from otoliths determined that the animal had eaten about 50 spotted cusk-eels, *Otophidium taylori*; 35 plainfin midshipmen; 10 rockfish; one flatfish; and two brown catsharks, *Apristurus brunneus*. The stomach also contained some unidentifiable teleost bones and an elasmobranch veterbral column.

Fiscus examined the stomach contents of four elephant seals found dead on Oregon beaches in 1973 for R. Stroud, School of Veterinary Medicine, Oregon State University, Corvallis, and identified the following species of cephalopods: Gonatidæ, 2 *Gonatus* sp., *Gonatopsis borealis*, *Chiroteuthis* sp., *Octopoteuthis* sp., *Onychoteuthis borealijaponicus*, *Rossia pacifica* and *Octopus* sp. In addition to the squids, the Pacific lamprey was found in two stomachs, and two species of flatfishes, Pacific sanddab, *Citharichthys sordidus*, and rex sole, were found in one stomach. From these records, it would appear that the elephant seal feeds principally on benthic neritic and demersal prey but does prey to some extent on epipelagic and mesopelagic species.

Identified prey species and pinniped population estimates are summarized in Table 2.

PREDATORS ON PINNIPEDS

Suspected predators of these pinnipeds are sharks of several species and killer whales. Rice (1968) listed the remains of California sea lions, northern sea lions, and northern elephant seals from the stomachs of killer whales, *Orcinus orca*. Kenyon (1959) identified the remains of California sea lions from the stomach of a white shark, *Carcharodon carcharias*.

DISCUSSION

Comparatively little is known about pinniped movements and feeding habits at sea, with the exception of the northern fur seal. We can, however, make some generalizations about feeding activites and foraging strategies of these six species by using available data.

In California waters, the schooling fishes and squid (Pacific hake, northern anchovy, jack mackerel, and the squid *Loligo*) are all commonly preyed on by otariids. We can assume that epipelagic and mesopelagic foraging is usual among otariids from what is known about the movement of these species both in coastal and offshore waters. Feeding in the epipelagic and mesopelagic zones is particularly true for the wintering northern fur seal when it arrives in California waters in December (from the northern rookeries) until it departs again in spring (Fiscus and Kajimura 1967, 1969).

The northern fur seal is the most pelagic of the four otariid species and seldom approaches land, whereas the two sea lion species do feed in the nearshore areas and to

TABLE 2

Summary of Prey Species and Pinniped Population Estimates in the CalCOFI Study Area.

Scientific name	Common name	Zalophus californianus (80,000 to 125,000)	Eumetopias jubatus (2,300)	Callorhinus ursinus 2,388 residents, [1] unknown number of winter migrants	Arctocephalus townsendi (2,000)	Phoca vitulina richardii (3,127)[1]	Mirounga angustirostris (60,000)
				Prey species [2]			
Eptatretus stouti	Pacific hagfish						C
Entosphenus tridentatus	Pacific lamprey	C	N	C			
Cephaloscyllium ventriosum	swell shark						
Apristurus brunneus	brown catshark						C
Squalus acanthias	spiny dogfish		N				C
Raja sp.	skate						C
Hydrolagus colliei	ratfish		N				C
Clupea harengus pallasi	Pacific herring	C	N	C		N	
Alosa sapidissima	American shad			C			
Sardinops sagax	Pacific sardine						C
Engraulis mordax	Northern anchovy	C		C			C
Oncorhynchus sp.	salmon	C	N	C		N	
Osmeridæ	smelt		N				
Hypomesus pretiosus	surf smelt			C			
Thaleichthys pacificus	eulachon			C			
Tactostoma macropus	longfin dragonfish			C			
Myctophidæ	lanternfish	C		C			
Paralepis atlantica	barracudinas			C			
Tarletonbeania crenularis	blue lanternfish			C			
Porichthys notatus	plainfin midshiman	C		C		C	C
Merluccius productus	Pacific hake	C	N	C		N	
Microgadus proximus	Pacific tomcod	C				N	
Theragra chalcogramma	walleye pollock		N			N	
Otophidium taylori	spotted cusk-eels						C
Cololabis saira	Pacific saury			C			
Antherinopsis californiensis	jacksmelt	C		C			
Trachipeterus altivelis	king-of-the-salmon			C			
Syngnathus californiensis	kelp pipefish			C			
Trachurus symmetricus	jack mackerel	C		C			
Scomber japonicus	chub mackerel			C			
Genyonemus lineatus	white croaker	C		C			
Seriphus politus	queenfish			C			
Rhacochilus vacca	pile perch					C	
Zalembius rosaceus	pink sea perch	C					
Ammodytes hexapterus	Pacific sandlance		N				
Peprilus simillimus	Pacific pompano	C					
Sebastes sp.	rockfish	C	C	C		N	C
Anoplopoma fimbria	sablefish			C			
Brama japonica	Pacific pomfret			C			
Medialuna californiensis	halfmoon			C			
Hexagrammidæ	greenling		N				
Cottidæ	sculpin		N				
Leptocottus armatus	Pacific staghorn sculpin					N	
Citharichthys sp.	flounder			C	C		
Citharichthys sordidus	Pacific sanddab						C
Pleuronectidæ	flatfish		N	C			C
Atheresthes stomias	arrowtooth flounder		N				
Glyptocephalus zachiris	rex sole	C					
Lyopsetta exilis	slender sole	C		C			
Parophrys ventulus	English sole	C					
Platichthys stellatus	starry flounder					N	
Pleuronichthys sp.	turbot			C			
Decapoda	squid		N			N	
Rossia pacifica	squid						N
Loligo opalescens	squid	C		C			C
Octopoteuthis sp.	squid			C			N
Onychoteuthis borealijaponicus	squid	C		C			N
Moroteuthis robusta	squid			C			
Gonatidæ	squid	C					N
Berryteuthis magister	squid			C			
Gonatus sp.	squid			C			N
Gonatopsis borealis	squid			C			N
Histioteuthis sp.	squid	C					
Dosidicus gigas	squid			C			
Chiroteuthis sp.	squid						N
Abraliopsis sp.	squid			C			
Octopoda	octopus	C	N	C		C	N
Pelecypoda	shellfish		N			N	
Crustacea	crab and shrimp		N			N	

[1] Actual count
[2] C=known prey in CalCOFI area. N=known prey north of the CalCOFI area.
[3] No prey species identified to date.

some extent in estuarine waters on seasonally abundant anadromous species of fish Fiscus (in press). Both species of sea lions and the northern fur seal apparently feed opportunistically on a variety of different prey. Some of these prey species are frequently preyed upon when they become more abundant during their seasonal migrations into nearshore waters and over the continental shelf and slope. Opportunistic feeding is substantiated by several reports on seasonal variations in feeding behavior of California sea lions (Ainley et al. 1977), northern fur seals (Fiscus and Kajimura 1967, 1979), and northern sea lions (Spalding 1964). We assume that Guadalupe fur seals exhibit feeding behavior similar to that of the other otariids, although studies of the food of this species have not been carried out.

Unlike the otariids, harbor seals and northern elephant seals most commonly feed on demersal prey species, although in different zones. Harbor seals probably forage near shore in less than 80 m of water, since flounder, sculpin, octopus, crustaceans, and bivalve mollusc are common food items (all from northern population; Spalding 1964 and Calambokidis et al. 1978). Harbor seals also feed opportunistically on seasonally abundant small schooling fishes that migrate near shore. Spalding (1964) reported relatively high consumption of salmon by harbor seals only during the fall migratory season in nearshore and estuarine waters.

The northern elephant seal feeds on several demersal and benthic species commonly found in water to 180 m (Huey 1930; Morejohn and Baltz 1970). Prey records of this species by Anthony (1925), by Townsend (1912), by Brown and Norris (1956), and the results of this study indicate that epipelagic and mesopelagic foraging also occurs when prey are abundant.

We assume that opportunistic feeding on a variety of prey species is common among these pinnipeds, and that during times of abundant food supply, foraging areas of different species overlap. One of us (C.H.F.) has personally observed California sea lions, northern fur seals, the saddleback dolphin, *Delphinus delphis*, and the Pacific whiteside dolphin all actively feeding on a single school of anchovies. When prey concentrations disperse, overlapping and competition in foraging areas declines. Thus, during a period of low prey abundance, one might expect to see the greatest degree of species separation as foraging occurs in the epipelagic and mesopelagic zones (>150 m) for northern fur seals, the neritic zone for both species of sea lion, the nearshore area for harbor seals, and the offshore demersal and benthic zone for northern elephant seals. During these same periods, we will also see a greater variety of prey species consumed.

The Guadalupe fur seal population is so small (a total population of probably no more than 2,000) that it could not significantly affect the abundance of fish and cephalopod resources of the region. The other three species of otariids (California sea lion, northern sea lion, and the northern fur seal) have populations that are large and are known to feed on a variety of commercially important fish and squids, including northern anchovy, salmon, Pacific hake, jack mackerel, and squid. The degree of pinniped predation on these species, however, is impossible to determine at this time since so little is known about the foraging behavior of these animals.

Information about the feeding habits of the two species of phocids (harbor seal and northern elephant seal) that inhabit the California Current region is extremely scarce. It is possible, however, that both species may affect the abundance of nearshore schooling fishes and squids, such as northern anchovy and *Loligo*. Furthermore, when elephant seals feed in deeper water there is a potential for competition with certain fisheries, such as longline fisheries for bottom fish.

It is possible that all fish species taken in the commercial fisheries might be potential food of these pinnipeds because of their opportunistic feeding behavior. At the present time, however, the effect of pinniped predation on the major commercial fisheries in the CalCOFI area cannot be determined. The establishment of the Fishery Conservation and Management Act of 1976, and the possibility of increased commercial fishing activities in pinniped foraging areas, could be of major concern in the future.

In addition to their potential impact on valuable commercial stocks, pinnipeds at times interact directly with commercial fishing operations. Briggs and Davis (1972) reported on damage caused by California sea lions in the sport and commercial troll fishery for salmon in Monterey Bay. Interactions between pinnipeds and other fisheries such as the purse seine fishery for anchovy and squid occur. California coastal marine mammal-fishery interaction studies are presently being implemented by the National Marine Fisheries Service through contract with the California Department of Fish and Game.

It is apparent that because of our general lack of knowledge of pinniped foraging habits, a great deal of research must be completed before we will be able to evaluate the impact of these marine mammals on commercially valuable marine resources. Preferred foraging habitats, distribution at sea, and seasonal feeding habits of different age groups and sexes are all topics that must be addressed in order to better understand predator-prey relationships.

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THE SEA OTTER IN CALIFORNIA

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ABSTRACT

The segment of the sea otter population in California from Monterey to Morro Bay appears to be at equilibrium. As in Alaska and the Commander Islands, the primary limiting factor is starvation. Shark predation and adverse human interactions are incidental and not limiting. The primary social behavior to ensure total utilization of food resources is the food stealing dispersal mechanism. Dominant males exert "territorial" dominance within their visual zone wherever they may be and will steal food from females and subdominant males. To avoid food stealing harassment, foraging sea otters, both in the established population and the migrant front aggregates, disperse during feeding bouts. The migrant front animals remain in a particular area at the periphery until food resources become limiting. When these front animals move into the next adjacent food-rich area, productive animals (females) will occupy the abandoned area and reach a food supply equilibrium at a density per unit of habitat much below that maintained by the front aggregate males.

RESUMEN

El segmento de la población de la nutria marina en California desde Monterey hasta Bahía Morro parece estar en equilibrio. Como en Alaska y las Islas Commander, el factor limitativo primario es la inanición. La predación por tiburones y las interacciones adversas con el hombre son incidentales y no limitativos. El comportamiento social principal para asegurar la utilización total de los recursos de comida es el mecanismo de dispersión producida por el robo de comida. Los machos dominantes ejercen un dominio "territorial" dentro de su zona visual dondequiera que estén y les roban la comida a las hembras y a los machos subordinados. Para evitar que les roben la comida, las nutrias marinas en busca de comida, tanto en la población establecida como en los agregados frontales migratorios, se dispersan durante los períodos de alimentación. Los animales del frente migratorio permanecen en un área particular en la periferie hasta que los recursos de comida llegan a estar limitados. Cuando estos animales del frente se trasladan a la zona adyacente rica en comida, los animales productivos (hembras) ocupan el área abandonado y así encuentran un equilibrio en el suministro de comida a una densidad por unidad de hábitat muy por debajo de la mantenida por los machos del agregado frontal.

THE SEA OTTER IN CALIFORNIA

From a single remnant of 50 to 100 sea otters, *Enhydra lutris,* near Point Sur in the early 1900's, the California population now totals around 2,000 animals. The increase averaged around 5 to 6% per annum up to the last total census in 1976. Sea otters in Alaska increased at a slightly faster rate, and the 1,000 to 2,000 animals in six isolated remnants has increased to 100,000 to 140,000 (Interagency Task Group 1978). Under full protection under state law since 1913, the return of the sea otter has been a success, and a viable and safe population now occupies 180 miles (290 km) of coastline from Santa Cruz to Pismo Beach.

This return has not been without some anguish to certain recreational and commercial shellfish users. The sea otter is the one marine mammal that man cannot compete with at the same time and place, due to its efficient foraging of the entire exposed habitat within its range from the lower intertidal zone out to at least 20-m depth. Unless the sea otter is eventually contained, the State's pismo clam, sea urchin, abalone, certain crabs, and possibly lobster fisheries will be precluded. Otters do not extirpate these shellfish stocks, they merely reduce the exposed biomass to densities well below those necessary for profitable commercial exploitation or satisfactory recreational use. In all cases where otters have moved into either pristine areas where there has been no human take (in natural preserves such as Point Lobos and Hopkins Marine Station) or in zones of utilization, there has been a reduction of over 90% in numbers of shellfish counted on transects (Burge 1973; Miller et al. 1975; California Department Fish and Game 1976). The only remaining macro-invertebrates of edible size are observed deep in crevices where otters cannot reach them (Ebert 1968; Lowry and Pearse 1973; Cooper et al. 1978). Whenever one of these large forage items leaves its protective habitat where otters are established, it apparently quickly becomes otter food.

Foraging strategies in the established range results in all the food available to the reproductive population being consumed. Food stealing by dominant animals results in distribution wherein sea otters tend to feed apart from one another. An otter foraging within sight of a dominant animal may lose its food item; thus, the food stealing dispersal mechanism ensures that all foraging habitat is utilized almost constantly in the established range. Len-

sink (1962) reported that the limiting factor of the otter in Alaska was food, with starvation being more acute than chronic. This acute food shortage in late winter was also reported by Kenyon (1969) for Alaska and by Barabash-Nikiforov et al. (1947) for the Commander Islands and is also evident in California (Morejohn et al. 1975).

There are no endemic diseases associated with the sea otter as is characteristic with pinnipeds, and the sea otter has no ectoparasites in its fur. There are no natural predators in California except for the great white shark. The apparently infrequent shark predation and occasional shooting by humans (around two animals per year have been found shot) has not kept the population from steadily increasing. Oil contamination appears to be the only form of pollution that could presently adversely affect the sea otter. Pesticide residues and heavy metal concentrations in sea otter tissues have been below levels considered injurious.

A major portion of the California population appears to be at equilibrium level with its habitat, or at carrying capacity. There are three major social attributes of the California population. These are the established population, the migrant front, and the colonizers:

1. The *established population* is at equilibrium with its food supply and habitat. There is a preponderance of females in the area from Monterey to Morro Bay. The population within these boundaries for years has remained stable in numbers with food stress most prevalent during the late winter.

2. The *migrant front* is an aggregate of almost entirely males, mostly subadults, at the two range peripheres. The fronts in 1978 were at Soquel in the north and near Pismo Beach to the south. These aggregates remain at the peripheral areas until food becomes limiting, then move into the next unforaged food-rich area. Some or possibly all of the males in these front aggregates may be surplus to the population, and those that may seasonally move back into the established population compete for food and may even lower the carrying capacity for the reproductive segment of the population.

3. The *colonizers* are the animals that move into or remain in an area that has most recently been abandoned by the migrant front. Here new reproductive female areas are established. The geographically linear population increases only in these areas. The increase in range has averaged about 2.5 miles (4km) per year since 1913 with an average increase in numbers of around 30 otters per year. Considering that the potential annual births in California may be as many as 400, it is obvious that most of the annual crop does not survive due to starvation, or that possibly there is a large turnover of adults resulting in

a relatively high reproductivity and survival of young animals. This latter condition has not as yet been adequately determined. A young animal must either occupy an area left "vacant" by an adult, by chance move into a colonizing area or migrant front, or die.

The dynamics of the California population, which is at equilibrium level throughout most of its range but still expanding slowly in distribution and numbers, presents a unique management problem. There are surplus animals in the established range as well as possibly in the migrant fronts in a still expanding linear population. In the Aleutian Islands, the expansion has been insular with island habitats progressively becoming saturated (reaching food supply limits) with the surplus animals moving to nearby islands or dying. Under Alaskan conditions, the U.S. Departments of Interior and Commerce (Interagency Task Group 1978) has approved* an annual take of otters in the island groups in which the population is at carrying capacity. There is no such plan to take otters in California except possibly to capture animals for research purposes and to establish another subpopulation of animals captured in California.

A recent serious problem has become evident in respect to areas into which sea otters in California may be moved. This concerns the subspecific determination of the sea otter which in itself has become a controversial issue. In brief, Merriam (1904) established *E.l. nereis* on the basis of the structures of one skull from San Miguel Island when compared to Alaskan skulls from the Bering Sea. This subspecies was recognized until researchers working with the otter failed to notice any behavioral or other differences between otters in Alaska and California. Scheffer and Wilke (1950) and Kenyon (1969) did not accept the subspecific division between Alaskan and California otters. Consequently, when otters were translocated to near Sitka, Vancouver Island, Washington, and Oregon, the federal and state agencies cooperating in these translocations did not consider it inappropriate to mix otters from Amchitka and Prince William Sound. Recent taxonomic interpretations (Davis and Lidicker 1975; Rice 1977) would consider the area from Prince William Sound into California as the previous range of *E. l. nereis* with the Aleutian Island animals belonging to *E. l. lutris*. The California Department of Fish and Game follows the interpretation that there is but one genetic stock in the eastern North Pacific (Scheffer and Wilke 1950; Kenyon 1969; Roest 1973, 1976; Woodhouse et al. 1977; Interagency Task Group 1978). The problem now arises as to where animals should be captured if more subpopulations are to become established in the Oregon to Prince William Sound areas. Now that there is an admixture of animals from two sub-

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*Approval was made but subsequently the State of Alaska has rescinded its request for the return of management of certain marine mammals, including the sea otter.

species, if one follows this taxonomic interpretation, *E. l. nereis* may have ranged north only to the Strait of Juan de Fuca or possibly "1500 miles" farther north (Federal Register 1977). The animals translocated to Washington and Oregon came from Amchitka; 68% of the otters released at Vancouver Island came from Prince William Sound with the remainder from Amchitka, and 82% of the animals moved into the Sitka area came from Amchitka with the remainder from Prince William Sound. There has never been any publication that presented evidence for any distributional break in the otter distribution throughout its entire pristine range from Japan to lower Baja California. Even the animals in the Commander Islands, which are 180 miles from the Aleutian chain, are of the same subspecies (Barabash-Nikiforov et al. 1947), and this is the widest open water space within the entire range. The Strait of Juan de Fuca is 11 nautical miles wide at the narrowest part and could not possibly represent a pristine geographical barrier. The end result has been that there is much confusion among policy makers as to where California type animals may be moved and whether they can be "mixed" with or put near animals from parts of Alaska. The California population is still considered threatened by the Federal Government (the Department of Fish and Game does not agree with this decision); however, all parties concerned wish to establish another population of these animals somewhere along the Pacific Coast. The problem now is where.

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Part III

SYMPOSIUM OF THE CALCOFI CONFERENCE

IDYLLWILD, CALIFORNIA
OCTOBER 23-25, 1979

CLIMATE AND ECOLOGICAL REGIMES

THE EFFECTS OF CLIMATE ON TERRESTRIAL AND MARINE POPULATIONS

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ABSTRACT

Climate impacts all biological systems. Human culture and health have been related to climatological variables.

Terrestrial biological populations are regulated by both intrinsic (e.g. genetics, physiology, behavior) and extrinsic (e.g. climate, predators, competitors, parasites, food, shelter) agents. Climate appears to be a major extrinsic regulatory agent for some organisms, most notably the more r-selected ones. Random meteorological events are reflected in environmental and population variability and instability. In some cases, it may be that regularly recurrent climatic patterns generate cyclic biological fluctuations.

The variability associated with marine populations in the California Current system is largely due to climatic fluctuation. The interplay of short (upwelling) and longer term (water mass influx) changes in the physical environment have been shown to regulate diatom blooms. In most cases, however, the mechanisms involved in climatic-biological interaction are not yet clear.

RESUMEN

El clima afecta todos los sistemas biológicos. La cultura humana y la salud han estado relacionadas con variables climatológicas.

Las poblaciones biológicas terrestres están reguladas por agentes intrínsecos (p. ej., genética, fisiología, conducta) y extrínsecos (p. ej., clima, predadores, competidores, parásitos, alimento, habitición). El clima parece ser un agente regulatorio extrínseco de mayor importancia para algunos organismos, notablemente para los más r-selectos. Acontecimientos meteorológicos del azar se reflejan en la variabilidad e inestabilidad del medio ambiente y las poblaciones. En algunos casos, puede ser que patrones climáticos que regularmente se repiten generen fluctuaciones biológicas cíclicas.

La variabilidad asociada con poblaciones marinas en el sistema de la Corriente de California se debe principalmente a la fluctuación climática. Se ha mostrado que el juego entre los cambios de períodos cortos (surgencias) y más largos (influencia de las masas de agua) en el ambiente físico rige los florecimientos de diatomeas. Sin embargo, en la mayoría de los casos, los mecanismos que intervienen en las interacciones climáticas y biológicas aún no están definidos.

INTRODUCTION

Environment is the setting in which an organism lives and functions. One may safely assume then that changes in the environment affect the resident biota. Considering that climatic change alters both terrestrial and marine environments, one can then state that climatic change will impact the biological community. It is difficult not to accept this point of view. Nevertheless, the effects of climatic change on biological populations have been one of the most controversial subjects in the history of science. The major part of this controversy has not been whether climatic change affects organisms, but rather how important those effects are in regulating the distribution and abundance of organisms comprising a population. In this paper, we review literature dealing with this subject. The extensive literature precludes a comprehensive review but allows for flexibility in approach.

The study of climate's impact on biological systems requires an interdisciplinary approach, integrating biological and meteorological time series of sufficient length and regularity as to yield significant results. Partly because of this constraint, most research effort has been directed toward terrestrial populations where time series are more readily available.

TERRESTRIAL STUDIES

Man

The preoccupation with climate-induced changes on human populations reaches back to early stages of human culture. Hippocrates in "Airs, Waters, Places" made an elaborate attempt to explain cultural differences between various races and nations (Greeks, Scythians, Egyptians, etc.) on the basis of different climatic regions. One of the most influential and lasting contentions of Hippocrates was that diseases were caused not by divine forces, but by atmosphere, waters, and places. As has been pointed out by Glacken (1973), by the time Huntington's "Main Springs of Civilizations" appeared in 1945, investigators of various disciplines had discussed the relation of environment—particularly climate—to health and disease, diet, creativity, labor efficiency, mental diseases, genius and intelligence, race, social and political organization, national character, and the suitability of the tropics to white settlement.

Because of direct relevance and potential beneficial application, there has been considerable effort to eluci-

date the functional role of climate in relation to human health. For instance, Sulman (1976) discusses the role of weather in producing hormonal change, psychic reactions, and ailments. He claims that the positive electric field, which surrounds living organisms, interacts with the strong negative field on Earth to cause headaches, eye flickering, and other disturbances. He suggests that neurohormonal changes in the blood may account for psychological depression of populations in northern countries which experience long, cold, gloomy winters.

Climatological variables, such as electromagnetic waves, barometric air pressure, temperature, and oxidative potential, have been related by Petersen (1947) to mortality, disease, and blood pH. He emphasizes Aristotle's concept of Man as a cosmic resonator, relating solar (sunspot cycle) and lunar rhythms to human health. In another article, Petersen (1940) concludes, "It is very likely that many as yet unexplainable observations in the biological literature will become understandable when once the major changes in the meteorological environment of the time are taken into consideration."

Climate and Other Terrestrial Organisms

Factors that regulate the number of organisms in a given population have been of great interest to population biologists. According to Krebs (1972), prior to 1950 three schools of thought predominated, which stressed extrinsic factors as regulatory agents: the "climate," the "biotic," and the "comprehensive" schools. Later, another theory evolved, emphasizing intrinsic regulatory factors. This "self-regulation" school (Chitty 1960) developed theories based on genetics (Pimentel 1968) and behavior (Wynne-Edwards 1965).

The concepts of density dependence and density independence were introduced by Smith (1935). These terms, interlaced among the various theories on population regulation, are discussed in detail by Solomon (1958). Smith (1935) stated that density-dependent factors are mainly biotic (e.g. competition, predation), whereas density-independent factors are mainly abiotic (e.g. climate). The biotic school views climate as operating density independently, thus claiming that climate cannot function as a regulatory mechanism per se.

In opposition to this view, Andrewartha and Birch (1954) maintain that weather can operate density dependently in some cases. They believed that density-independent factors, in a strict sense, do not exist. Klomp (1962) concluded that if weather operates density independently, it alone cannot regulate animal numbers. However, in conjunction with density-dependent factors, such as limited shelter or a density-related genetic change, weather may serve as a regulatory agent.

Environmental and biological systems exhibit a high degree of natural variability. Solomon (1949) reviews

theories attempting to explain periodic fluctuation, based on overpopulation, predator-prey relationships, and meteorology. Palmgren (1949) suggested that population cycles may be regarded as random fluctuations with serial correlation between populations of successive years (autoregression). This interpretation has been both supported (e.g. Cole 1954) and refuted (e.g. Keith 1963). Overall, this theory has proved invaluable, since it has prompted critical reinspection of data series that had previously been regarded as cyclic. Furthermore, it has shown the value of a stochastic approach to understanding biological systems.

Slobodkin (1961) notes that because population numbers can be assessed only theoretically, the reality of oscillations must be interpreted in this context. The appearance of cycles may be attributed to data smoothing or unreliable census counts. Slobodkin concludes, moreover, that population fluctuations are intrinsically regulated and do not necessarily reflect a one-to-one correspondence with environmental fluctuations.

From an evolutionary standpoint, several theories have been formulated to explain biological-environmental interaction. Using the theory of r- and K-selection (MacArthur and Wilson 1967), based on population levels in relation to the carrying capacity of their environment, Pianka (1970) presents the following correlates: 1) r-selection with variable or unpredictable climate, density-independent mortality, and unstable population size; 2) K-selection with constant or predictable climate, density-dependent mortality, and stable population size. Pianka (1970) suggests that insects, for example, are more r-selected, whereas terrestrial vertebrates are more K-selected.

Prior to 1930, population studies dealt mainly with insects. The study of other invertebrate, vertebrate, and plant populations had scarcely begun. Experimentally, the impact of the physical environment on insect populations has been demonstrated (e.g. Gause 1932). In the field, it has been shown that the distributional range of some insect populations is controlled by climate (e.g. Morris 1963).

One way to examine the effect of climate on higher vertebrate species is to focus on a classic example from the literature that deals with fluctuations of northern wildlife populations. Keith (1963) reviews these fluctuations. Most of this literature concerns the 3-4-year (e.g.Pitelka 1958) and the 9-10-year (e.g. Elton and Nicholson 1942) cycles with mammal and bird populations in northern latitudes.

Elton (1924) speculated on astronomical and geophysical causes of these animal fluctuations. He suggested that sunspots, lunar tides, and volcanoes may indirectly generate periodic cycles of abundance among mammal and bird populations. Lack (1954) claims that

there exists no clear evidence that these fluctuations are due to climate, since different geographic regions within the same climatic zone often cycle out of phase.

A popular example of a 10-year fluctuation is the North American snowshoe hare-lynx cycle. This 10-year cycle was first observed in the late 1700's from records provided by the fur trade industry in Canada (Keith 1963). Moran (1953) proposed that the lynx-hare cycle is a classic predator-prey type relationship. However, since the oscillations are so strongly synchronized over all of Canada, he reasoned that large-scale meteorological factors must be responsible for this synchronicity. He cites two observations that conflict with the predator-prey interpretation but support the sychnronicity by meteorological factors. These are 1) other animals not dependent on snowshoe hares were synchronously fluctuating, and 2) introduced hares on lynx-free Anticosti Island were apparently cycling together with those on the mainland.

To determine how climate affects the lynx-hare cycle, Moran (1953) studied several potentially climate-influenced targets: lynx birth and death rate, snowshoe hare food source, and trapping effeciency. The inclusion of trapping efficiency, which implies unreliable census data, is interesting in that the observed correlations between temperature and lynx numbers may result from the effect of climate on trappers (i.e. unfavorable climate for trapping) rather than on the lynx. Although the effect of climate on vegetation is likely to be the root cause of synchronizing the 10-year lynx-hare cycle, Moran (1953) concludes only that climate is the synchronizing agent and that these populations are dependent on meteorological factors.

MARINE STUDIES IN
THE CALIFORNIA CURRENT SYSTEM

Compared to a large number of terrestrial studies, some of which have been briefly summarized in the preceding section, marine studies dealing with the biological effects of climatic change have been few in number (this article does not deal with paleobiological studies; for those, see Soutar and Isaacs 1969). This is not due to lack of interest but rather to a scarcity of time series that are both reliable and of sufficient length. Despite these shortcomings, however, during the last few years there has been an efflorescence of studies relating climatic fluctuations to changes in the distribution and abundance of marine organisms.

The groundwork for these types of studies was laid by the pioneering work of Hubbs and Schultz (1929) and Walford (1931). They noted that during the anomolously warm years of 1926 and 1931, a heavy influx of southern fish species into the waters of California occured. Radovich (1960) reached similar conclusions after comparing fish catch statistics of the 1957-58 period, which again

was characterized by anomously high sea-surface temperatures, with the catch statistics of the preceding years. For the same 1957-58 period, Brinton (1960) reported a northerly extension of several species of euphausiids which, in previous years, were confined to more southerly latitudes. Similarly, Balech (1960) stated that during the 1957-58 period, "one is impressed with the striking change in the character of the planktonic populations from south to north and the far northward extension of typically warm water forms."

These findings are what one may expect from purely physical oceanographic considerations. According to Reid et al. (1958), four distinct water masses characterize the surface waters of the California Current system. These come from the north (California Current), west, south, and below (due to upwelling). Changes in the circulation patterns of these water masses frequently occur, and these changes are reflected in sea-surface temperature (SST), salinity, nutrient concentration, and sea level. A lessening of the flow of the California Current, for example, results in the incursion of a subtropical water mass into the region, which in turn is reflected by higher SST, salinity, and sea level, but lower nutrient concentrations. Hydrodynamically passive organisms, such as diatoms, are expected to be carried along with the water masses they inhabit. Mobile organisms, either due to temperature tolerances or feeding strategies, may also undergo a geographical shift. Since these shifts are accompanied by anomolous circulation patterns in the atmosphere (for various physical aspects of climatic changes, see Namias 1975), climatic change has been implicated as an important factor in regulating the abundance and distribution of several organisms as well as the composition of species inhabiting the California Current system. However, due to mixing, food considerations, and wide differences in species temperature tolerance, a complete community shift rarely occurs.

Obviously, long-term changes (months, years) in the circulation pattern of water masses can account for only part of the variability observed in marine populations. For example, unlike climatic change, upwelling is a short-period phenomenon (weeks) which is important in promoting diatom blooms (e.g. Moberg 1928). However, as has been shown by one of us (Tont 1976, in preparation), although upwelling is a short-period phenomenon, its efficacy depends on long-term changes that precede its occurrence. Thus, if upwelling takes place after the influx of subtropical water masses into the region, its effectiveness in bringing nutrients to the surface from a water mass already low in nutrients is clearly limited. The reverse is true if upwelling occurs when the flow of California Current, which is the chief supplier of nutrients in this region, is strong. Indeed, diatom blooms observed during periods of high SST's and sea levels were smaller

by several orders of magnitude than those observed when conditions were reversed. Thus, occurrence of diatom blooms off the coast of southern California is regulated by weather (upwelling instigated by alongshore wind stress), but the magnitude of each bloom, in turn, is modulated by climatic change (large-scale atmospheric change coupled with similar change in the ocean).

Wind-induced upwelling, which results in diatom blooms, may have opposite effects on dinoflagellate concentrations, according to Lasker (1978). His examination of a major upwelling event that occurred in February of 1975 indicates that dinoflagellates, which were abundant before the upwelling, were dissipated because of it.

Recent work by the Food Chain Group at Scripps Instutution of Oceanography (SIO) further illustrates the interconnection between variables, some of which are clearly related to climatic changes. According to Eppley et al. (1978), much of the spatial and temporal variability in phytoplankton standing stocks near the coast of southern California is related to changes in the vertical concentration gradient of nutrients and is reflected in sea surface temperature anomalies. Based on these findings, Eppley and McPeak (in preparation) hindcasted Z_n—the depth were nitrate concentration becomes measurable—from SIO pier temperatures and correlated these values with the commercial kelp harvest. They found that although natural mortality appears to be a chief determinant of kelp biomass, variation in the estimated Z_n accounted for 10% of the variability in the kelp harvest overall and for 20% if only the fall averages of both variables are used.

DISCUSSION

It should be apparent from this brief review that climate is an important factor regulating both the abundance and distribution of terrestrial and marine organisms. Further research is needed, however, to differentiate between the various pathways through which climatic change impacts a biological population. These effects could be *direct*, such as when high mortality rates occur due to temperature changes, or *indirect*, as when climatic change alters the nutrient concentration available to the organisms in question. Another important point to consider is that climatic change may have different effects upon the various life stages of an organism. Perhaps more importantly, climatic change may be correlated with several interrelated trophic levels. That is, a change in the abundance of a particular prey species may be the result of the effect of climatic change on the predator species or vice versa, as in the lynx-hare system. Increased data collection over a long period of time and careful analyses will undoubtedly answer these questions.

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REGIMES AND EVENTS IN RECENT CLIMATIC VARIABLES

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ABSTRACT

Nonseasonal behavior of the marine and atmospheric environment in the eastern North Pacific and western North America are participants in the variability of a larger climate system. Recent climatic history displays extreme events and some longer term regimes that are often related. These extreme events are examined in the context of the overall variability, and details of their time and space scales are discussed.

RESUMEN

El comportamiento no estacional del ambiente atmosférico y marino en el Pacífico Norte oriental y Norteamérica occidental son participantes de la variabilidad de un sistema climático mayor. La historia climática reciente exhibe efectos extremos y algunos regímenes de período más largo que están frecuentemente relacionadas. Estos efectos extremos son examinados en el contexto de la variabilidad total, y se discuten los detalles de sus escalas tiempo y espacio.

INTRODUCTION

An excellent example of short-period climatic variability is provided by the surface temperature in the central and eastern North Pacific Ocean over the last few decades (see Figure 1). The heat stored in large regions of the North Pacific has apparently undergone considerable interannual or anomalous fluctuations, with time scales ranging from a few months to a few decades. The longer time scale variations, emphasized by the dark low-pass filtered curve in Figure 1, has the quality of regimes, whereas the unfiltered curve shows the shorter term variations, which one might call events. Instead of being randomly distributed in time, the extreme events are mostly found in the midst of a general anomalous period. Thus, although they are often regional in scope, the extreme events are usually linked to a broader scale and longer lived condition (i.e. a regime). Since both time scales have important effects on biota, etc., both, to some degree, are treated in this article.
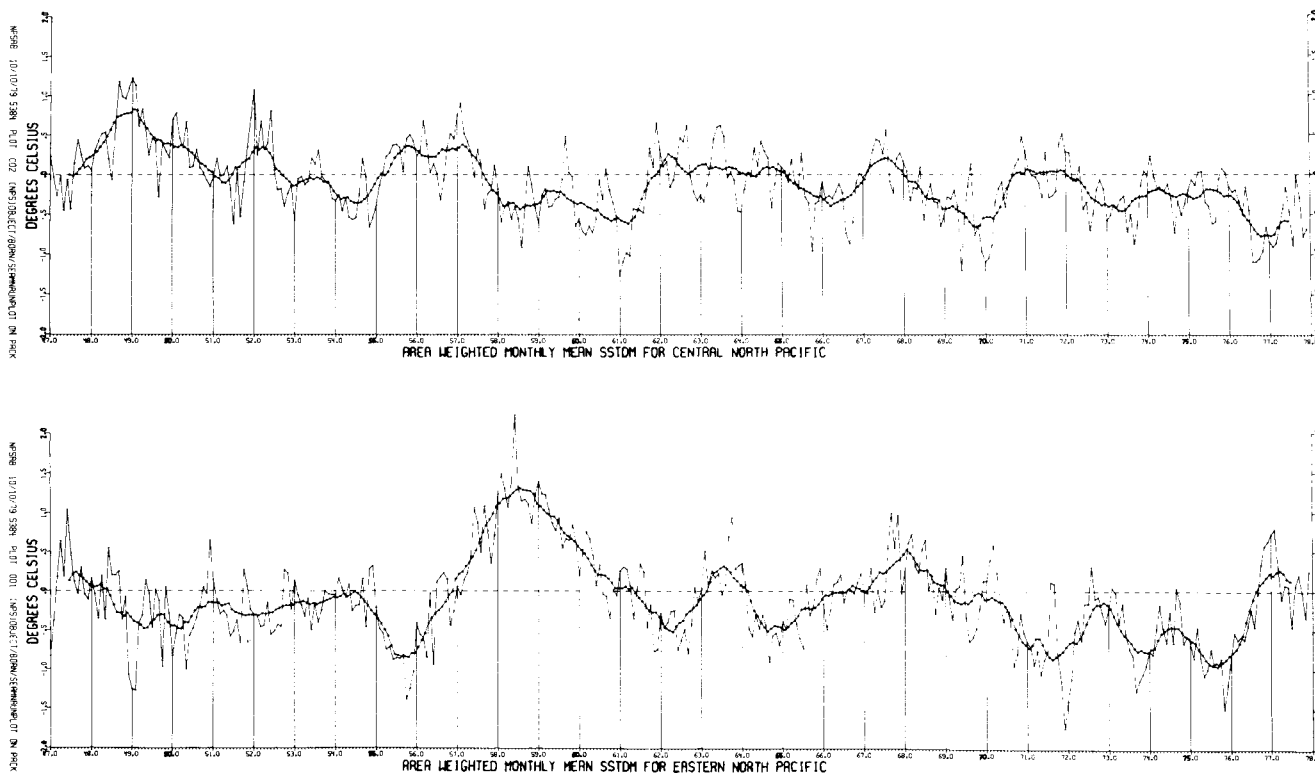

Figure 1. Area weighted sea-surface temperature (SST) for the central (30°N to 50°N, 150°W to 180°W) and eastern (20°N to 55°N, and east of 130°N) North Pacific. Light curve is monthly anomaly, dark curve is 12-month centered running mean; both are in degrees Celsius.

This report is concentrated on short-term climatic variations. These are just a small subset of the continuum of scales that represent the climate variability. For instance, the proxy records of tree rings and marine sediments, discussed by Douglas (this volume) and Soutar and Crill (1977), offer a look at climatic fluctuations on a scale beyond that of the directly measured data, which is what is treated here. Reliable direct observations of atmospheric, oceanic, and other climate variables are limited to the most recent few decades and are in many ways insufficient for thorough statistical descriptions of climate variability or for adequate verification of many theories of climatic change. However, they do provide a valuable glimpse of recent short-period fluctuations, with some notable extremes and regimes.

Examples shown here are taken from the eastern North Pacific and west coast of North America, of general interest to the CalCOFI audience. This material is descriptive. The major issues addressed are the spatial and temporal scales of anomalous variability, seen through the window of directly sampled observations. Events (relatively short-period fluctuations) are mentioned as well as regimes (more persistent, longer term fluctuations), because the mechanisms that force physical and biological transitions are often confined to these short storm-like periods. It is clear that these extreme events are sometimes linked to the background provided by the larger scale regime (see Namias 1973). This short-period climatic time scale is important because it contains significant variability and includes the periods of months to years over which many important management decisions must be made.

## THE NATURE OF THE RECENT CLIMATIC RECORD

The longest directly measured climatic variables are surface temperature and precipitation, with some records of the west coast of the United States extending back into the 1800's (see Roden 1964, 1965; Kuhn in preparation). However, it is well known that the weather at the surface is influenced by the character of mid-troposphere, where adequate records have been collected routinely only since the end of World War II. Recent work has established the important role of other members of the globally linked climate system, such as the Southern Hemisphere, the polar ice sheets, and marine atmospheric and oceanic conditions. Unfortunately, the sampling of the entire climate system has been spatially nonuniform and temporally erratic. It is only during the last few years that serious attempts have been made at truly global sampling, which naturally needs many years of data to establish a clear description of the climatic scale of variability. A concerted effort to monitor global weather is underway by several worldwide cooperating institutions in the Global

Atmospheric Research Program (GARP; see Fleming et al. 1979).

Much of the climatic information over the oceans is derived from island stations, ocean weather ships, routine surface marine reports from merchant and naval vessels, and recently from satellites. Despite all this, a reliable climatology is still hard to establish: island stations are not uniformly positioned, especially in the extratropics; many of the ocean weather station occupations have been recalled due to expense of operations, ending several unique series of nearly continuous open ocean data; satellite measurements are presently only marginally accurate (Barnett et al. 1979). For much of the synoptic scale ocean surface climatology, merchant ship observations provide the wealth of information. However, there are also numerous problems associated with these data. They are nonuniformly sampled in space (depending on ship tracks) and time (depending on season, etc.), and rather coarse areal and time averaging is necessary to construct meaningful maps of surface variables. Not only is there the usual seasonal variation in sampling density, but there have been large changes in the number of data from year to year and decade to decade, as illustrated for the Atlantic Ocean Marsden Square areas of sea-surface temperature in Figure 2. Part of this has historical causes, such as the general drop off in sampling density during the World War II period, but it appears that some of these aberrations, such as pre-1964 and post-1970 on Figure 2, resulted from a failure of various agencies to completely compile or process the data (not a trivial task). This
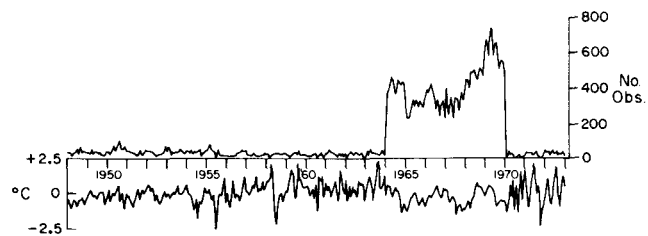
Atlantic SST (lower) and Number of Observations (upper) at Marsden Square 1
Latitude 5°N, Longitude 5°W
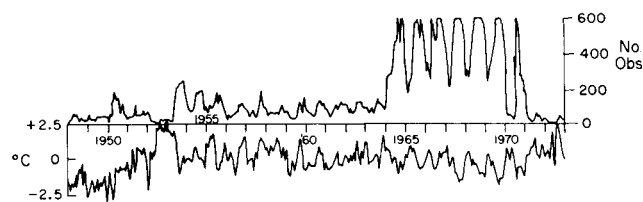
Atlantic SST (lower) and Number of Observations (upper) at Marsden Square 184
Latitude 55°N, Longitude 35°W

Figure 2. Examples of sea-surface temperature (SST) records in the North Atlantic for 10 degree (Marsden Square) averages centered as indicated; numbers of observations per month (upper) and monthly anomalies (lower). Notice how number of observations are modulated by time of year in Marsden Square 184 and also large difference in number over time. Also see how SST variance changes with sampling density.

inhomogeneity introduces artificial variability into the data series. Finally, a subtle, but serious, problem arises from the fact that most vessels avoid storm regions and hence the sampling misses the extreme portion of the variability in the surface data fields, which account for a large part of the interaction in the air-sea system.

Subsurface oceanic characteristics are known only in a long-term-mean sense, except for a few selected points and areas. This is due to a lack of routine synoptic sub-surface sampling, which is more costly and time consuming than surface monitoring and is of little interest in routine maritime operations. There are, of course, several climatologies in the long-term-mean sense (see Levitus and Oort 1977), but the interannual variability of such important fields as the upper ocean thermal field is quite poorly known except for a few rather specialized points or areas (see White and Haney 1978). The upper oceanic thermal field is of interest because it plays an important role in the global heat budget of the climate system.

Despite its less than perfect state, the recent, directly observed record has yielded an interesting picture of the workings of the climate system on time scales of months to a few years, a few details of which are discussed below.

INTERANNUAL VERSUS ANNUAL VARIATIONS

It is important to distinguish between regular annual variations and the differences from normal, or the inter-annual variations (called anomalies, deviations from nor-mal, or deviations from the long-term mean). The normal, or annual, signal of a particular variable is in practice con-structed by taking the mean over some extended period of time for each sub-period of the year (months or seasons in this case). The interannual or anomalous signal is the difference between the observed value and this long-term-mean. In the case of events and regimes, we focus on these interannual components of the variability.

First, we compare the size of interannual variability to the size of annual variability. This is shown in the West-ern Hemisphere on a surface area temperature in the three panels of Figure 3, which presents the standard deviation of seasonal anomalies, root mean square (RMS) value representing the seasonal cycle, and the ratio of these two quantities. From this comparison, it is seen that the seasonal interannual variability is smaller than the regular seasonal amplitude, but of the same order of magnitude, which indicates the importance of the sea-sonal variability. There is a large contrast between the ratio of interannual to annual variability for continental and oceanic situations. Although the anomalous compon-ent is generally much greater on the continent than the ocean, the seasonal cycle is proportionately greater still, and in this sense the relative importance of the inter-annual variability is greatest over the oceans. Finally, note the general increase in the ratio toward tropical lati-tudes, caused by large seasonal anomalies (like El Niño) superimposed on a rather small seasonal signal.

Hence, we find a large, important interannual signal in low latitudes. Also, the smaller scale "noise" tends to be smaller in lower latitudes with less transient storm occur-rence. The temperature fields, as well as other important variables, have large spatial coherence (see Barnett 1978b). This suggests that lower latitudes embrace areas where the interannual variation plays an important part in the overall dynamics of the short-term climate system. The low latitudes, then, offer a fruitful region of study to augment the understanding of the climate system gained from higher latitudes.

TIME SCALES AND SPECIFIC EXAMPLES

Short-term regimes in atmospheric and oceanic vari-ables are hard to define. There are always transient (storm-like) disturbances that obscure the lower frequen-cy components, particularly in the atmosphere. On the other hand, the anomalous component of the oceanic thermal structure has been shown to exhibit persistence over periods of several months. This contrast between the upper ocean and the faster changing lower troposphere is illustrated with autocorrelation functions of North Pacific sea-surface temperature and 700 mb height in Figure 4 (see Namias and Born 1970). It is thought that this dis-parity between time scales causes the upper ocean to act as a stablizing agent for the rather turbulent atmospheric circulation regime. For this reason, sea-surface tempera-tures have been explored as prime candidates for short-term climate predictors (see Namias 1975; Barnett 1978b; and Newell 1979).

Striking examples of regimes are the El Niño condi-tions usually centered in the eastern tropical Pacific, often in the Southern Hemisphere. El Niño is the occurrence of abnormally warm ocean surface temperature off the coast of Peru usually during northern winter, with associated atmospheric aberrations, such as heavy precipitation in the central Pacific (see Figure 5). The low latitude atmo-sphere-ocean system, as mentioned in the previous sec-tion, possesses strong, rather low frequency anomalous behavior, of which El Niño plays a major part (region-ally). El Niño occurrences are spaced at roughly 6-year intervals (but nonperiodic), with varying degrees and duration, as seen from the time series in Figure 5. Per-haps the most impressive El Niño occurrence in recent times was the 1957-58 case, when the warming spread far beyond the lower latitudes into the eastern North Pacific (see Figure 6). This coupled oceanic and atmospheric system conspired to produce such anomalies in the physi-cal realm as to decimate or translate entire biological populations and alter the distribution of species for sev-eral seasons. The "regime" that prevailed during 1957 and 1958 was the topic of an exciting past CalCOFI Sym-
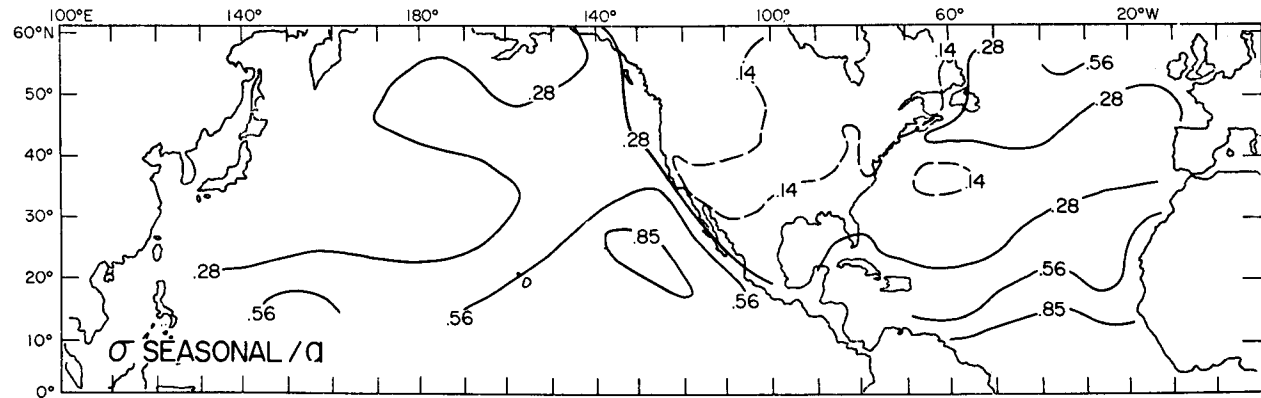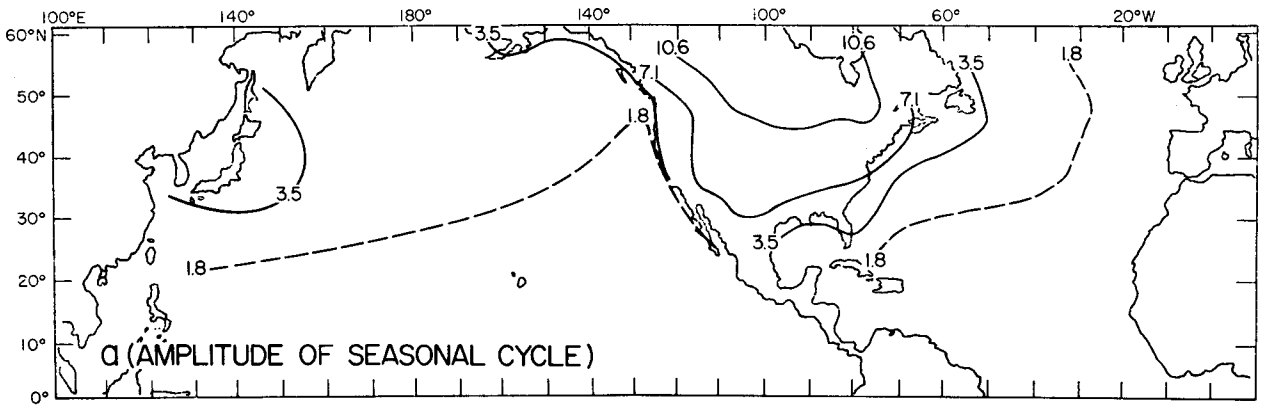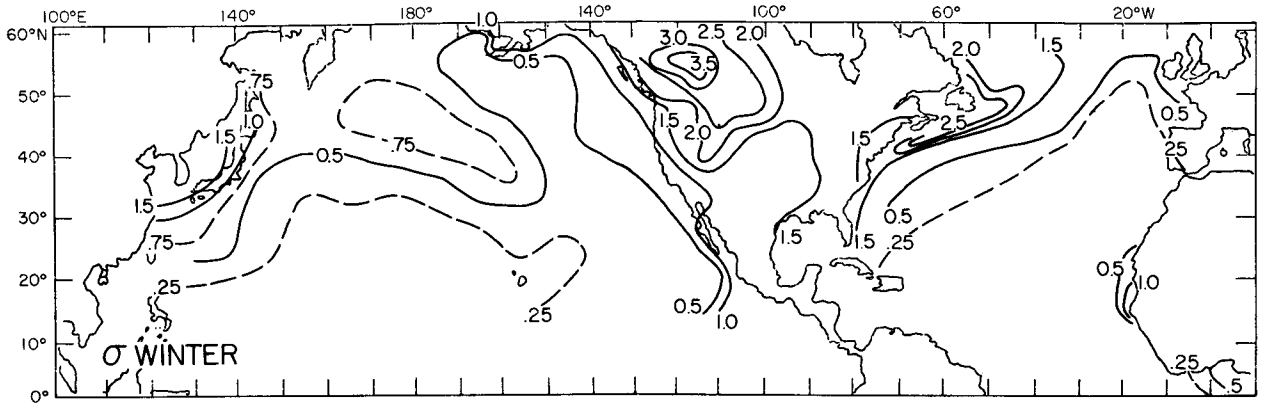
Figure 3. Seasonal versus interannual variability for oceanic and continental surface temperature.

posium (see Sette and Isaacs, eds., 1960). In fact, Namias (1972) contended that this 1957-58 event "ushered in a new regime that has a relatively warmer eastern North Pacific and cold central Pacific" that lasted through the 1960's (see Figure 7). The impact in higher latitudes during 1957-58 is indicated by a graph showing seasonal temperature anomalies at San Diego (Figure 8). It is interesting to note that the extreme short-period events that contributed to these various seasonal averages were not isolated random cases but seem to be fostered by the general large-scale regime.

Another striking example of an intense regime in the short-term climate system is the sequence of droughts that plagued the State of California and other parts of the west coast of North America during the winters of 1976 and 1977 (see State of California 1977; Namias 1978 a,

1978b). Persistent high pressure and the usual accompanying subsidence resulted in the diverting of winter storms (from which California gets most of its precipitation) to the north, and consequent dry conditions prevailed (see Figure 9). The unusual nature of the situation involved the tenacity of the dryness and the fact that two dry winters occurred back-to-back. Again, the ocean was a partner, with concomitant strong anomalous sea-surface temperature patterns in the North Pacific (see Namias 1979). Although cause and effect relationships between the upper oceanic thermal structure and the overlying atmospheric flow pattern are still uncertain and require further research, it is clear that large, persistent sea-surface temperature anomalies are *strongly* associated with their atmospheric counterparts.

SPATIAL BEHAVIOR

A most remarkable feature of monthly and longer scale anomalous variability in the atmosphere and in the ocean is the large continuous nature and rather large amplitude of the spatial patterns that often exist. The length scales are on the order of hundreds to a few thousand kilometers. Although it might seem that an average over these periods (monthly and longer) of seemingly noisy, transient daily events would approach zero, it in fact has amplitudes that in many cases rival that of the daily events. Although explanations for this quasi-stationary standing wave tendency of the short-term climate system are not completely known, part of the reason for this behavior is probably intrinsic to the interactive behavior of the atmospheric and oceanic flow systems. Stabilizing influences might come from the lower boundary in the form of upper ocean and cryospheric heat sources, soil moisture transfers, and other surface characteristics that might influence albedo.

The spatial coherence is well illustrated in numerous West Coast and eastern Pacific examples. The large-scale nature of the mid-latitude surface temperature field, extending from the eastern North Pacific through the western half of the United States, is illustrated in Figure 10, in this case with the aid of empirical orthogonal
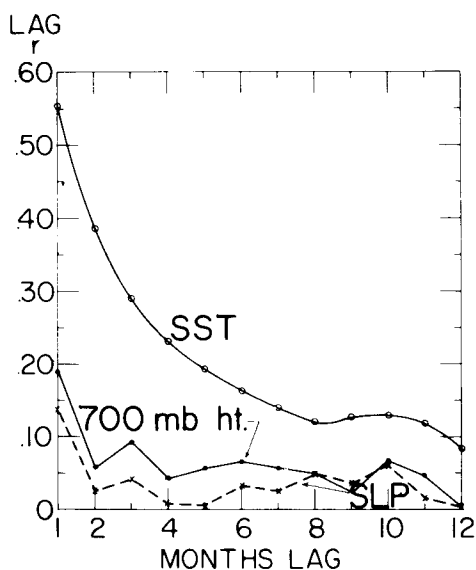
Figure 4. Overall autocorrelation functions at monthly lags for patterns of sea-surface temperature (SST), 700 mb height, and sea-level pressure (SLP) in the North Pacific. (After Namias and Born 1970).
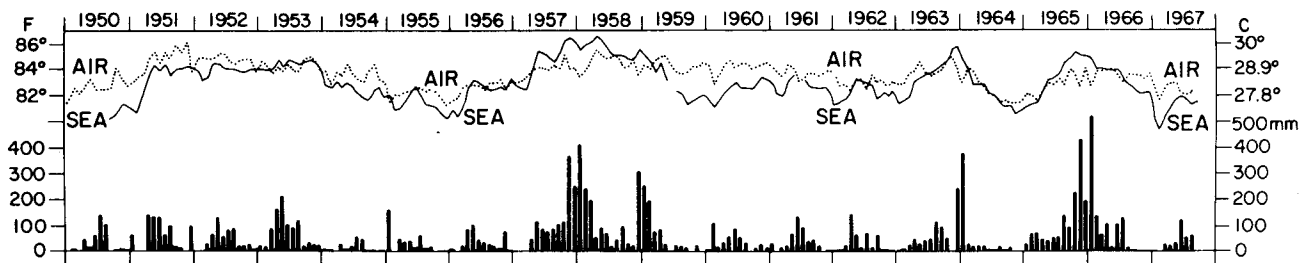
Figure 5. Time series of air temperature (dark curve in °F), surface temperature (dotted curve in °C), and precipitation (bar graph in mm) at Canton Island (172°W, 3°S). (After Bjerknes 1969.)
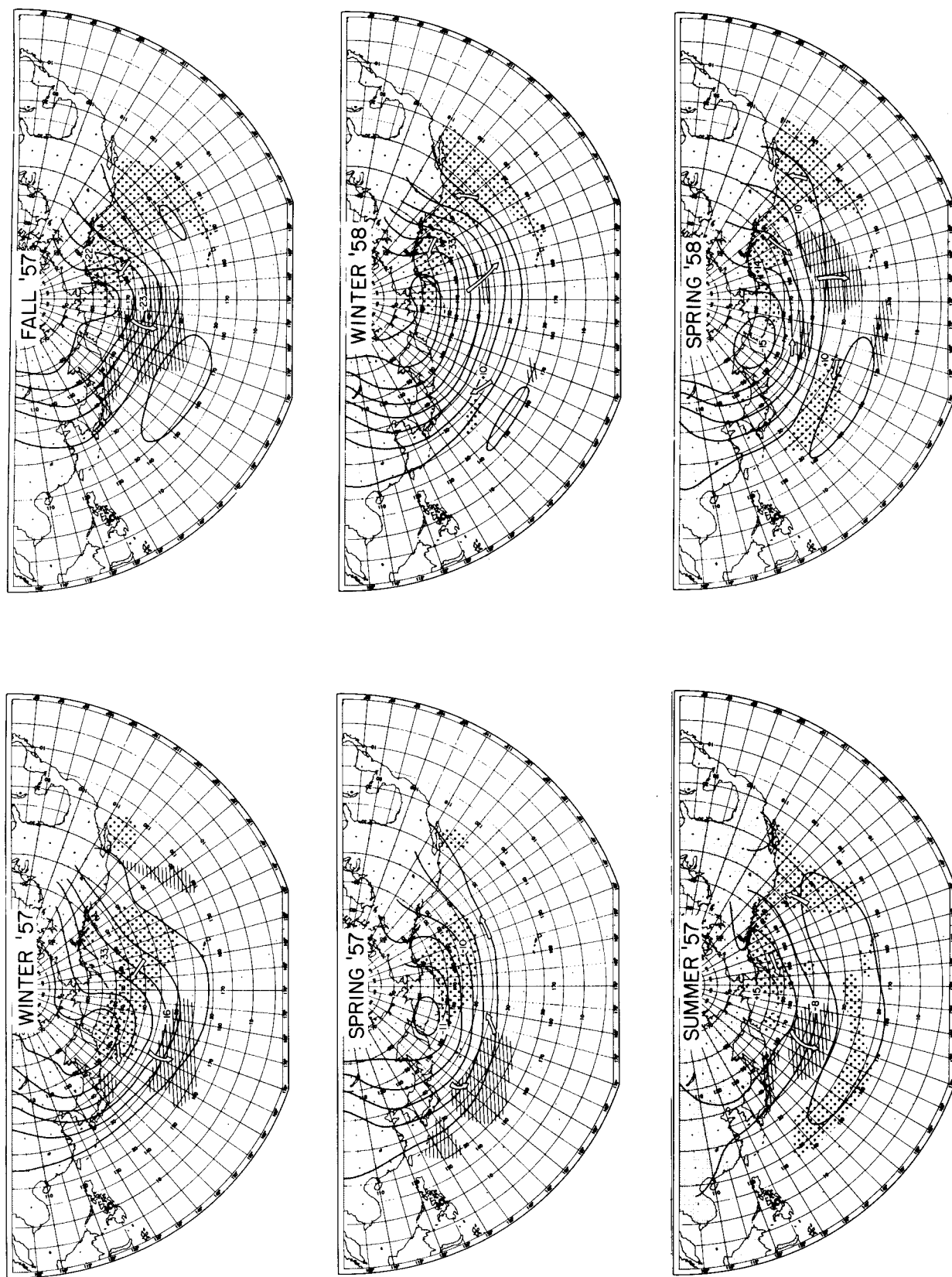
Figure 6. Sea-surface temperature (SST) anomalies (base period 1947-66) and 700 mb contours for winter, 1956-57. Stippled areas are more than 1°F below 20-year mean and hatched areas more than 1°F below. Numbers (expressed in tens of feet) are placed at centers of 700 mb anomalies. Arrows fly in direction of principal anomalous geostrophic flow (i.e. parallel to isopleths of height anomaly which are not reproduced). (After Namias 1972).
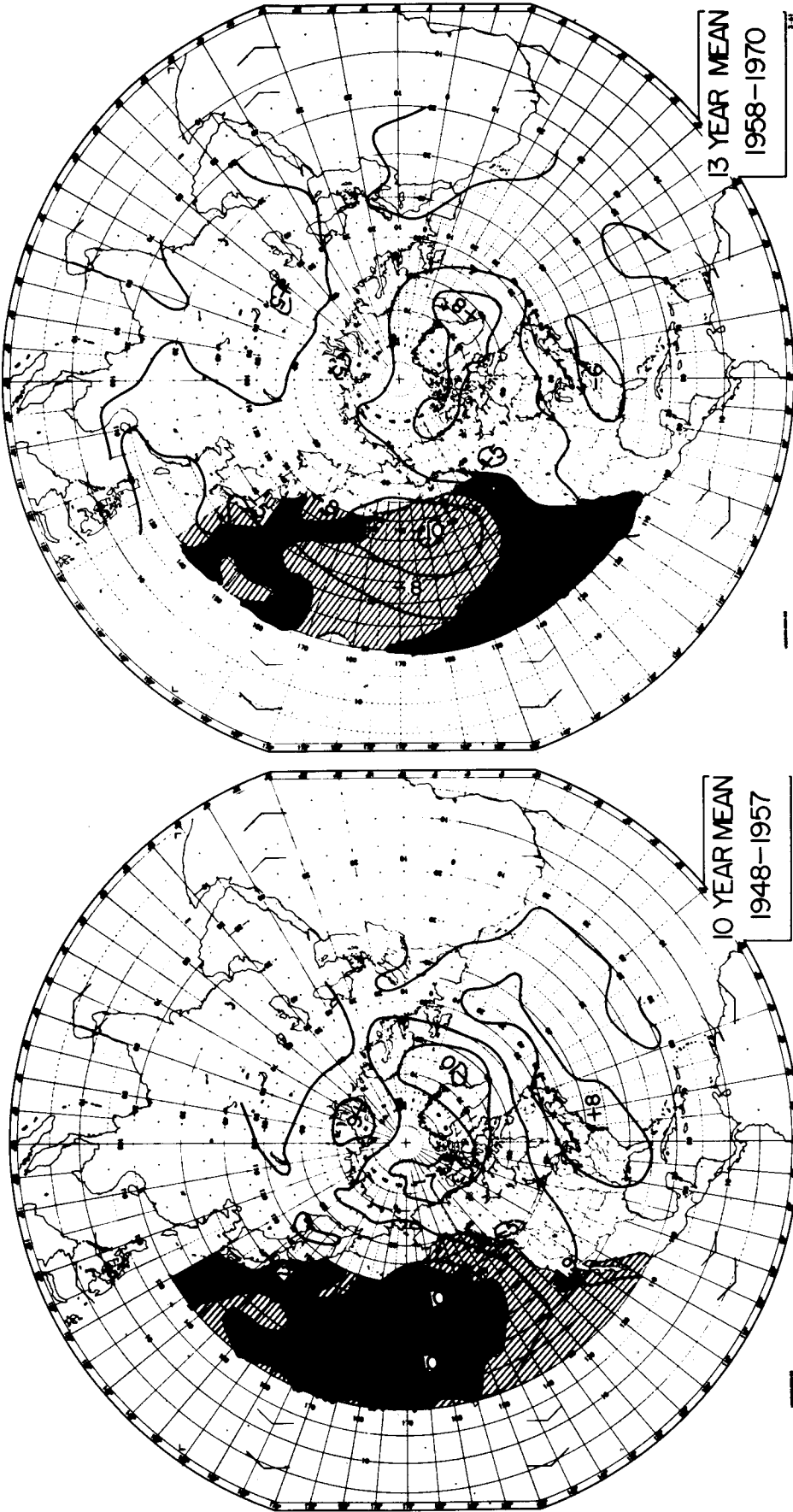
Figure 7. Comparison of anomalous Pacific sea-surface temperature (SST) and hemispheric 700 mb height over the 10-year period 1948-57 and 1958-70. Shaded and hatched areas represent SST anomalies greater than and less than zero, respectively. Note the shift in pattern between the two periods.
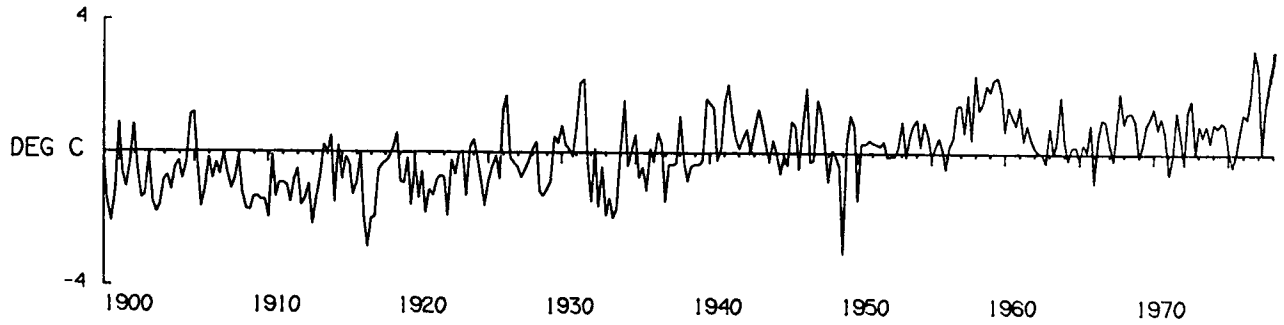
SAN DIEGO SEASONAL TEMPERATURE DEPARTURE 1899-1978

Figure 8. San Diego seasonal temperature departure (1899-1978). Notice the prolonged warm period centered around 1958.

Principal Tracks of Centers of Cyclones at Sea Level, North Pacific
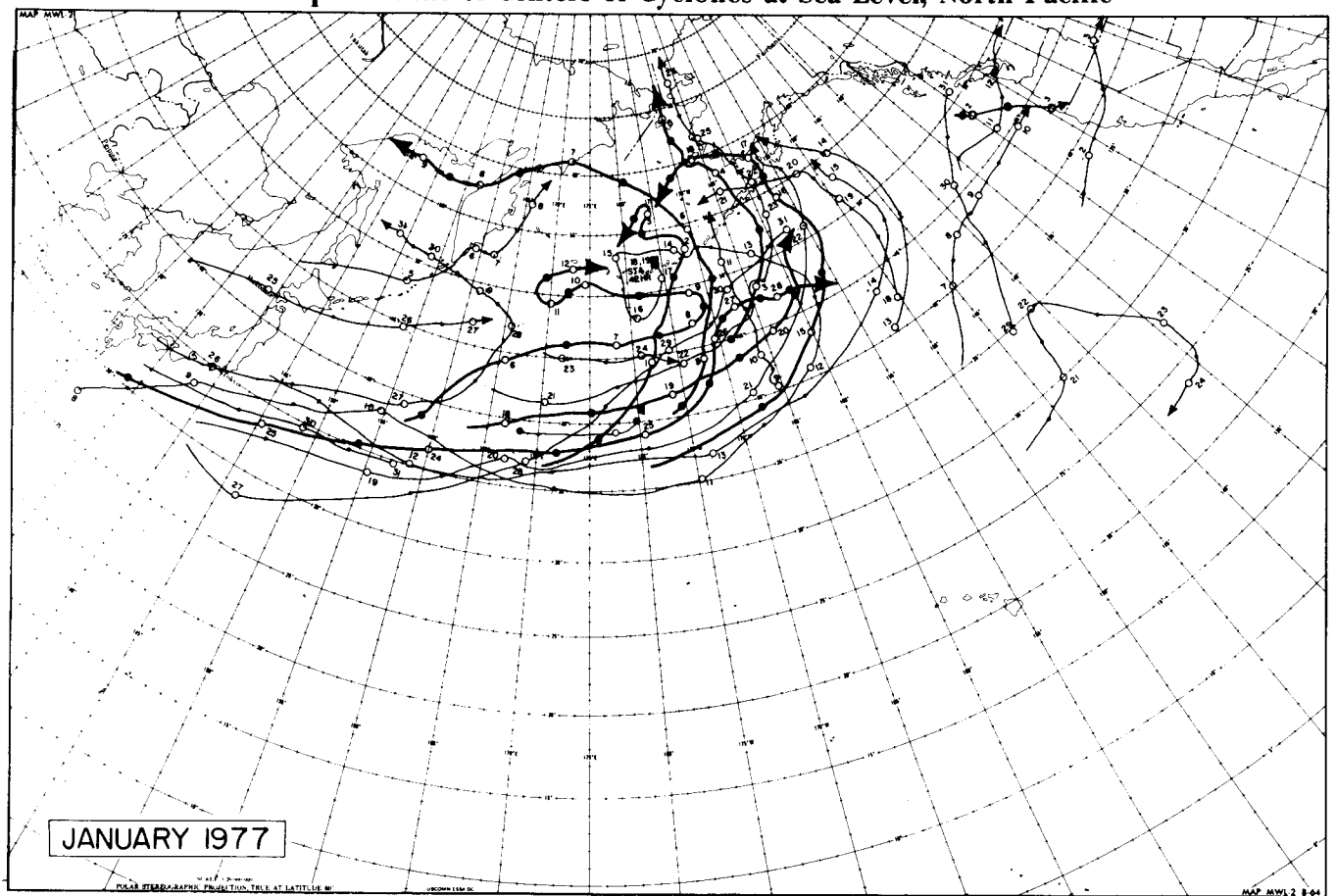
JANUARY 1977

Figure 9. North Pacific storm tracks observed for January, 1977. Notice the relative absence of storms entering the West Coast region due to the strong ridge that was present during the heart of the 1977 drought. (From U.S. Department of Commerce, Mariners Weather Log, 1977.)
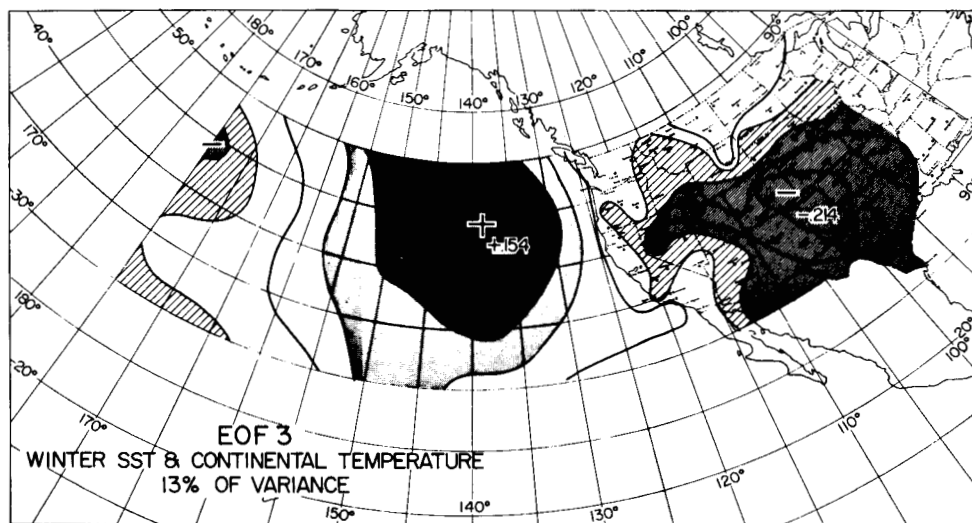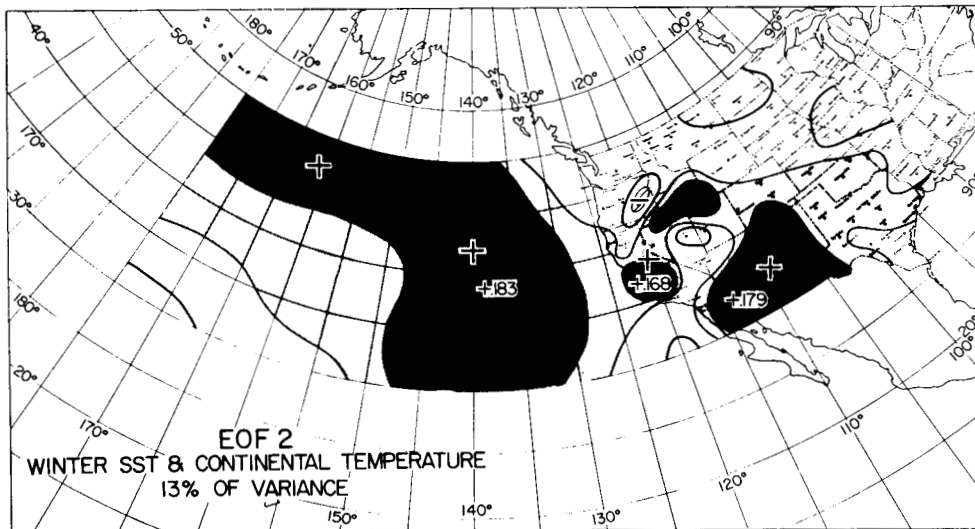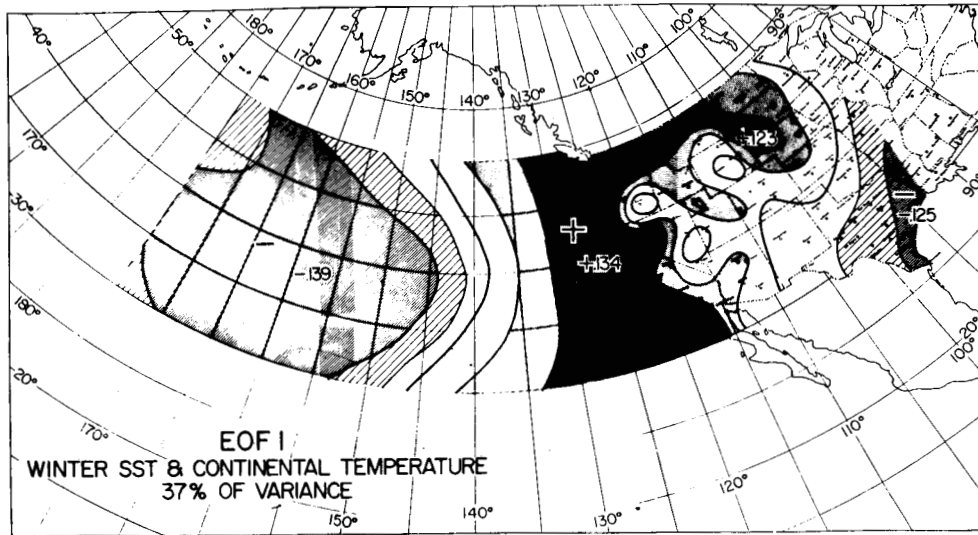
Figure 10. Empirical orthogonal functions (EOF) of surface temperature field based on winter data from 1948-72.

functions (EOF's). The first three patterns of covariability indicate a planetary wave length scale (4,000-6,000 km in this case) and together account for over 60% of the total surface temperature field. These patterns indicate that much of the anomalous temperature variability occurs in the zonal direction, also indicative of atmospheric long waves. Also, the patterns seen in this subarea of the Northern Hemisphere are reflective of larger patterns for the entire Hemisphere (see Barnett 1978a).

Focusing on a smaller region, the west coast of the United States, we can examine the variability in a nearly meridional cross section, with the help of surface temperature and precipitation. First, a chart of the time series of monthly temperature anomalies for 21 stations along the coast indicates the signal level and a large degree of correspondence between neighboring stations (Figure 11). The ability of empirical orthogonal functions (EOF's) to reduce a highly interrelated data set like this is illustrated in Figure 12. The first two EOF's (patterns shown in Figure 12), comprise roughly 83% and 70% of the variance of entire temperature and precipitation field, respectively, of the 21 stations. In both, the first EOF exhibits the tendency for the anomalous variability to be of like sign all along the coast (for instance all stations warmer than normal or all stations colder than normal), which agrees with our first example showing zonal alignment. This pattern dominates both the temperature and precipitation fields. It would prevail in a winter such as 1976-77 (see Figure 9), when a strong ridge dominated the entire west coast of the United States with resulting warm, dry conditions. In contrast, the second EOF shows a smaller scale meridional behavior, with warm in the north, cold in the south anomalous conditions (or vice versa). Again this function appears for both the temperature and precipitation fields. Physically, it probably represents the occurrence of a northern or southern storm track in the winter period. Notice that EOF 2 accounts for at most half of the variability of the first function.

FINAL REMARKS

There is considerable physical evidence for the occurrence of large space and time scales of interannual variability. In the physical realm, much work is needed to understand the causal mechanisms and interactions of this scale of behavior in order to predict their occurrence. In the biological realm, there are indications of important influences by short-term climatic fluctuations on various biological populations (see McGowan 1974; Tont and Platt 1979), which are discussed in part by Tont and Delistraty (1980) in this symposium. This area of application of climate research is in many ways interesting to those concerned with the growing problem of resource management, and it deserves greater attention.

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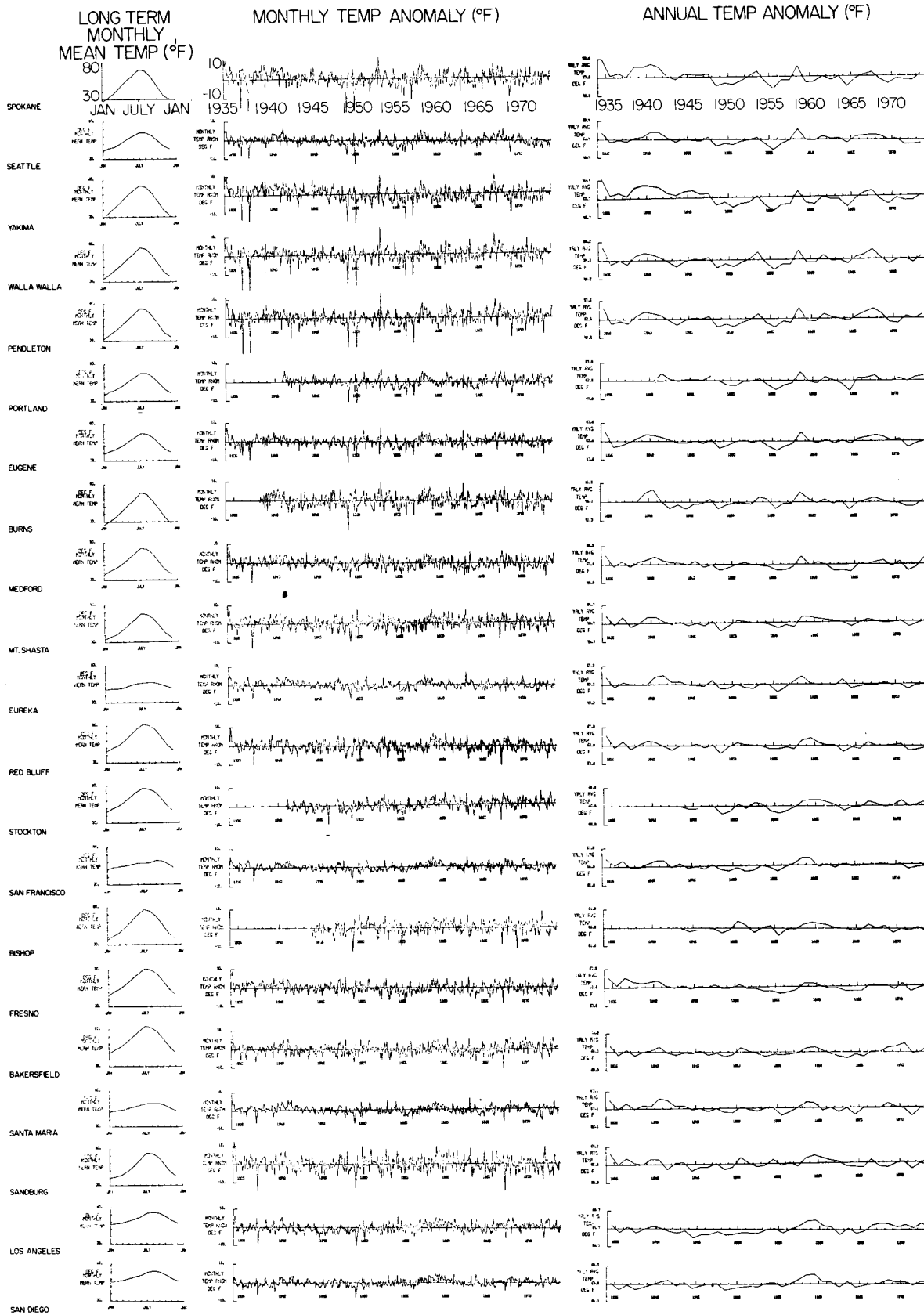
Figure 11. Surface temperature at 21 stations on the west coast of the United States. Graphs of long-term mean, monthly anomalies, and annual anomalies for (1934-73). Note the coherence between stations.

NORMALIZED WINTER TEMP. 1934-1973

EOF 1
66.7% of variance

EOF 2
16.6% of variance

NORMALIZED WINTER PRECIP. 1934-1973

EOF 1
41.9% of variance

EOF 2
28.4% of variance
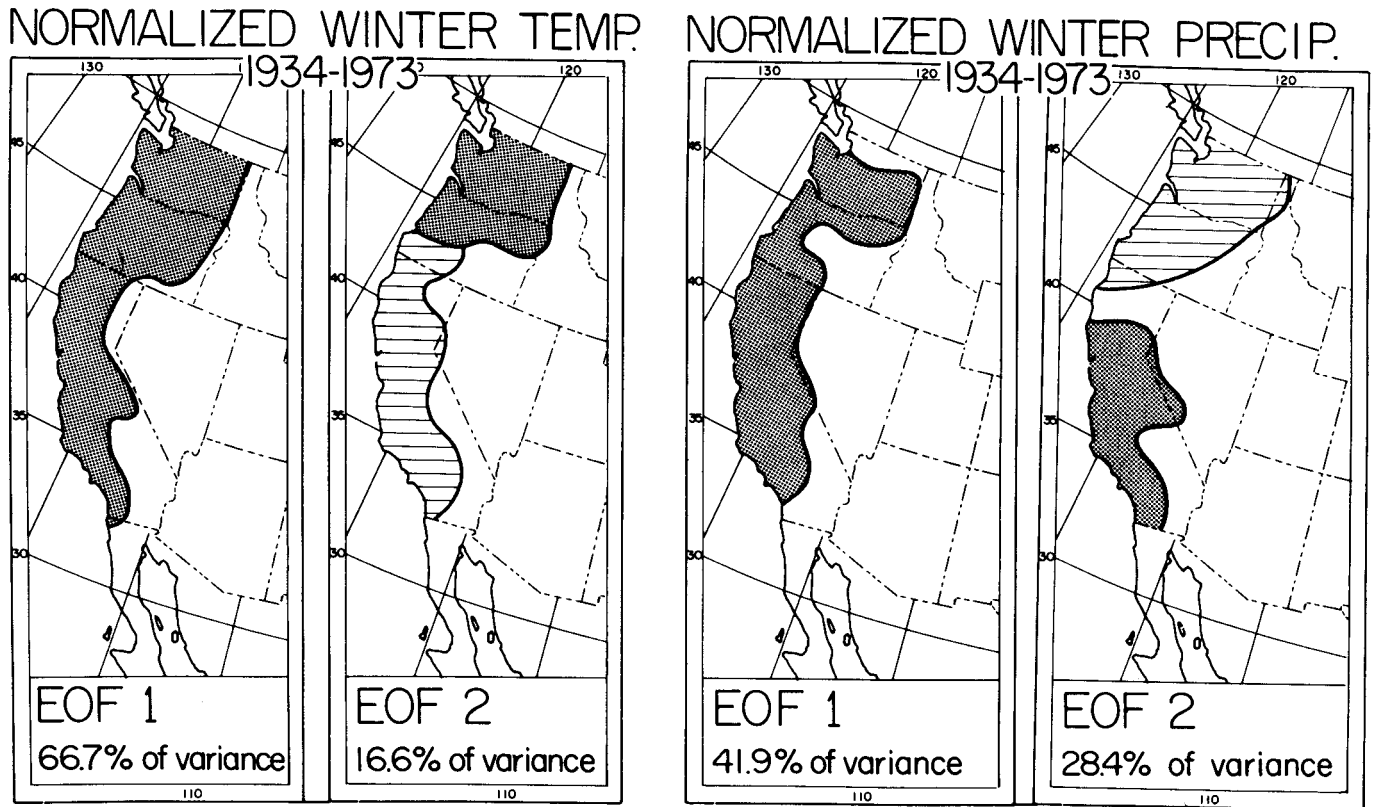
Figure 12. The first two empirical orthogonal functions (EOF) of surface temperature and precipitation for the 21 West Coast stations shown in Figure 11.

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GEOPHYSICAL ESTIMATES OF SEA-SURFACE TEMPERATURES
OFF WESTERN NORTH AMERICA SINCE 1671

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ABSTRACT

Sea-surface temperature (SST) data, which are reflective of air-sea interactions, are only available for the periods 1924 to 1940 and 1949 to 1972. In order to augment this short-term data, reconstruction of SST data are made using climatically sensitive tree-ring data. This involves multiple linear regression analyses between SST for 1° squares off southern California and Baja California (22°N to 33°N) and tree-ring data from seven sites in western North America.

A reconstructed summer SST series is shown to be negatively correlated ($r = -0.49$) with anærobic sediment core estimates of variations in northern anchovy populations off southern Baja California since 1785. Examination of the reconstructed SST reveals that the period 1671 to 1800 was typified by warm winter SST's and cool summer SST's. By the early 1800's, summers became anomalously warm off Baja California, and this summer warming climaxed in the 1840's and 1850's. During this warm summer period, SST anomalies were in excess of $+2.0°C$, and this is equivalent to a 2° latitudinal shift in SST fields, and a 2° northward shift in the oceanic front off southern Baja California.

RESUMEN

Datos de temperatura de la superficie del mar que reflejan las interacciones aire-mar solamente se han obtenido para los períodos de 1924 a 1940 y de 1949 a 1972. Para aumentar estos datos de corto plazo, se hacen reconstrucciones en los datos de temperatura de la superficie del mar usando los datos climáticamente sensitivos de los anillos anuales arbóreos. Esto implica unos análisis de regresión linear múltiple entre las temperaturas de la superficie del mar para cuadrados de 1° frente al sur de California y Baja California (de 22°N a 33°N), y datos de anillos anuales arbóreos de siete localidades en el oeste de Norteamérica.

Una serie reconstruída de temperaturas de la superficie del mar en el verano muestra tener una correlación negativa ($r = -0.49$) con cálculos tomados de núcleos de sedimento anaerobio, de las variaciones en las poblaciones de anchoveta del norte frente a Baja California desde 1785. Una examinación de las temperaturas reconstruídas revela que, en el período de 1671 a 1800, las temperaturas de la superficie del mar en el invierno eran típicamente cálidas y en el verano eran frescas. Por la época inicial de los años 1800s los veranos llegaron a presentar una anomalía cálida frente a Baja California, y este proceso

de calentamiento en los veranos tuvo su clímax durante el decenio de 1840 y de 1850. Durante este período cálido de verano, las anomalías de temperatura de la superficie del mar eran en exceso de $+2.0°C$, y ésto equivale a un cambio de 2° latitudinales en los campos de las temperaturas de superficie, y un cambio en el frente oceánico frente al sur de Baja California de 2° hacia el norte.

INTRODUCTION

Objective of the Investigation

Sea-surface temperature anomalies in the eastern North Pacific have been linked to fluctuations in climate across western North America (Allison et al. 1972; Bjerknes 1969; Namias 1969; Pyke 1972). It has been demonstrated that a long-term record of climatic fluctuations in western North America can be obtained from tree-ring data (LaMarche and Fritts 1971; Fritts et al. 1971). One should, therefore, be able to make inferences about past sea-surface temperature (SST) anomalies, as well as climatic anomalies, based upon analyses of tree-ring data.

This study is concerned with the reconstruction of SST data based upon analyses of tree-ring data in southwestern North America. Tree-ring data are useful in paleoclimatic reconstructions due to the availability of a large number of trees, the longevity of trees, and the critical fact that the climatic information they provide is accumulated during a specific year. Douglas (1973) has found that seasonal SST data can be extracted from tree-ring series. By calibrating tree-ring series from western North America against SST data, reconstruction equations can be made for estimating seasonal SST based upon the tree-ring data. In this project, reconstructed SST anomalies are used as indicators of past air-sea interactions off California and Baja California.

Previous Investigations

An apparent relationship between ocean temperatures and precipitation in California was first suggested by McEwen in 1925, who hypothesized that ocean temperatures should influence the atmospheric pressure patterns of the North Pacific region. He suggested that ocean temperatures should also influence the amount of atmospheric moisture available for precipitation. With these ideas, he attempted to forecast cool season precipitation in California based upon previous summer ocean temperatures. These forecasts were reasonably accurate con-

sidering his lack of open ocean data. He noted that the predicted departures in precipitation values agreed with the sign of the observed anomaly about 80% of the time.

In 1931, Lynch suggested the possibility of reconstructing past precipitation anomalies in southern California based on annual widths of tree rings. He found that the correlation between tree growth and precipitation was sufficiently high that he could calculate expected rainfall departures back to the 1700's. Using more advanced statistical techniques, LaMarche and Fritts (1971) showed that large-scale tree growth anomalies in the western United States for the past few centuries are a reflection of changes in seasonal precipitation patterns. Variations in precipitation patterns are ultimately linked to changes in large-scale circulation patterns across western North America and the North Pacific. Strong links between anomalies in atmospheric pressure, oceanic and continental precipitation, and SST have been demonstrated by Allison et al. (1972), Bjerknes (1969, 1974), and Namias (1969, 1971, 1972, 1973, 1974). Debate continues as to which variable, pressure or SST, is the most influential in creating climatic fluctuations, but once these variables do become anomalous, they can perpetuate or terminate each other through numerous and complex positive and negative feedback mechanisms.

Success has already been achieved in coastal SST reconstructions (Douglas 1973), and thus, the next step should be the reconstruction of open ocean data. The recent processing of SST data from ship logs dating up to 1972 has allowed this study to concentrate on a larger oceanic area for a longer time period (post-1924) than has previously been possible.

PROCESSING AND SEASONALIZATION OF SST DATA

Prior to forming a set of seasonalized SST data to be calibrated against tree-ring data, the monthly SST data, 1900 to 1972, were examined for possible observational errors and missing data. This involved checking the standard deviation of each average monthly SST value for each 1° square (Figure 1) and comparing all monthly SST values with the data from surrounding 1° squares. Virtually complete records were found to exist from 1924 to 1940 and 1949 to 1972. Only one monthly mean was found to be anomalously low compared to values from nearby squares. This incorrect value plus five missing values had to be estimated. These six monthly values were estimated by calculating the average SST for the two adjacent 1° squares that were north and south of the square with the missing data.

The three seasons examined include winter, spring, and summer, each of which contains four months. These seasons were based on natural criteria in the following ways. From March through June, the cyclonic eddies that
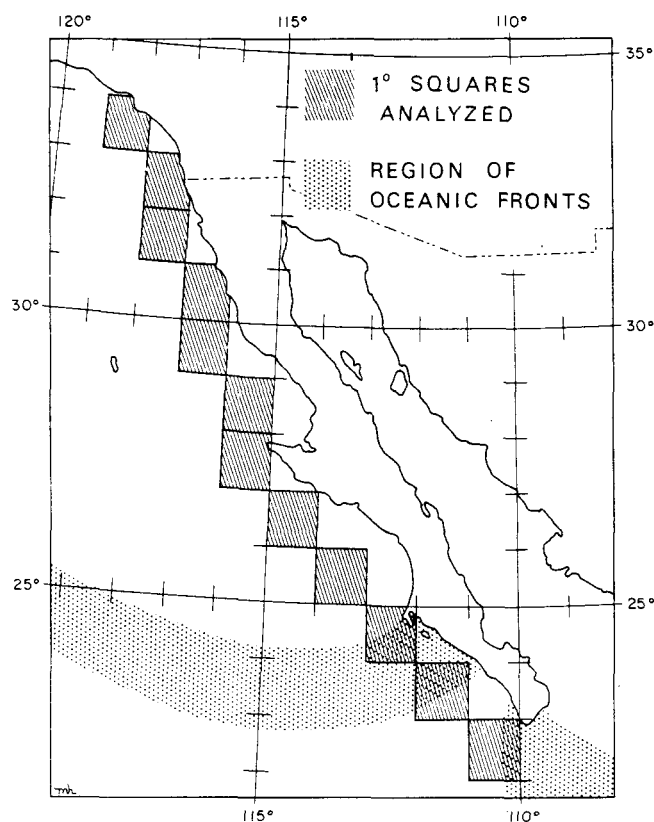
Figure 1. Location of 1° squares for which sea-surface temperature data are analyzed. General areas of oceanic fronts are shaded.

are commonly observed off southern California and Baja California become weak or nonexistent. During this spring period the California Current swings into the inshore waters from California southwards to the southern tip of Baja California. This is a result of an Ekman transport of water towards the south and southwest in association with strong north or northwesterly winds along the entire coast. The thermocline or mean mixed layer depths of spring are of intermediate depth to those of winter and summer.

The cyclonic eddies become established in July as the strongest winds become located farther offshore. During the summer period, July through October, a shallow thermocline is often present in the quieter coastal areas. The summer period is marked by a shallow thermocline and cyclonic eddy development off southern California and Baja California. This period is also characterized by the movement of an oceanic front up the coast of Baja California beginning in July. In June the 25° isotherm which marks this boundary is south of this region of the study, but by July it has advanced to near 23.5°N, 111.5°W and by October it has reached its northernmost position near 25°N.

By November, winter storminess greatly increases along the Pacific coast resulting in the mixing of the shallow thermocline of summer. The deepest thermo-

clines normally occur by January. Deepening of the thermocline plus decreased incoming solar radiation combine to initiate pronounced surface cooling across the area. At the same time, however, periods of southerly and southwesterly winds become more frequent, and this precludes cooling due to upwelling processes. The southerly winds also promote a strengthening of the cyclonic eddies and a surfacing of the northward flowing Davidson current. The winter season, November through February, is thus characterized by a deep thermocline and northward flowing water in the inshore regions.

DENDROCHRONOLOGY AND DENDROCLIMATOLOGY

Previous Investigations

Relationships between atmospheric circulation anomalies, precipitation anomalies, and tree-ring growth anomalies in North America have been discussed by LaMarche and Fritts (1971). They found that the growth of a tree can be directly or indirectly affected by variations in seasonal temperature and precipitation. These climatic fluctuations influence the energy balance and other physical or physiological conditions in the tree. With respect to trees in the warm parts of southwestern North America, low precipitation and high temperatures during the growing season are linked to the formation of narrow rings in arid site trees (Fritts et al. 1971, Model A). The narrow ring is the result of low soil moisture and increased evaporation which lead to increased water stress in the tree.

In a detailed analysis of the effect of climate on tree growth, Fritts et al. (1971) have obtained growth response fluctuations that indicate the relative effect of monthly temperature and precipitation upon the width of a given year's ring for different tree species on different sites. His analysis has indicated that a given species' response to climate may vary due to differences in location (e.g. differences in elevation, site aspect, substratum, or associated biota). It was also found that climatic conditions during given months may affect one tree species while having no effect on other tree species at the same site. Tree-ring chronologies of a single species at a given site will also contain "hold over" effects of previous climatic anomalies on successive annual rings. The number of years of "hold over" in different species has become a critical part of Fritts' response functions.

The most effective way to reconstruct different year-round conditions of past climate is to obtain a sample from diverse sites and several species within each region. The differences and similarities among sites provide added climatic information. Climatic reconstruction can sometimes be improved by using previous and following years' growth as predictors to handle the effects of food

storage or changes in root or shoot area. Thus, the climatically induced growth responses of trees for several sites with different species, and for several years (lagged tree-ring data) may be necessary to accurately predict the climatic conditions during a given season or sets of months.

Chronologies from Southwestern North America

In view of the above findings by Fritts, a number of species from diverse sites throughout southwestern North America have been examined for use in reconstructing seasonal sea-surface temperatures (Figure 2). The need for this diversity was recognized in an earlier analysis of SST reconstructions in which it was found that chronologies from high and low elevation sites contained different climatic information than did chronologies of different species (Douglas 1973). The three most useful chronologies from the earlier study were used in this analysis. They include the *Pseudotsuga macrocarpa* chronology, which is from the steep slopes of the coastal Santa Ana Mountains of California, elevation 1,214 m (Douglas 1973). A *Pinus ponderosa* chronology from California was selected from the gentle slopes of the Baldwin Lake area of California, elevation 2,231 m (Stokes et al. 1973). The high altitude *Pinus flexilis* chronology from Mount San Gorgonio, California, elevation 3,281 m, was also retained for this study (unpublished data on file at the Tree-Ring Laboratory, University of Arizona).

In addition to these chronologies, four more sites (Figure 2) were chosen for their possible usefulness in reconstructing SST's. In northern Baja California two
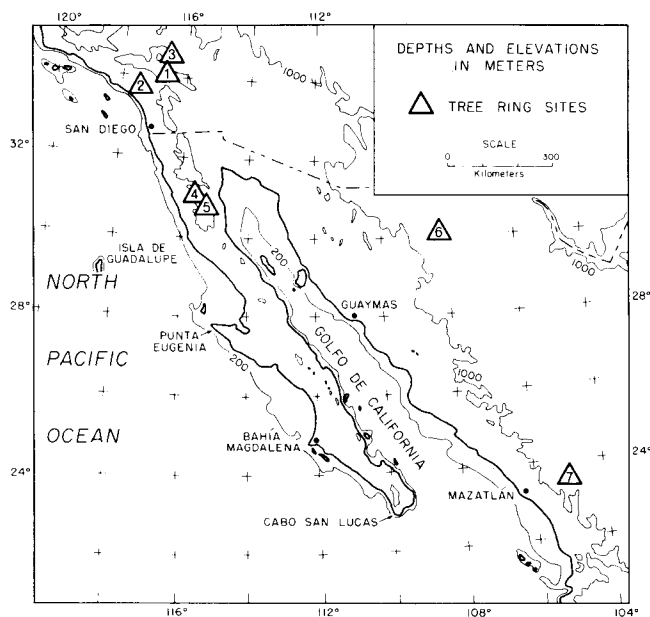

Figure 2. Location map of tree-ring sties and general area from which sea-surface temperature data are available. Sites include: 1) San Gorgonio; 2) Santa Ana Mountains; 3) Baldwin Lake; 4) San Pedro Martir; 5) Tasajera; 6) Rancho Escondido; and 7) El Salto.

chronologies from the San Pedro Martir range were selected: San Pedro Martir (low) and Tasajera. The San Pedro Martir (low) *Pinus jeffreyi* chronology was obtained from a site with a moderately low elevation (1,976 m), as was the Tasajera site chronology (elevation 2,218 m).

Unfortunately, no tree-ring chronologies have been developed for southern Baja California. For this reason two mainland site chronologies east of Baja California were chosen for their known usefulness in reconstructing climate. The northernmost Mexican mainland chronology is from Rancho Escondido, Chihuahua, where the sampled trees, *Pinus ponderosa*, grow at 2,128 m. Farther south in western Durango, Mexico, a *Pseudotsuga menziesii* chronology was selected (elevation 2,432 m).

The latitudinal coverage of the tree-ring chronologies is from 23°N to 34°N, which is about the same latitudinal area for which SST data are available. Most of the chronologies are from the northern sector of the study region because the availability of good long-term tree-ring data precludes any other choice of sites. The greater number of northern tree-ring sites may actually prove useful in reconstructing SST data for waters off western Baja California since the northern region is the source of the southward flowing California Current water.

The chronologies used in this analysis were developed by using the techniques of Fritts et al. (1969). This involves taking the measured raw tree-ring data and fitting the data to a modified exponential curve (growth function), thus producing indices. The indices were obtained by dividing the respective ring widths by the corresponding value from the growth curve, so that the mean of the series is 1.00 or 100% (Figure 3). This conversion is quite useful since the raw ring-width data show a considerable growth trend through time. The trend is induced by increasing age and not climate. Low frequency or long-term variance at frequencies of decades and centuries is preserved in this procedure, but trend is eliminated.

In most cases two cores from each tree are sampled and averaged into a tree chronology. This tree chronology represents an integrated climatological record with reduced nonclimatic noise. A given annual ring around the radius of the tree will minimize these nonclimatic abnormalities. Merging a large number of tree chronologies into a mean site chronology further minimizes the noise caused by growth variations within and between the trees, and the desired climatic information common in all trees is retained.

In developing a chronology from a large sample size (about 12 trees at each of the seven sites), a reliable estimate is obtained of the average limiting effects of climate on the trees. A plot of the final site chronologies for the seven localities is given in Figure 3. Similarities in growth can be noted in the low elevation sites of the north, while
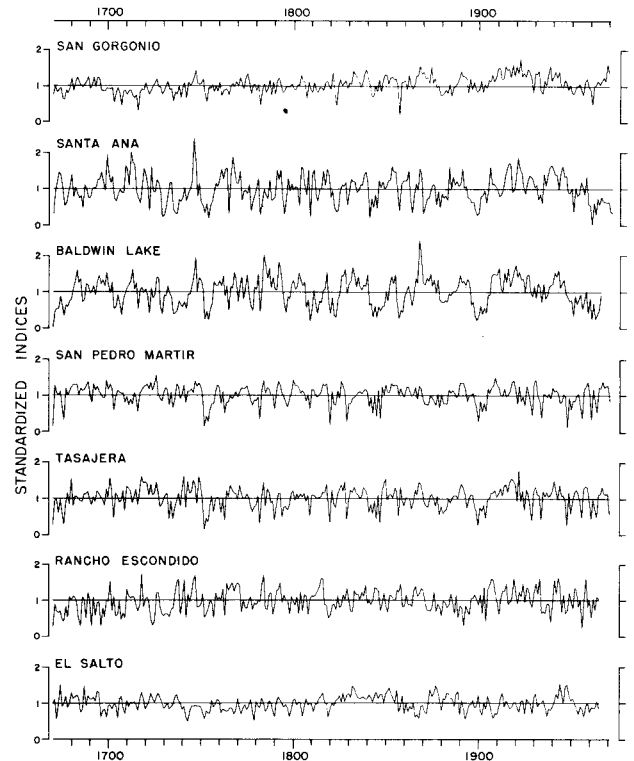
Figure 3. Tree-ring indices for seven sites in the western United States and Mexico. See Figure 2 for the location of sites.

the mainland Mexico chronologies do not appear to be highly correlated with the chronologies to the northwest. Less agreement is found between the high and low elevation chronologies.

SST RECONSTRUCTIONS

Tree-Ring Reconstructions of Climatic Parameters

Tree-ring data are useful in long-term climatic reconstruction due to the fact that the climatic information in tree rings is accumulated over a specific time period. In addition, one can obtain specific climatic information from tree-ring data that is for a given set of months or natural season. In the southwestern portion of North America, the vast majority of the dendroclimatic work has dealt with trees that are long-lived and sensitive to climatic changes. The following is a brief review of the development of dendroclimatology as it pertains to this study region in western North America.

In 1947, Schulman noted a positive correlation between tree-ring widths and rainfall in southern California. He felt that tree-ring data were reliable indicators of past wet or dry periods in southern California back to 1789. Schulman (1947) calculated a correlation coefficient (r) of 0.86 between tree-ring data from *Pseudotsuga macrocarpa* and rainfall for southern California. Correlation between Los Angeles annual temperature and tree growth was determined to be nonexistent by Schulman ($r = \pm 0.00$). Temperatures in May, June, and July were

found, however, to be slightly negatively correlated with tree growth ($r = -0.13$).

Large-scale and prolonged anomalies in precipitation are often linked to detectable changes in the atmospheric circulation. This immediately suggests the possibility of reconstructing past atmospheric pressure anomalies based upon tree-ring data over a large grid such as western North America. Anomalies in the atmospheric circulations of the western portions of North America since 1700 based upon tree-ring data have been calculated by Fritts et al. (1971). Their reconstructions are in the form of surface pressure anomaly maps reconstructed from various tree-ring sites in western North America. Both the surface pressure data (1900-62, excluding 1939-44) and the tree-ring data were subjected to eigenvector analysis before the calibration of the two data sets. The authors noted a good statistical relationship between the reconstructed surface pressure anomaly maps and known sea level pressure anomalies in the North Pacific during the 19th Century.

Growing evidence suggests that surface and upper level pressure anomalies near and over the North Pacific are linked to SST anomalies (Allison et al. 1972; Namias 1969; Bjerknes 1969). This linkage between SST and pressure may involve both positive and negative feedback mechanisms, depending upon the oceanic region and the season. Douglas (1973) took the relationship between climatic anomalies and SST anomalies to be an indication that SST data could also be reconstructed from tree-ring data. The results for southern California were encouraging with about 50% of the variance in SST being explained by the tree-ring data when using a simple multiple linear regression analysis. This type of reconstruction is of interest to both meterologists and oceanographers since SST anomalies have been shown to initiate major pressure, temperature, and precipitation anomalies in North America (Allison et al. 1972; Bjerknes 1969; Namias 1969; Pyke 1972). In addition, the reconstructed SST data could be used to infer changes in ocean currents (Douglas 1973). Reconstructed SST data also serve as an independent check upon other long-term reconstructions of precipitation, air temperature, or sea level pressure.

Multiple Linear Regression Analysis

The reconstruction of a given climate variable from tree-ring data lends itself to multiple linear regression analysis. In this project a stepwise multiple linear regression technique was used for reconstructing seasonal SST records. This is the same procedure used previously by Douglas (1973) in reconstructing coastal SST data for southern California. In the present investigation, however, the desired seasonal reconstructed temperature data

are the 5-m depth at La Jolla and SST data at 1° squares (predictands) from southern California southwards to the southern tip of Baja California. The set of seven tree-ring chronologies which were analyzed in the previous section are used as the independent variables (predictors).

The regression equation is an equation for estimating a variable, say Y_1 (seasonal SST), from a number of other variables $X_1, X_2 \ldots$ (the tree-ring data). In the case of the seven tree-ring chronologies the number of independent variables can vary, but the regression equation has the form

$$Y_1 = b_1 + b_2 X_2 + b_3 X_3 \ldots$$

where $b_1, b_2, b_3 \ldots$ are fitted constants.

As noted earlier, the climatic information for a given year can be "held over" into the rings of the following years. In order to extract this climatic information which is "held over," data from each of the seven chronologies were placed in a matrix of tree-ring data representing the lags over four years. That is, seasonal SST at time "t" could be considered a function of the tree-ring data X at times:

$$X_{t-3}, X_{t-2}, X_{t-1}, X_t$$

$$X_{t-2}, X_{t-1}, X_t, X_{t+1}$$

$$X_{t-1}, X_t, X_{t+1}, X_{t+2}$$

$$X_t, X_{t+1}, X_{t+2}, X_{t+3}$$

The reconstruction equations which on the average account for the greatest percent variance are those with the following lagging: $X_{t-1}, X_t, X_{t+1}, X_{t+2}$ (Douglas 1973). The seasonal SST data were calibrated against the tree-ring data for the following years: 1924 to 1940 and 1949 to 1963 for the 1° squares; and 1927 to 1963 for a 5-m temperature record at La Jolla.

The signficance of the regression equations and their variables can be determined by F-testing (Draper and Smith (1966). In these analyses the cutoff level for including a variable into the equation was an F level of 3.0 or greater. It should be noted, however, that a majority of the equations are totally composed of variables that entered the equations at F levels above 4.0.

Considering the length of record at each 1° square (32 years) and La Jolla (37 years), an F ratio for the reconstruction equation of 4.2 or greater indicates that the equation is significant at the 95% level. An examination of the regression equations reveals that all of the equations are significant at the 95% level, and in fact the majority are significant at the 99% level. Only 1 of the 175 regression coefficients was found not to be significant at the 95% level based upon "Students" t distribution. This

one regression constant is used in the summer reconstruction equation for the 1° square at 28.5°N, 115.5°W. Since all regression equations are significant at or above the 95% confidence level, it is probable that 9 or less of the 175 variables used have been chosen by pure chance.

When the coefficient of determination r^2 is multiplied by 100, this gives the percent variance explained by the equation. Values for the variance explained range from a low 30% at 33.5°N, 118.5°W during the summer, to a high 77% at 22.5°N, 110.5°W during the summer. The average percent variance explained at the 1°squares is 53% in winter, 54% in spring, and 55% in summer. Viewed in another way, this indicates a correlation coefficient (r) of about .74 between the tree-ring data and the seasonal SST data. These correlation results are somewhat better than those previously obtained from correlating tree-ring data with shore station SST data from southern California ($r = .67$, N averaging 41 years; Douglas 1973). This difference in r values probably reflects the fact that the oceanic data from south of 30°N are more representative of anomalies across broad areas of the eastern North Pacific. In contrast, shore SST data from California may at times reflect periods of tide-induced upwelling which have little relationship to broad-scale air-sea interactions.

Reconstructed SST and Verifications

Using the equations derived from the multiple linear regression analyses, reconstructions were made of the seasonal SST data and the 5-m temperature data for La Jolla back to 1671 (Figures 4 to 12). In the testing of the reconstructions, the physical reasonableness of the reconstructed data and the relation of the reconstructed data to independent data are important factors to be considered. An examination of the plots of the SST data (Figures 4 to 12) indicates that there is considerable correlation between the reconstructed SST data sets. Occasionally during the winter and summer, however, the reconstructed SST data for the southern California eddy region may show little correlation with the reconstructed SST data for southern Baja California (e.g. winters of 1868 and 1869 and summers of the 1870's). This is not an unusual condition since in the winter above-normal seasonal cooling can take place in the southern California eddy region when strong winter winds enhance oceanic mixing, while to the south lighter winds may allow the warm surface waters of late summer to persist. At times during the summer, anomalously warm waters may be restricted to the coast off southern Baja California. This anomaly pattern develops when the North Pacific Equatorial Current moves northward and influences this region earlier in the season.

A verification of some of the predicted SST data can be made by using SST data that were withheld from the calibration—i.e. the SST data prior to 1924 or from 1941-1948. In Table 1 actual and reconstructed seasonal SST data are presented for four 1° squares. This table shows that many of the reconstructions are within .5°C of the actual observed SST. Since extremes of SST are often emphasized in studying climatic anomalies, it was decided to test the predicted data with the observed data in a method that would stress the accuracy of reconstructing the extremes. A test utilizing specific class limits was developed in the following manner. Three class limits of the seasonal SST data were determined so that, on the average, three-tenths of the observed SST's would fall in each of the above-normal and below-normal classes, and the remaining four-tenths would fall in the normal class. An above-normal class reconstruction was thus considered correct if the actual observed value was above or near normal (100% accuracy), and it was considered incorrect if the actual value was below normal (0% accuracy). A tabulation of the results in Table 1 reveals an 81% accuracy in winter, an 83% accuracy in spring, and an 86% accuracy in summer. This gives an overall accuracy of 83% for the reconstructions.

The poorest reconstructions are for the winters of 1923 and 1945 and for the springs of 1917 and 1922. In these four cases, the actual observed SST anomaly patterns were found to have been undergoing major changes. In 1917 and 1922, rapidly warming conditions characterized the end of the spring, even though the March through June SST averages were below normal. Above-normal seasonal cooling occurred during the winter of 1923, following an anomalously warm summer in 1922. Anomalously cool summer waters in 1944 were followed by relatively warm winter waters in 1945. This analysis suggests that in examining the reconstructed SST data, the major anomalies that lasted for a number of seasons are probably correct, though the exact season in which the given anomaly ended may, at times, be off by one season.

An examination of the predicted summer SST data for all stations suggests an anomalously warm summer period from 1841-59 (Figures 10 to 12). Based on the reconstructions, this mid-1800's summer warmth has never been equalled during the period of actual SST records. The apparent accuracy of this reconstruction is borne out by marine fish collections from off southern California during 1853-60. Hubbs (1948) noted that the fish fauna of San Diego " . . . was definitely more tropical than that of any subsequent decade. Of the 30-odd species reported, six (about 20%) do not now occur so far north or have been so rare recently that one certainly would not expect any to be caught at present by such incomplete and superficial collecting as that of the 1850's and 1860's" (page 464). An examination of the SST plots (Figures 10 to 12) clearly indicated anomalously cold summers from
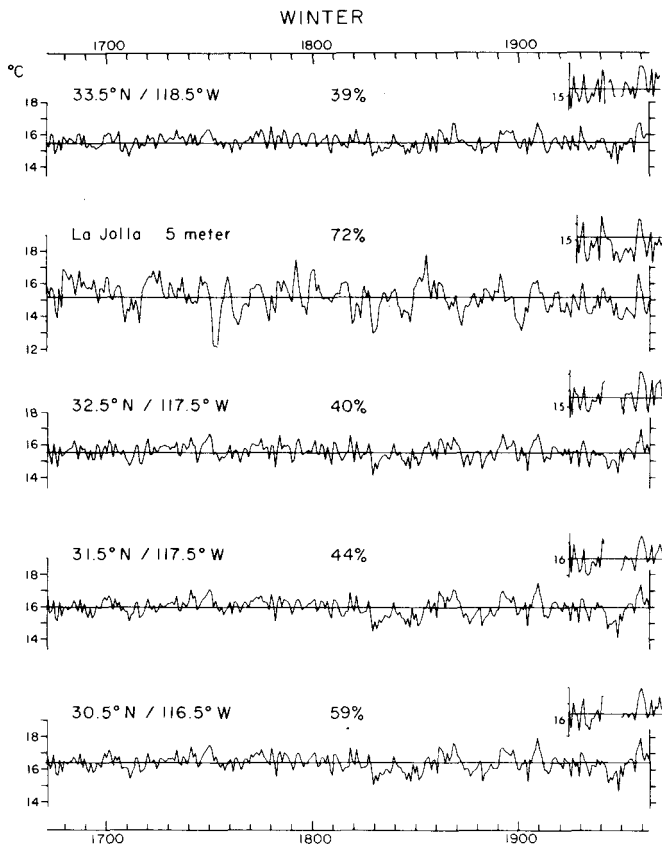
WINTER

WINTER

Figure 4. Reconstructed winter sea-surface temperatures for 1° squares from 30°N to 33°N. Winter reconstructed sea-surface temperatures with actual temperature data above each reconstruction. Solid lines through the curves are the means.

WINTER

SPRING

Figure 5. Reconstructed winter sea-surface temperatures for 1° squares from 26"N to 29"N.

Figure 7. Reconstructed spring sea-surface temperatures for 1° squares from 30"N to 33°N.

SPRING

Figure 8. Reconstructed spring sea-surface temperatures for 1° squares from 26°N to 29°N.

SUMMER

Figure 10. Reconstructed summer sea-surface temperatures for 1° squares from 30°N to 33°N.

SPRING

Figure 9. Reconstructed spring sea-surface temperatures for 1° squares from 22°N to 25°N.
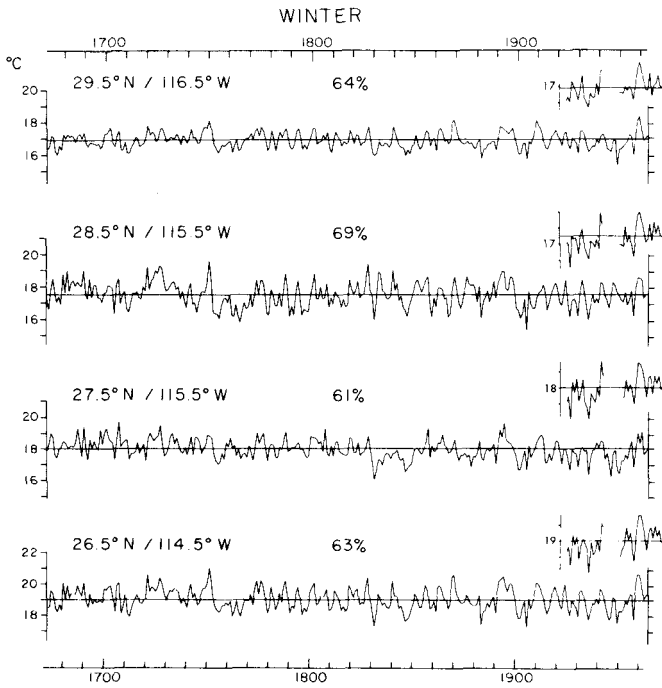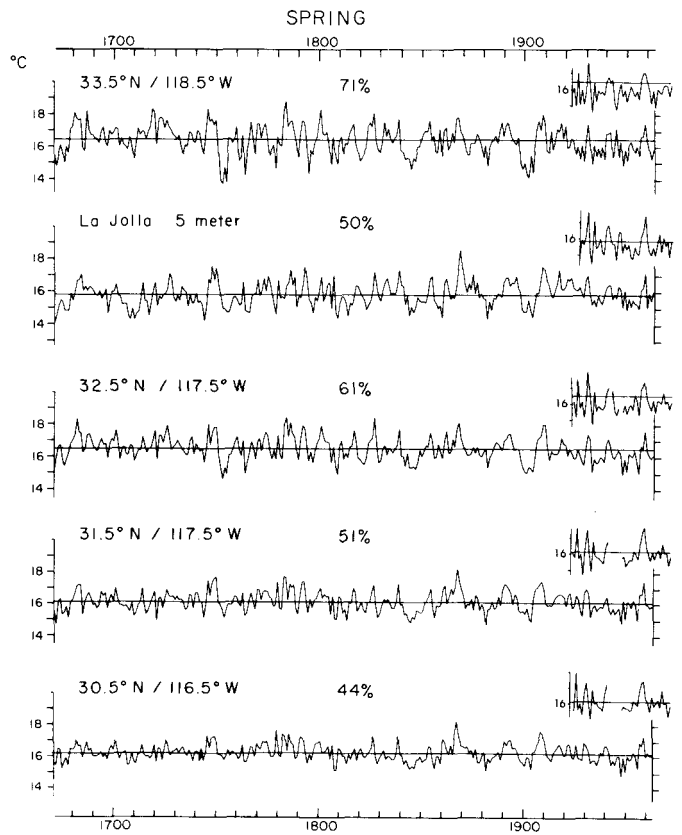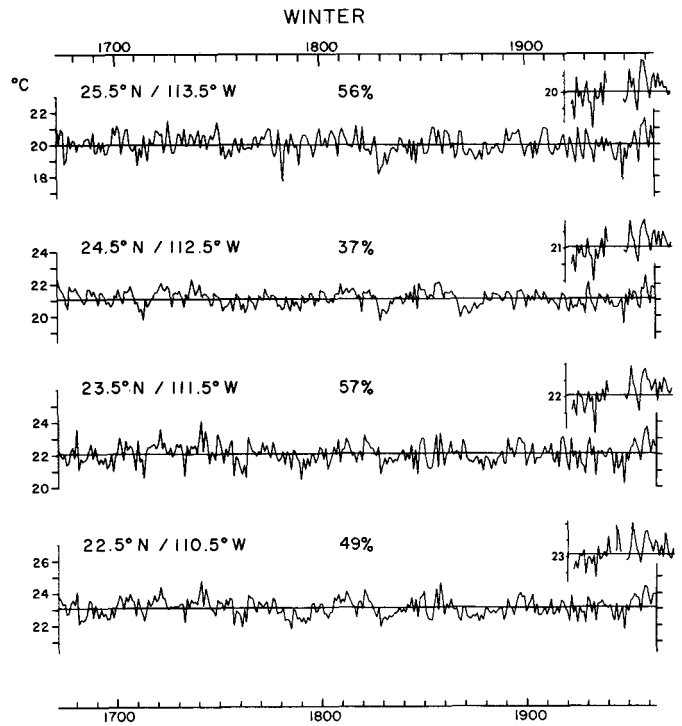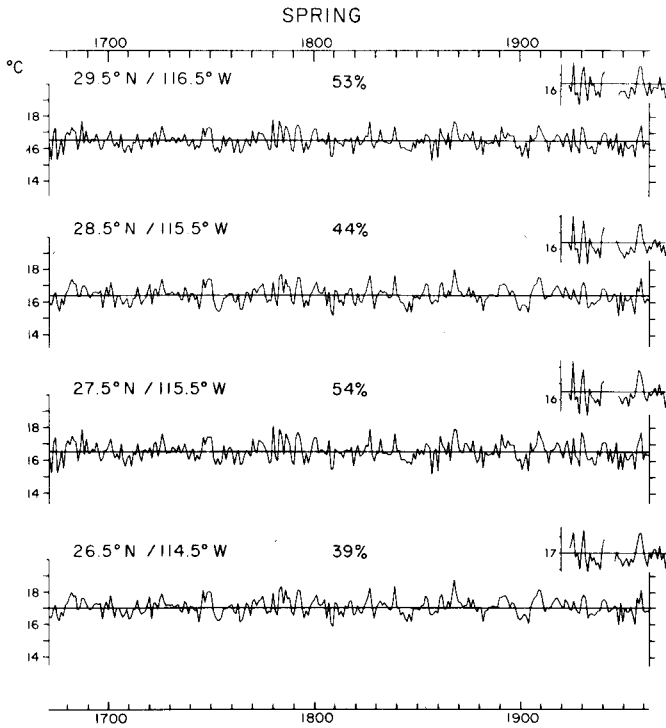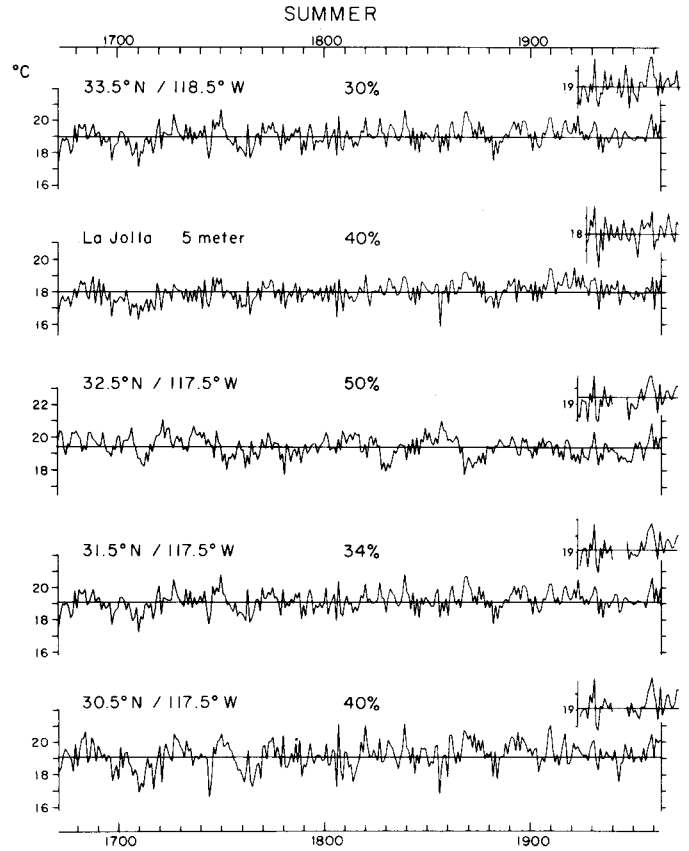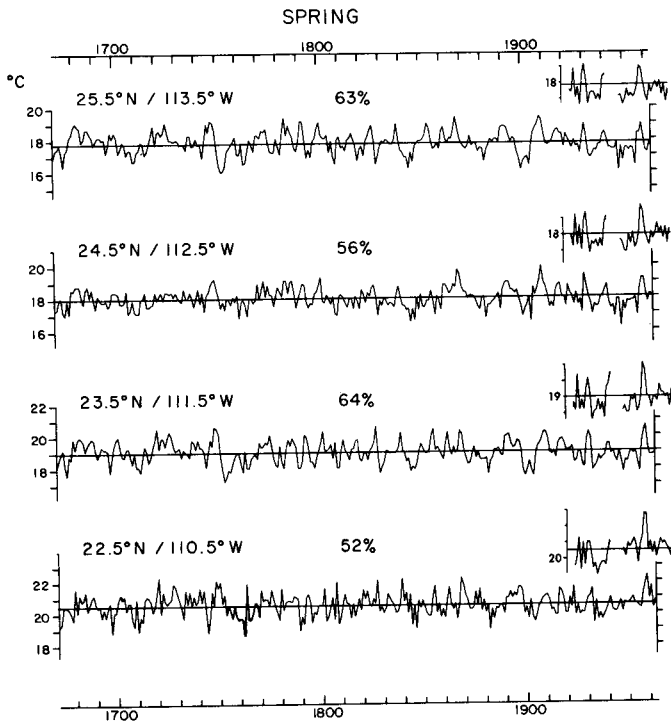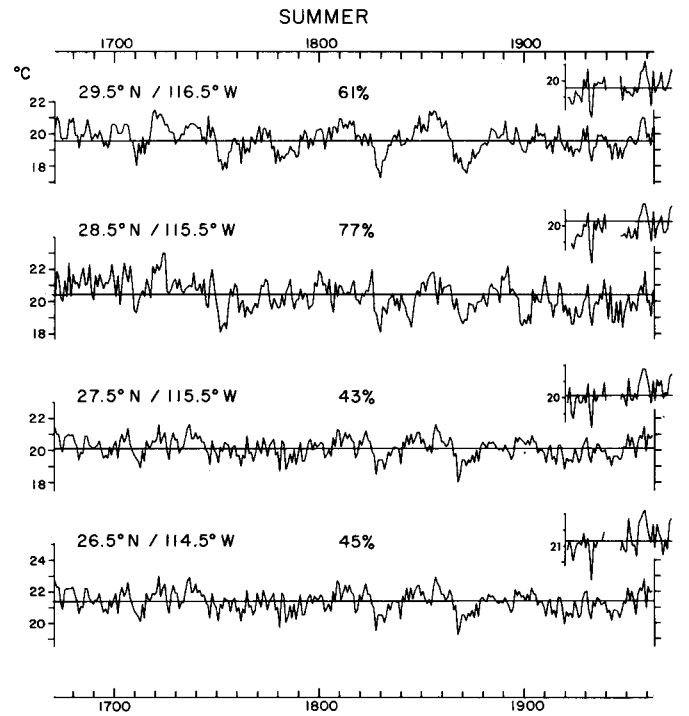
SUMMER

Figure 11. Reconstructed summer sea-surface temperatures for 1° squares from 26°N to 29°N.
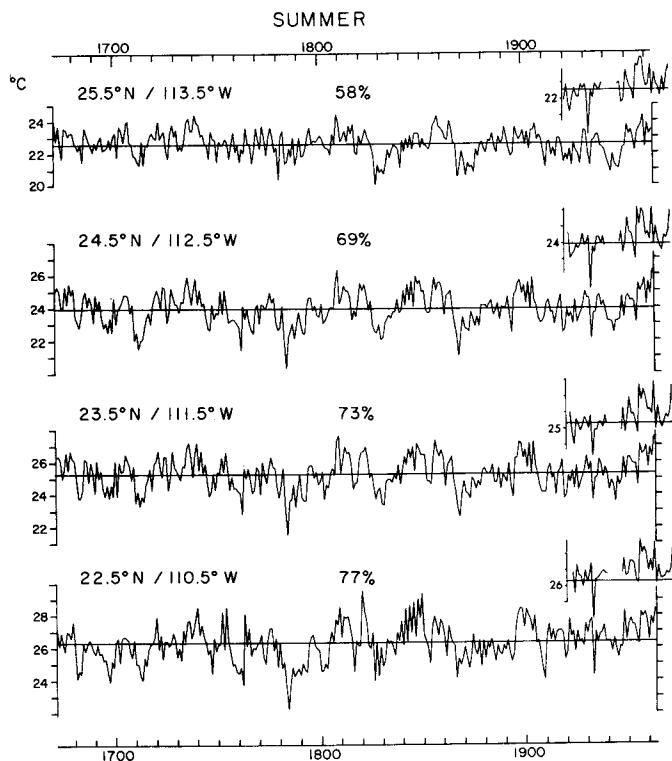
SUMMER

Figure 12. Reconstructed summer sea-surface temperatures for 1° squares from 22°N to 25°N.

1860 to 1880, a condition that undoubtedly resulted in a southward depression of the northern limits of these tropical fish. This reconstructed summer anomaly of the mid-1800's is the most impressive anomaly of any season during the past 200 years (Figures 4 to 12). It is highly encouraging to find that the historical fish-catch records also clearly indicate this to be an unduplicated event.

Hubbs (1948) further noted that long-term SST anomalies along the California coast can affect the distribution and population sizes of numerous marine organisms. An excellent measure of fish population changes can be derived from an examination of anaerobic coastal sediments. Such a record exists for the Soledad Basin off Bahia Magdalena (Figure 2, near 25°14'N, 112°41'W). Soutar and Isaacs (1974) found large variations in the population sizes of the northern anchovy (*Engraulis mordax*) as determined from scale counts (Figure 13). These population changes may indicate climatic changes since Baxter (1967) states that "During periods of warmer-than-average water temperatures, adult anchovies became less available in the inshore waters" (page 110). Off central and southern Baja California, 65% of the fish catch is taken in water temperatures ranging between 17.0° and 21.5°C. It would seem, therefore, that anomalously warm periods would favor a paucity of fish, while anomalously cold periods could result in a sizeable increase in the fish population.

TABLE 1
Comparison of the Actual with the Reconstructed Sea-Surface Temperatures at Four Locations.[1]

1° Square	Year	Winter Actual	Winter Recon.	Spring Actual	Spring Recon.	Summer Actual	Summer Recon.
33.5°N/	1921					18.9	19.9
118.5°W	1923	13.6	15.8	15.7	16.5	18.5	20.4[2]
	1941	16.1	15.7	16.8	16.8		
	1942			16.4	16.9	18.7	19.4
	1943	15.8	14.8	16.6	15.4	19.6	18.3
	1944	16.1	14.9[2]	15.2	16.0	18.3	18.5[2]
	1945	15.7	14.4	14.7	17.1[2]	18.8	19.1
	1946	15.0	15.3	15.9	15.3	20.4	19.4
	1947	15.1	15.5	16.4	16.3	19.5	19.1
	1948			15.5	14.9	17.7	19.0
29.5°N/	1914	16.7	16.3				
110.5°W	1921					19.0	19.5
	1922					19.0	18.8
	1923	16.0	17.5[2]			18.6	19.2
	1941	17.9	17.2	17.2	17.0		
	1945					20.1	19.4
	1947					20.3	19.1[2]
	1948			15.8	15.6	18.8	18.4
26.5°N/	1914	18.7	18.1	17.4	16.9		
114.5°W	1917			16.2	17.5[2]	22.1	21.6
	1919	19.7	19.4				
	1921					20.8	20.7
	1922			15.4	17.5[2]	21.4	20.4
	1923	18.3	20.0[2]			20.0	20.6
	1941	19.9	19.6	17.9	17.5		
	1945					23.6	20.8[2]
	1946	19.1	19.2	16.5	17.1		
	1947			17.1	17.0	20.7	20.4
	1948			16.7	15.9	21.3	20.7
22.5°N/	1914	23.1	22.7				
110.5°W	1917			19.6	21.3[2]	27.2	27.0
	1921					26.1	27.7
	1922			18.4	20.3		
	1923	22.2	22.7			26.9	26.9
	1941	23.2	23.2	21.1	20.9		
	1944	24.9	23.3				
	1945	24.3	22.2[2]	21.6	20.3	26.6	25.3
	1946	23.3	22.7	23.3	20.7		
	1947					26.6	25.9
	1948			20.6	20.6	27.7	28.2
Verification Scores		81%		83%		86%	

[1]Data comparison is for the periods not included in the calibrations. Seasonal verification scores are given for each season (see text for details).
[2]Received scores of 0%.

A simple correlation analysis was run between the fish scale count data and the reconstructed summer SST at 25.5°N, 113.5°W (5-year averages for 1785-1919). The results show an *r* value of −0.49 (*N* = 27), which is significant at the 95% level. This significant negative correlation indicates that from 1785-1923 the northern anchovy was probably common off Bahia Magdelena during cool summer periods (e.g. 1825-34 and 1870-79) and rare

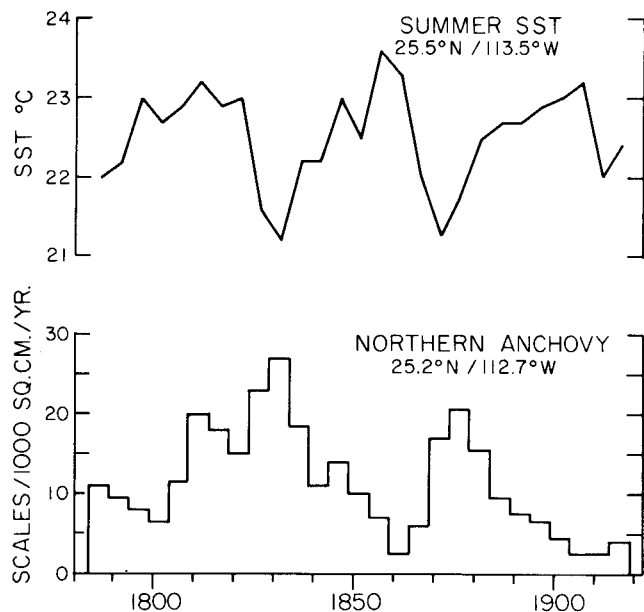Figure 13. The total number of northern anchovy scales (5-year totals) collected in deep-sea cores from off central Baja California (from Soutar and Isaacs 1974). Plot of reconstructed summer sea-surface temperatures at a nearby location is given for comparison.

during warm-water periods (e.g. 1845-64). The correlation between the northern anchovy and the reconstructed SST might have been higher if it was based on yearly data rather than 5-year means which unfortunately often overlapped apparent warm and cold periods (e.g. late 1830's-early 1840's). This correlation analysis clearly stands out as a verification of these two independent data sets back to 1785.

CONCLUSIONS

Analyses of average monthly SST data for 1° squares off southern California and Baja California indicate that there were two periods of virtually complete records: 1924 to 1940 and 1949 to 1972. Standard ring-width series from western North America were examined for their potential use in reconstructing these SST records back to the 1600's. Climatic information for all months of the year appears to be contained in the tree-ring series. Presumably, tree species were indirectly influenced in their growth by SST changes during the past in a manner similar to that for the period in which the reconstruction equations have been developed (1924 to 1940 and 1949 to 1963).

The average percent variance of the SST data that is explained by the tree-ring series is 53% in winter, 54% in spring, and 55% in summer. This amounts to a correlation of about 0.74 ($N = 32$) between the tree-ring series and the SST series. Tree-ring series are highly correlated with the summer SST off southern Baja California (r values of about 0.85). Less correlation is noted between

the tree-ring series and the SST data for off southern California (r values of about 0.65). Apparently the complex oceanographic conditions of this region are not as well related to widespread changes of climate in the eastern North Pacific.

The reconstructed records of SST indicate a number of changes in seasonal SST patterns since 1671. From 1671 until about 1800 there are suggestions of relatively warm winters and cool summers. This indicates a southward shift in the oceanic regime of the eastern North Pacific, because suppressed seasonal ranges in SST are more typical of central California.

The mid-1800's were characterized by anomalously warm summers and an apparent northward shift in the mean position of the summertime oceanic front off western Baja California. The SST departures from normal during some of these summers exceeded $+2.4°C$, and this is equivalent to about a 2° latitudinal shift in the SST fields and the oceanic front.

A general upward trend in SST is noted in the 5-m temperature reconstructions for La Jolla, California. This rise in ocean temperatures coincides with the warming at the end of the Little Ice Age, and thus this event may be detectable in SST reconstructions. The rise of about 1°C in the 5-m temperatures is most noticeable during the seasons of upwelling, spring and summer, and may reflect warming of the subsurface water mass off southern California, which originates to the south. It was noted that anomalously warm summer conditions commenced in this southern region about 1800, and this coincides with the beginning of the warming at 5 m.

Verification of the reconstructed SST data was accomplished through a number of methods using different sources of data. The SST data from the periods prior to 1924 or from 1941 to 1948 tended to indicate a fairly high degree of accuracy in reconstructing SST extremes (an 83% accuracy). In most cases the reconstructed anomalies were within 0.5°C of the actual anomalies. Reconstructions were not as accurate during periods of major SST reversals, with the actual season of reversal occasionally being miscalculated by one season.

Verification of the reconstructions for the 1700's and the 1800's involved comparing the reconstructed SST data with deep-sea varve data. The varve data provide estimates of relative variations in northern anchovy populations from 1785 to present. These estimates of fish populations showed a significant negative correlation with summer SST for off southern Baja California (r value of -0.49). Plots of the two data sets indicate that the fish species was less common in the warmest summers, and this is in agreement with data that indicate the species is seldom caught when water temperatures rise to about 21.5°C.

ACKNOWLEDGMENTS

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Part IV

SCIENTIFIC CONTRIBUTIONS

EFFECTS OF SEAWATER TEMPERATURE ON SPAWNING, EGG DEVELOPMENT, HATCHING SUCCESS, AND POPULATION FLUCTUATIONS OF THE DUNGENESS CRAB, *CANCER MAGISTER*

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ABSTRACT

Dungeness crab (*Cancer magister*) fishery landings in central California declined in the early 1960's and have continued at low levels to the present. In the laboratory, female crab spawning, egg development, and hatching success were affected variously by seawater temperatures ranging from about 10 to 17°C. Crabs tended to spawn later in colder water. The time required for eggs to develop from spawning to hatching ranged from an average of 64 days at 16.7°C to 123 days at 9.4°C. Egg survival and hatching success were significantly better the cooler the water. The average number of larvæ hatched per crab egg mass ranged from 14,000 at 16.7°C to 685,000 at 10.0°C. Unusually high ocean temperature during the egg brooding period in 1957 preceded the decline in landings by three years, and landings have remained low as ocean temperatures, on the average, have remained relatively high. A similar relationship also exists between ocean temperature and fluctuations in crab landings in northern California.

RESUMEN

Las capturas del cangrejo Dungeness, *Cancer magister*, en California central disminuyeron a principios de la década de 1960 y han continuado a niveles bajos hasta el presente. En el laboratorio, el desove de las hembras, el desarrollo de los huevecillos, y el éxito de eclosión se vieron afectados por variaciones en la temperatura del agua marina, fluctuando entre 10 y 17°C. Los cangrejos tendían a desovar más tarde en agua más fría. El tiempo requerido para el desarrollo de los huevecillos, desde el desove hasta la eclosión, varió desde un promedio de 64 dias a 16.7°C, hasta 123 dias a 9.4°C. La supervivencia de los huevecillos y el éxito de la eclosión eran significativamente mejores cuanto más fría estaba el agua. El promedio de larvas eclosionadas por masa de huevecillos de cangrejos varió desde 14,000 a 16.7°C, hasta 685,000 a 10.0°C. Temperaturas oceánicas extraordinariamente altas durante la época de incubación de los huevecillos en 1957, precedieron por tres años la disminución de las capturas, y éstas han permanecido bajas mientras las temperaturas oceánicas, en un promedio, han permanecido relativamente altas. Una relación similar existe también entre las temperaturas oceánicas y fluctuaciones en la captura de cangrejos en el norte de California.

INTRODUCTION

The Dungeness crab, *Cancer magister*, supports important commercial fisheries along the west coast of North America from central California to Kodiak, Alaska (Figure 1). Wide fluctuations in landings have been characteristic of these fisheries, but the landings in California, Oregon, and Washington have fluctuated somewhat synchronously over the years. However, in the early 1960's, landings in central California declined drastically and have continued at unprecedented low levels to the present while the landings in northern California (and northward along the coast) have continued to fluctuate widely (Figure 2).
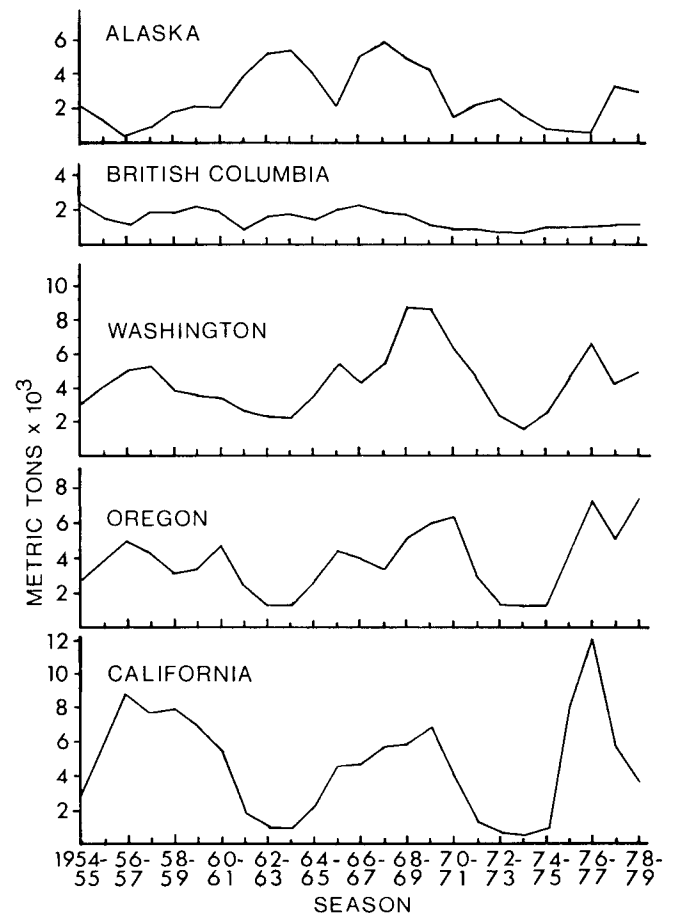

Figure 1. Dungeness crab commercial fishery landings by season, 1954-55 through 1978-79, except Alaska and British Columbia seasons are in calendar years, i.e. 1954-55=1955.
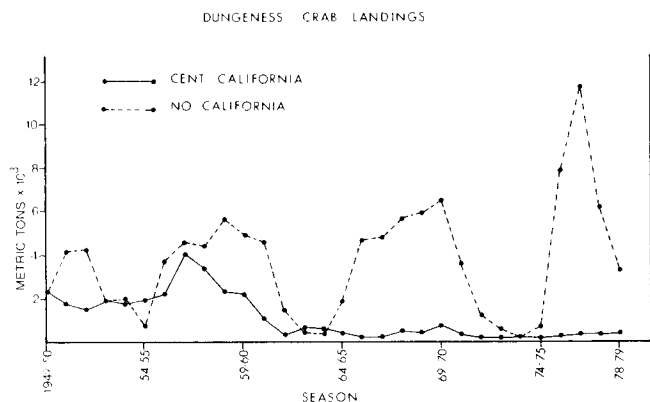
Figure 2. Northern and central California Dungeness crab commercial fishery landings by season, 1949-50 through 1978-79.

The long-term decline of the central California crab fishery has been of much concern to fishermen, dealers, consumers, and fishery biologists. In 1974 the State Legislature, by Senate Bill 1606, directed the California Department of Fish and Game (CDFG) to conduct an investigation into causes of the decline and to make recommendations to protect and increase the crab resource.

In response to the Legislature, the Department established an intensive Dungeness Crab Research Program which has been studying crab life history, pollution, and oceanographic factors for possible relationships to the decline (Orcutt et al. 1975, 1976; Orcutt 1977, 1978; Farley 1979). These studies have shown no significant relationships to environmental pollutants (pesticides, oil, chlorine-treated domestic and industrial wastes, etc.) that can explain the decline or that would prevent recovery of the crab resource. These studies do indicate that long-term oceanographic conditions may be at least partly responsible.

The present report presents information from laboratory studies on seawater temperature and Dungeness crab reproductive biology and comparisons of crab landings and ocean temperatures which suggest a possible explanation for the central California decline and for some of the fluctuations in Dungeness crab landings on up the coast.

DUNGENESS CRAB REPRODUCTIVE BIOLOGY

In California, most Dungeness crab mating occurs in the spring from about March through June. Mating occurs between a hard-shelled male and a newly molted soft-shelled female (Snow and Neilson 1966). Sperm are stored internally in the female's paired spermathecæ until spawning, which usually occurs in the fall from late September to November in California. The eggs are fertilized as they pass through the spermathecæ at the time of spawning and are extruded from the reproductive tract through paired ovipores on the crab's sternum. The eggs form in a spongelike mass (Figure 3) as they adhere

individually to the pleopodal hairs on the crab's abdomen where they are brooded until they hatch. A crab must be at least partially buried in sand for the egg mass to form. An egg mass may contain as many as one to two million eggs. Egg masses are usually bright orange in color when spawned and gradually change to dark brown as the developing embryos deplete the yolk, and pigmentation and eye spots appear before hatching. Most egg brooding (ovigerous) crabs are generally found in central California from about October through December and in northern California from about October through January. Hatching in central California usually occurs from late December to early February and in northern California from about January to early March. Ovigerous females are found even later in the year on up the coast, where temperatures are cooler and the egg brooding period is longer. The newly hatched larvæ are planktonic and metamorphose through six larval stages before the benthic crab stage is reached three or four months later.

METHODS AND MATERIALS

Adult female Dungeness crabs were collected from San Francisco and Eureka areas (central and northern California respectively) during late May, June, or July of 1977, 1978, and 1979 and were transported to the Department's Marine Culture Laboratory near Carmel, California. Crabs that had obviously molted recently and thus presumably had mated were selected at the laboratory for the experiments. Twenty crabs were used in 1977, 24 in 1978, and 24 in 1979. These crabs ranged in size from 130 to 156 mm in carapace width (excluding the 10th antero-lateral spines).

The crabs were held in separate compartments in fiberglass aquaria, four crabs (two from each area) in each aquarium. The aquaria were equipped with sand and aerated sub-sand filters and were supplied with seawater in an open (non-recirculating) system. The seawater was

Figure 3. Dungeness crab with egg mass.

pumped from the ocean nearby and was filtered and ultraviolet-treated at the laboratory.

Three seawater temperature regimes were used each year, including one at approximately 17°C, one at approximately 10°C, and one at ambient which, fluctuating between the other two, averaged 13-14°C during 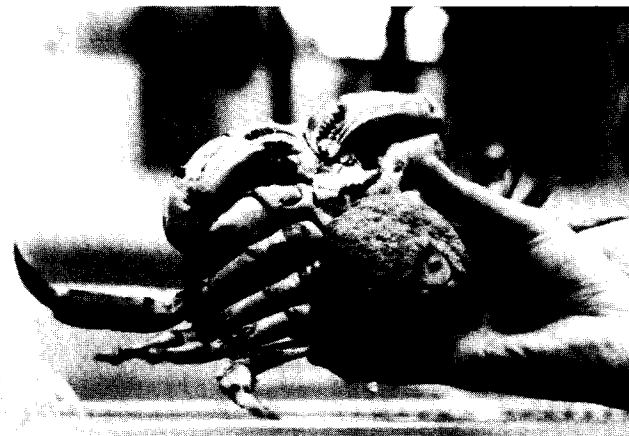the experiments. Ambient laboratory temperature approximates ocean tempreatures off San Francisco, whereas the other two are respectively higher and lower; the lower regime is closer to conditions off Eureka. The crabs were maintained at these temperatures during prespawning, spawning, egg brooding, and hatching periods.

Each experiment was begun with eight crabs in each temperature regime, except in 1977 when only four crabs were held in ambient. Also in 1977, air and seawater supplies to one warm aquarium malfunctioned, and all four crabs died before spawning, leaving only four crabs in warm seawater that year.

At least three times per week throughout each experiment, seawater temperatures were monitored, crab behavior was noted, and the crabs were fed. Food consisted of frozen market squid, Loligo opalescens, diced before feeding, and frozen ocean shrimp, Pandalus jordani.

During all three experiments, time of spawning, condition and color of the egg masses, and time of hatching were recorded. During 1978 and 1979, egg mass volumes were measured periodically and estimates of numbers of larvæ hatched were calculated by serial dilution and counting. Egg mass volumes were obtained by removing a crab from an aquarium, gently pressing seawater from the egg mass, and forming aluminum foil over it to form a cup, The cup was removed and filled with seawater, which was then measured in a graduated cylinder. The mean of about five repeated fillings was recorded as the volume. Of several methods considered, this method, although somewhat imprecise, was considered the least traumatic to the crabs and egg masses; also, it allowed for periodic measurements and gave values that were useful in comparisons of egg mass volumes within and between seawater temperatures.

RESULTS AND DISCUSSION

Spawning

All spawnings occurred between mid-September and early December, although most occurred before mid-November. A few crabs died before spawning, but all of the remaining crabs spawned during this period (Figure 4). Nonparametric Kruskal-Wallis tests (Hollander and Wolfe 1973) were used to determine the significance of differences in dates of spawning by year, by location, and by temperature.

There were no significant differences in dates of spawning by year within temperature regimes except in ambient
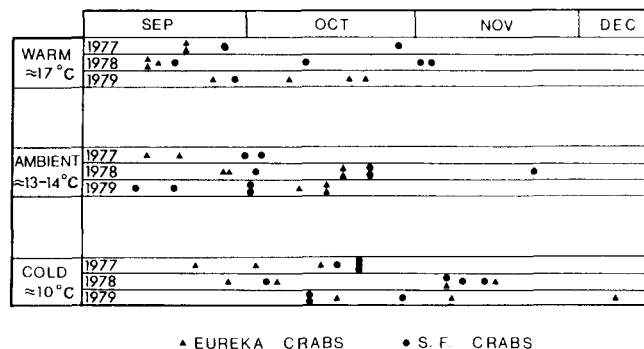
Figure 4. Spawning dates of female Dungeness crabs from Eureka and San Francisco areas in three different seawater temperature regimes in the laboratory during 1977, 1978, and 1979.

seawater where the differences were only slightly significant ($P = 0.076$) with spawning dates tending to be later in 1978.

When all temperature regimes are considered together, there was a tendency for Eureka area crabs to spawn earlier than San Francisco crabs in both 1977 ($P = 0.008$) and 1978 ($P = 0.045$) whereas in 1979 there was a tendency for San Francisco crabs to spawn earlier ($P = 0.041$).

There appears to be a trend towards crabs spawning later the colder the water. However, Dunn's multiple comparisons (Hollander and Wolfe 1973) show that spawning dates were not significantly different between ambient and warm regimes but they were significantly different between cold and ambient and cold and warm regimes with an experimental error rate 0.05. Therefore crabs in the coldest temperature tended to spawn later than those in either ambient or warm regimes.

One additional observation of interest is that spawning dates of San Francisco crabs in ambient seawater were not significantly different from Eureka area crabs in cold seawater ($P = 0.19$). In both cases, these crabs were in temperatures approximating their natural environments. This may suggest that crabs in San Francisco and Eureka areas tend to spawn at similar times.

The reversal in spawning trends by areas in the 1979 experiment may be due to differences in maturation rates of ovaries in crabs in these areas. Ovaries in Eureka area crabs in June 1979 were considerably delayed in development compared to ovaries in both San Francisco and Eureka area crabs in 1976-1978. San Francisco crab ovaries were not examined in 1979, but the laboratory results indicate that they matured earlier than Eureka crabs that year.

Egg Brooding Period

Differences in average egg brooding temperatures from year to year produced differing egg brooding periods even within regimes. The warmest regime averaged 16.7°C for
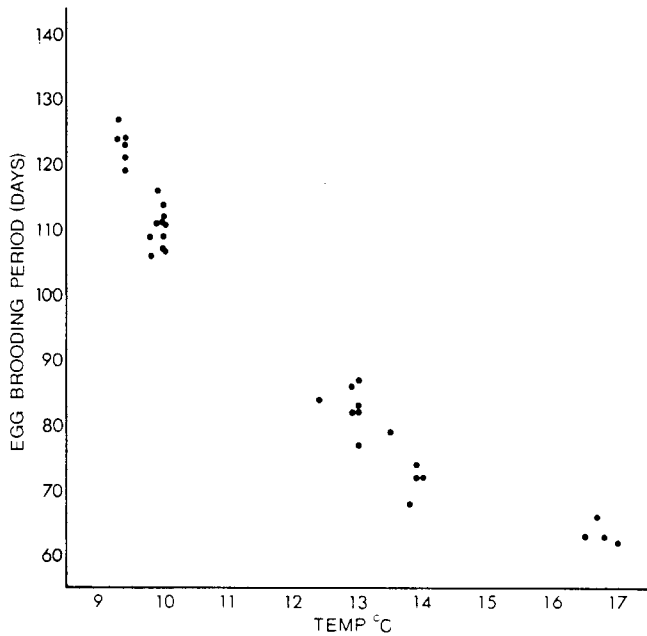
Figure 5. Dungeness crab egg brooding periods at various seawater temperatures in the laboratory.

all three years and varied the least in egg brooding periods. Average ambient egg brooding temperatures ranged from 12.9°C in 1978 to 13.9°C in 1979. Cold egg brooding temperatures averaged 9.4°C in 1977, and 10.0°C in 1978 and 1979. The egg brooding periods varied inversely with these seawater temperatures (Figure 5). Prolonged egg brooding periods in the colder water in the laboratory are consistent with prolonged occurrences of ovigerous crabs and cooler ocean temperatures progressively northward along the coast.

Hatching Success

Although the eggs developed faster at the warmer seawater temperatures, hatching success (the number of larvæ hatched from an egg mass) was lower the warmer the water. Lower hatching success at the warmer temperatures was the result of egg mortalities and deterioration of egg masses during the egg brooding period, which also resulted in declining egg mass volumes in warm and ambient regimes (Figure 6). These egg mass volumes declined even though the surviving eggs increased in size from about 0.4 mm in diameter at spawning to about 0.5 mm by the time they hatched. The increase in egg size resulted in increasingly larger egg mass volumes in the coldest temperature (Figure 6) where egg mortalities were the lowest and hatching success was the highest.

The average number of larvæ hatched per egg mass in 10.0°C seawater in 1978-79 was 685,000. Problems with a new seawater intake pump in late December 1979 after most hatching was completed in ambient and warm regimes resulted in high egg mortalities and low hatching success in the egg masses in cold water. This precluded an

evaluation of hatching success due to cold water in the 1979-80 experiment. In ambient seawater at 12.9°C in 1978, an average of 257,000 larvæ per egg mass hatched and in 1979 at 13.9°C, the average was 292,000. The overall average for ambient was 275,000. In the warmest regime at 16.7°C in both 1978 and 1979, the only egg mass that produced any significant amount of larvæ hatched approximately 110,000, at least half of which died shortly after hatching. Overall, the average hatch per egg mass in warm seawater was 14,000, but virtually no larvæ hatched from most of these egg masses. These data suggest that a temperature of about 16.0 to 17.0°C may represent an upper lethal temperature limit for developing Dungeness crab eggs.

In a study near Puget Sound, Washington, Mayer (1973) observed effects of seawater temperature on Dungeness crab eggs removed from females' pleopods and cultured at 5, 10, 15, and 20°C for about 15 days. Egg mortalities during this relatively short period were minimal at 5°C, reached about 20% at 10°C, showed "a significant increase in the slope of the mortality curve at
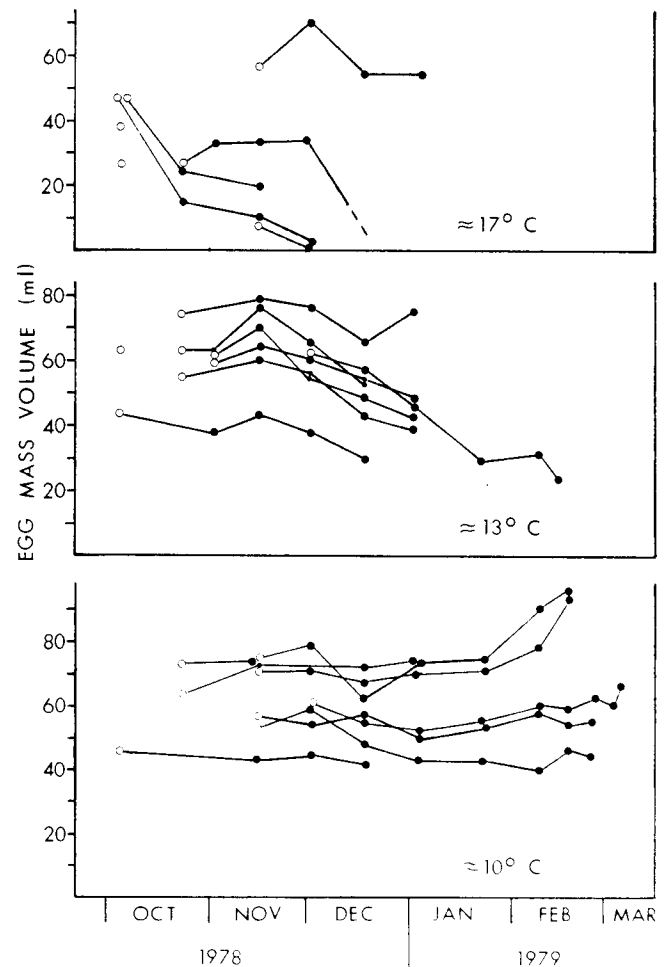
Figure 6. Progressive volumes of individual Dungeness crab egg masses in three different seawater temperature regimes in the laboratory in 1978-79.
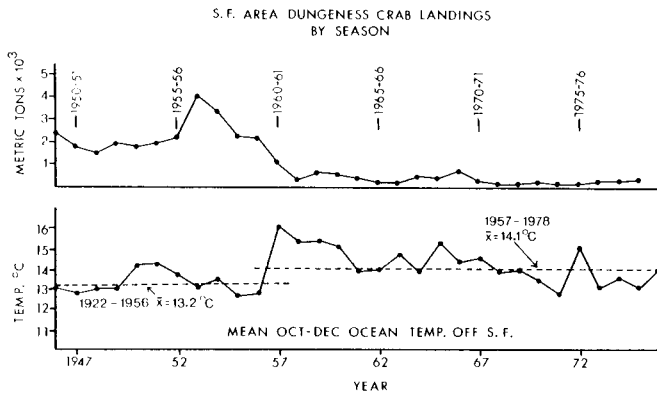
Figure 7. Commercial fishery landings of Dungeness crabs from the San Francisco area by season, 1949-50 through 1978-79; landings are shown lagged three years relative to mean October-December ocean temperatures.

15°C due to the effect of elevated temperatures between 10 and 15°C," and at 20°C, 100% mortality occurred in about 6 days.

Thus, laboratory studies indicate that seawater temperatures that are known to occur in central California could adversely affect the reproductive potential of crabs living there and thus could also affect Dungeness crab fishery landings.

Ocean Temperature and Dungeness Crab Fishery Landings

To determine if the central California crab decline could possibly be related to effects of ocean temperature on crab reproductive potential, historical ocean temperatures during the egg brooding period (October-December) off San Francisco were compared with commercial Dungeness crab fishery landings.[1] Only male crabs may be taken legally in the fishery, and male crabs in central California take about three years to reach legal size (159.0-mm carapace width). Thus, the onset of the crab fishery decline in 1960-61 coincides with a significant rise in mean October-December temperatures in 1957, and crab landings have remained low as ocean temperatures, on the average, have remained higher than for at least 35 previous years (Figure 7). This change in the ocean climate in the California current was well documented in a symposium on "The Changing Pacific Ocean in 1957 and 1958" (Sette and Isaacs 1960). Shifts in geographical ranges of many marine organisms were observed during this period (Radovich 1961). Huang (1972) analyzed sea-level fluctuations and contributing factors and concluded that changes observed in the ocean climate in 1957 persisted for at least a decade. Huang showed that the thermohaline effect, particularly during winter months, was the major factor contributing to the

variations in sea level.

Although recent ocean temperatures occasionally appear to have been more suitable for good crab production (Figure 7), sea levels (high sea levels are usually associated with higher ocean temperatures) at San Francisco at the same time did not return to pre-1957 values. Furthermore, the crab population in central California has been depressed for so many years that recovery of crab landings could require a few consecutive years of suitable temperatures. In northern populations and in pre-decline years in central California, a holdover of large stocks of females during a few years of low landings probably provided for rapid recovery when environmental conditions improved.

Comparisons of ocean temperatures during the egg brooding period in northern California (November-January) with crab landings four years later (crabs take about four years to reach legal size in northern California) show a relationship to fluctuations in crab landings there (Figure 8); landings in Oregon and Washington also have fluctuated similarly. The highest California crab landings in history were taken in northern California in the 1975-76 and 1976-77 seasons and were associated with the lowest November-January (1971) ocean temperatures since the 1940's (Figure 8.)

Therefore, information from laboratory experiments and comparisons of crab landings with ocean temperatures during the egg brooding periods suggest that the decline in central California Dungeness crab landings as well as fluctuations in landings northward up the coast may be related to effects of ocean temperature on survival of Dungeness crab eggs.

ACKNOWLEDGMENTS

Much of the assistance with this work came from a
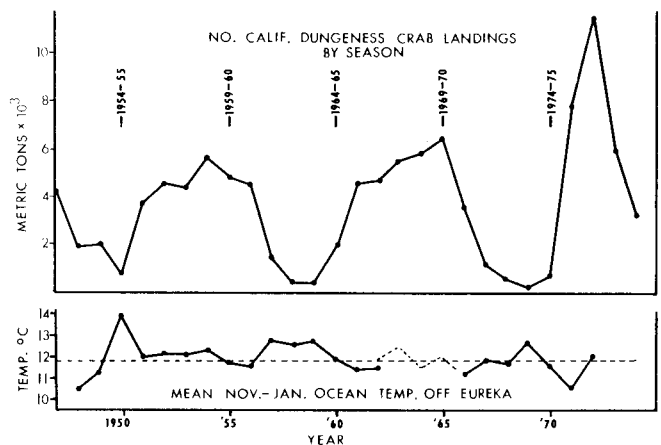
Figure 8. Northern California Dungeness crab commercial fishery landings by season; landings are shown lagged three years relative to mean November-January ocean temperatures. Dashed-line temperatures are Crescent City Harbor temperatures substituted for missing data in the offshore series.

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CHARACTERS USEFUL IN IDENTIFICATION OF PELAGIC MARINE FISH EGGS

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ABSTRACT

Characters of importance in identifying pelagic marine fish eggs can be divided into two categories: characters independent of the embryo and characters associated with the developing embryo. Characters independent of the embryo would include egg shape, egg size, character of chorion, character of yolk, presence or absence of oil globules, and width of perivitelline space.

Planktonic marine fish eggs are usually globular in shape and range in size between 0.5 and 5.5 mm. We estimate that over 40% of the kinds of pelagic eggs are under 1.0 mm in diameter, 30% are between 1.0 and 1.5 mm, 15% are between 1.5 and 2.0 mm, and that about 14% are over 2.0 mm in diameter.

The chorion is usually smooth, but can be variously ornamented (polygonal network, spines, swellings, etc.). The perivitelline space is usually narrow but is wide in eggs of some primitive teleost groups (Anguilliformes and many clupeids). The yolk can be segmented or homogeneous. Oil globules range in number from none or one to many. About 25% of pelagic fish eggs lack an oil globule, 15% have two to many oil globules, and 60% have a single oil globule.

Characters associated with embryos would include pigment patterns, number of myomeres, length of gut, type of fin fold, position of heart, state of development at blastopore closure and at hatching, shape of yolk sac on late-stage eggs and newly hatched larvæ, position of oil globule(s) in the yolk sac, and special embryonic characters such as the elongated fin rays that form in trachipteroid eggs.

RESUMEN

Los caracteres importantes para la identificación de huevecillos de peces marinos pelágicos pueden ser divididos en dos categorías: carácteres independientes del embrión, y carácteres asociados con el embrión en desarrollo. Los carácteres independientes del embrión incluirían la forma del huevecillo, el tamaño del huevecillo, el carácter del corión, el carácter del vitelo, la presencia o ausencia de gotas oleosas, y la anchura del espacio perivitelino.

Huevecillos de peces marinos planctónicos son generalmente de forma globular y varían en tamaño entre 0.5 y 5.5 mm. Calculamos que más de 40% de los tipos de huevecillos pelágicos son menos de 1.0 mm de diámetro, el 30% son de entre 1.0 y 1.5 mm, el 15% son de entre 1.5 y 2.0 mm, y alrededor del 14% son de más de 2.0 mm de diámetro.

El corión es normalmente suave, pero puede estar distintamente ornamentado (red poligonal, espinas, inflaciones, etc.). El espacio perivitelino es normalmente estrecho, pero es ancho en los huevecillos de algunos grupos primitivos de teleósteos (anguiliformes y muchos clupéidos). El vitelo puede ser segmentado u homogéneo. Gotas oleosas varían en número desde ninguna hasta una o varias. Como 25% de los huevecillos de peces pelágicos carecen de la gota oleosa, el 15% tienen de dos a varias gotas oleosas, y el 60% tienen una sola gota oleosa.

Los carácteres asociados con embriones incluirían patrones de pigmentación, número de miómeros, longitud del intestino, tipo de pliegue de la aleta, posición del corazón, estado de desarrollo en el cierre del blastoporo y el tiempo de eclosión, la forma del saco vitelino en la última fase de los huevecillos y las larvas recién eclosionadas, la posición de la(s) gota(s) oleosa(s) en el saco vitelino, y carácteres embriónicos especiales tales como las rayas de aleta elongadas que se forman en huevecillos traquípteros.

INTRODUCTION

Oviparous marine teleosts extrude their eggs in a variety of ways. Many inshore species have demersal eggs, which are often attached to rocks, shells, or seaweed. Some build nests, and eggs are guarded by the male during incubation. Some demersal eggs are initially released in the pelagic zone, fertilized, and then sink. The chorions of these eggs are characteristically mucilaginous, permitting eggs to cling to bottom objects or to each other. Pelagic spawners usually produce separate isolated eggs, but the eggs of some species can be aggregated in various ways. They may be aggregated into large gelatinous masses or balloons (as in most scorpænid genera, and in the ophidiid genus *Brotula*) or can be spawned in gelatinous ribbon-like sheets (*Lophius antennarius*). Another method of aggregation is attachment of eggs to each other by filaments, a form of aggregation found in most exocœtoid fishes and in many atherinid fishes. In our experience except for eggs of the scomberesocid fish, *Cololabis saira*, aggregated eggs are seldom taken in plankton hauls. The number and arrangement of chorionic fila-

ments can differ strikingly among species and genera of exocoetoid fishes and provide useful characters for identification.

We are primarily interested in identifying pelagic eggs that are collected on ichthyoplankton surveys for the purpose of determining distribution and spawning biomass of target species. There are numerous contributions that describe pelagic eggs of marine fishes in order to facilitate their identification in plankton collections. The majority of such contributions are based on rearing artifically fertilized eggs from known parents or rearing mixtures of eggs collected in plankton hauls through both the embryonic and larval periods to sizes that can be positively identified. Other contributors have used the historical method of identifying eggs collected in ichthyoplankton surveys by working backwards from late-stage larvae or juveniles that can be positively identified to earlier stage larvae and ultimately to yolk-sac larvae and eggs.

SUMMARY OF CHARACTERS

Plates 1 and 2

The characters of importance in identification of pelagic marine eggs are the following;

1) *egg shape*: spherical or otherwise;
2) *egg size*: pelagic marine fish eggs range in size from ca 0.5 to ca 5.5 mm;
3) *chorion*: ornamented or smooth, type of ornamentation, thickness;
4) *inner membrane*: presence or absence and location within egg;
5) *yolk*: segmented or homogeneous, nature of segmentation;
6) *perivitelline space*: width;
7) *oil globules*: number and size;
8) *embryonic characters*: state of development at blastopore closure, sequence of appearance and changes in pigmentation, pigment pattern at hatching, stage of development on late-stage embryos of various anatomical features such as eyes, mouth, fins, digestive tract, position of anus, and heart.

DESCRIPTION OF CHARACTERS

Egg Shape

Planktonic eggs are predominantly spherical, but there are some interesting exceptions. The engraulids afford the most striking exceptions; the eggs of most anchovies are ellipsoidal. The eggs of several species of engraulids approach the globular shape (*Thryssa mystax*, Delsman 1931; *Anchoa mitchilli*, Kuntz 1914; and *Setapinna phasa*, Jones and Menon 1952). Delsman (1931) described eggs of several species of *Stolephorus* that had a terminal knob at one end of the chorion. Planktonic eggs
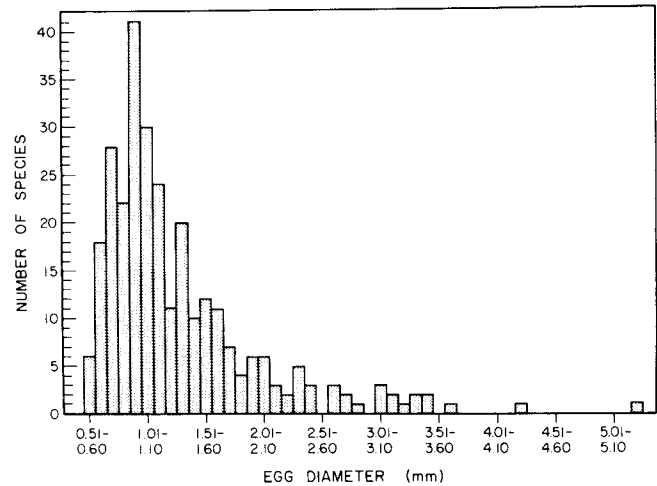
Figure 1. Frequency of egg diameter for 288 species with pelagic eggs, compiled from Mito (1961-63), Marinaro (1971), Robertson (1975), Russell (1976) and original data.

of some marine fishes in other families are not truly spherical but rather are somewhat off-round, as in the scomberesocid, *Scomberesox saurus* (Ahlstrom 1972) and in several ostraciontid species (Watson and Leis 1974; Plate 1).

Egg Size

Pelagic fish eggs range from 0.5 mm in diameter to about 5.5 mm (Figure 1). Among the smallest marine fish eggs are those of certain bothid flatfishes and labrids, whereas the eggs of the pleuronectid flatfish, *Reinhardtius hippoglossoides* (4.0 to 4.5 mm size range), and a muraenid eel from the Mediterranean (ca 5.5 mm) are the largest known. The majority of pelagic fish eggs are in the size range 0.6 to 1.6 mm. In some fishes, larger sized eggs result from the possession of a wide perivitelline space, as for example in some clupeids, most Anguilliformes, some stomiatoid fishes, and the pleuronectid flatfish genus *Hippoglossoides* (Plate 2). The yolk mass within some large eggs may be no larger than in eggs of less than 1.5-mm diameter that have a narrow perivitelline space. Some fishes that spawn larger sized eggs with the yolk mass almost filling the egg would include several pleuronectid flatfishes, most trachipteroid fishes, most exocoetoids that spawn separate pelagic eggs, various tetraodontiform fishes that spawn pelagic eggs, several argentinoid fishes, and some trichiurids and uranoscopids. This list could be made moderately extensive but, even so, would probably not include more than 10% of the kinds of pelagic marine fish eggs.

Chorion

The outermost structure of the egg is variously called the egg capsule, egg shell, vitelline membrane, egg membrane, or chorion. Although most fish eggs have smooth unornamented chorions, it can be variously and sometimes elaborately ornamented in some species. Such ornamentation can occur in several orders, including the

Salmoniformes, Myctophiformes, Gadiformes, Pleuro-nectiformes, Atheriniformes, Gobiesociformes, and Clu-peiformes (Rass 1972). In some species where the chor-ion appears to be smooth and unornamented, a careful in-spection, especially under higher magnification, shows the chorion to be striated or wrinkled. This is particularly true of the egg membranes of a number of pleuronectid flatfishes, which have striations or reticulations.

The ornamentation of the chorion can be limited or extensive. It can consist simply of a single protuberance or swelling, or a cluster of pustules or swellings surround-ing the micropyle (Plate 1). Mito (1963b) shows several types of flatfish eggs that possess a single swelling or protuberance, and Watson and Leis (1974) illustrate an egg with a more complicated protuberance that they also assigned to a flatfish. Eggs of ostraciontids are known to have a patch of pustules on the chorion surrounding the micropyle (Watson and Leis 1974).

Of those eggs with extensive chorion ornamentation, the most widespread type consists of a honeycomb-like polygonal network formed at the outer surface of the egg membrane (Plates 1 and 2). Usually the network is hexa-gonal, but in some species the polygons can have 4, 5, or 7 sides intermixed with the usual 6-sided pattern. The diameters of the polygons range for example from 0.015 in *Chirocentrus dorab* (Delsman 1923) to 0.18-0.24 mm in the soleid, *Aesopia cornuta* (Mito 1963b). The pattern is well shown on scanning electronmicrographs of the pleuronectid genus *Pleuronichthys* and the synodontid genus *Synodus*, two genera that are phylogenetically remote (Sumida et al. 1979). On eggs of the macrurid genus *Coelorhynchus*, the network is removed from the chorion itself and attached to it by a series of posts (Sanzo 1933). In the distinctive egg of the sternoptychid, *Mauro-licus muelleri*, the chorion is divided into a number of hexagonal facets, the junctions of which protrude as spine-like structures (Mito 1961a).

Another less common type of ornamentation on the chorion of pelagic fish eggs is spination. Spines can be relatively simple such as are found on the eggs of several exocoetids that spawn separate pelagic eggs, or they can be rather complex spine-like structures such as the orna-mentation found on several types of eggs referred to the Myctophiformes (Plate 1).

Only a few of the pelagic, separate exocoetid eggs have been confidently assigned to species. Identified eggs would include eggs of two species of *Oxyporhamphus* with quite short spines distributed over the chorion and two species of *Cheilopogon*, which have fewer but some-what longer and thinner spine-like filaments (Plate 1).

Delsman (1938) described two types of eggs that had strikingly ornamented chorions, which he referred to the Myctophoidea. The chorions are covered with short, trifid spines. On one type of egg the appendages are made up of three planes intersecting each other at an angle of 120° and ending in a point. In a second type of egg, the trifid spine-like structures end bluntly in a small hollow pit. Other eggs similar to Delsman's second type have been described from Japanese waters (Mito 1961a) and

from Hawaii (Watson and Leis 1974; Plates 1 and 2).

Instead of having ornamentation on the outer surface of the chorion, eggs of fishes belonging to the salmoniform suborder Argentinoidei have pustules or swellings on the inner surface of the chorion. The pustulation can be quite marked, as in the eggs of *Microstoma* or *Nansenia*, or hardly evident, as in eggs of some bathylagid smelts.

Inner Egg Membrane

Most pelagic fish eggs lack a free inner egg membrane. The presence of an inner egg membrane occurs, for example, in eggs of some anguilliform fishes (Mito 1961a shows several example; Plate 2), in some clupeiform fishes (Delsman 1926), and in some fishes of the sub-order Stomiatoidei (Sanzo 1931b; Ahlstrom and Counts 1958). The inner membrane can be quite firm, as in eggs of *Chauliodus sloani* (Mito 1961a), or it can be thin and irregular in outline, as in eggs of *Vinciguerra lucetia* (Ahlstrom and Counts 1958). In the latter, the inner membrane lies close to the chorion. In the egg of *Chauli-odus sloani*, which has a wide perivitelline space, the inner membrane is much closer to the embryo, and in the egg of *Argyropelicus hemigymnus* it adheres in places to the yolk (Sanzo 1931b).

Yolk

The yolk mass dominates the newly spawned fish egg and is usually translucent and unpigmented. The yolk is segmented in eggs of most "primitive" teleosts but is homogeneous in the majority of eggs of "higher" teleosts (Plates 1 and 2). Segmented yolk is found in some of the latter group (principally among the perciforms and pleuro-nectiforms) at the end of the embryonic period. In addi-tion to the character of segmented versus homogeneous yolk, the shape of the yolk sac, particularly in late-stage eggs or new-hatched larvæ, is a useful character. Also the presence of pigmentation and its characteristic distribu-tion may help in identification.

Segmentation of the yolk can range from coarse to fine. Delsman found the type of segmentation to be an impor-tant character for distinguishing the eggs of clupeoids. He found the yolk to be finely segmented in eggs of *Dussu-mieria hasseltii* (Delsman 1925), moderately fine in eggs of most species of *Ilisha* (Delsman 1932), and coarsely segmented in eggs of *Anodontostoma chacunda* (Dels-man 1926).

Segmentation of the yolk among eggs of a given species can be quite variable. Ahlstrom and Counts (1958) com-mented on the variability observed in eggs of the stomia-toid *Vinciguerria lucetia*, especially noticeable in early-stage eggs. The yolk in some eggs was nearly homo-geneous, in others partly segmented, and in still others completely segmented into globules.

In some "higher" teleosts the segmentation is con-fined to the periphery of the yolk, as in eggs of various soleids (see Russell 1976). In others, for example the carangid, *Trachurus symmetricus*, where segmentation becomes rather complete, it can progress from little or no segmentation in newly spawned eggs to rather complete segmentation in late-stage eggs (Ahlstrom and Ball 1954).

Explanation of Plates

Captions under each plate indicate the species and the diameter or dimensions of the egg in mm.

Plate 1

Uranoscopus scaber, from Dekhnik (1973).
Pleuronichthys cornutus, from Mito (1963b).
Leuroglossus stilbius, from Ahlstrom (1969).
Cheilopogon nigricans, from Parin and Gorbunova (1964).
Maurolicus muelleri, from Mito (1961a).
Aesopia cornuta, from Mito (1963b).
Cheilopogon katoptron, from Kovalevskaya (1965).
Myctophiform, from Watson and Leis (1974).
Pleuronectiform, from Watson and Leis (1974).
Oxyporhamphus meristocystis, from Parin and Gorbunova (1964).
Ceratacanthus cirrus, from Sanzo (1939).
Ostraciontid, from Watson and Leis (1974).
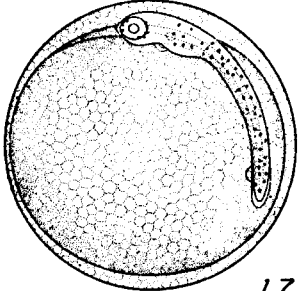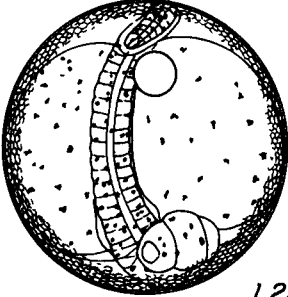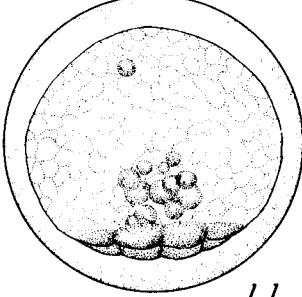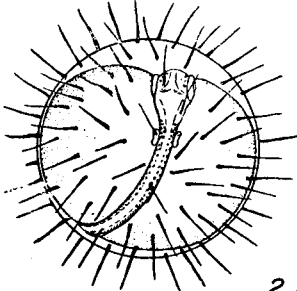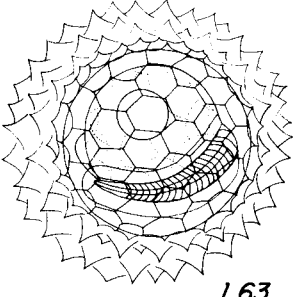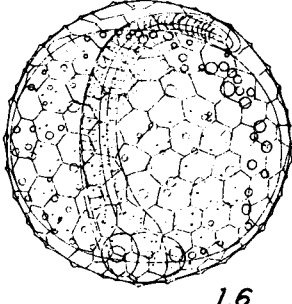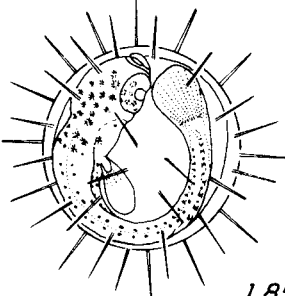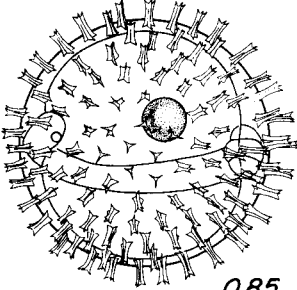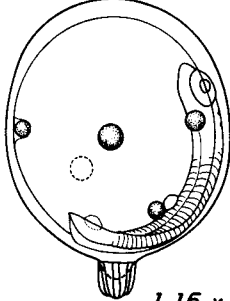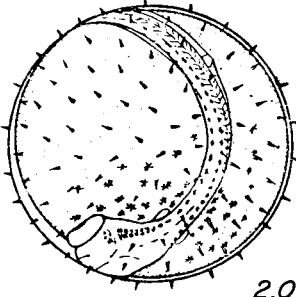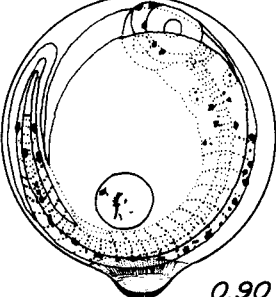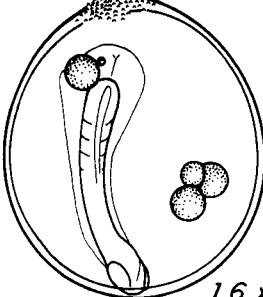
TYPES OF ORNAMENTATION ON CHORIONS OF PELAGIC MARINE FISH EGGS

0 OIL GLOBULE	1 OIL GLOBULE	2 OR MORE OIL GLOBULES
1.7 *Uranoscopus scaber*	1.22 *Pleuronichthys cornutus*	1.1 *Leuroglossus stilbius*
2.1 *Cheilopogon nigricans*	1.63 *Maurolicus muelleri*	1.6 *Aesopia cornuta*
1.85 *Cheilopogon katoptron*	0.85 *Myctophiform*	1.15 x 1.25 *Pleuronectiform*
2.0 *Oxyporhamphus meristocystis*	0.90 *Centracanthus cirrus*	1.6 x 1.9 *Ostraciodontid*

Plate 2

Synodus lucioceps, original.
Microstoma microstoma, from Sanzo (1931a).
Myctophiform, from Mito (1961a).
Muraena helena, from Grassi (1913).
Sardinops sagax, from Mito (1961a).
Anguillid, from Mito (1961a).
Etrumeus acuminatus, original.
Trachurus symmetricus, from Ahlstrom and Ball (1954).
Soleid, from Mito (1963b).
Glyptocephalus zachirus, original.
Merluccius productus, from Ahlstrom and Counts (1955).
Prionotus carolinus, from Kuntz and Radcliffe (1917).
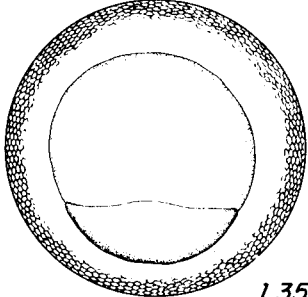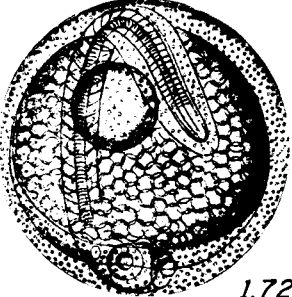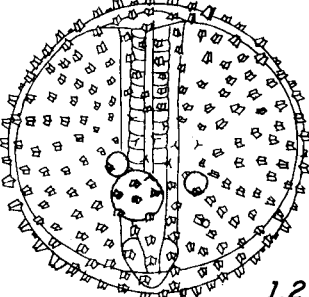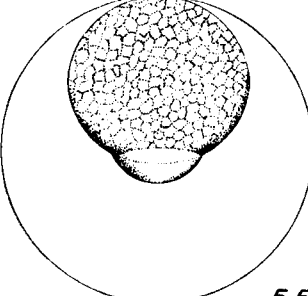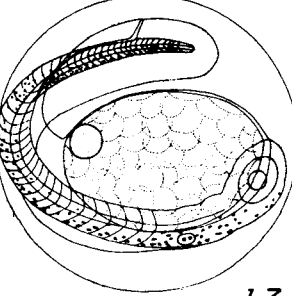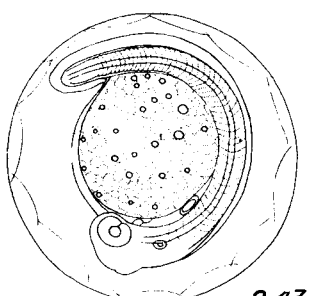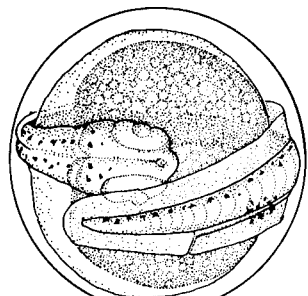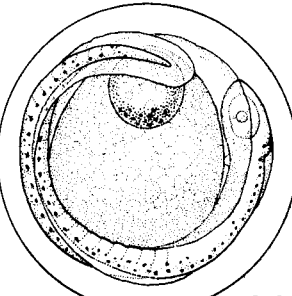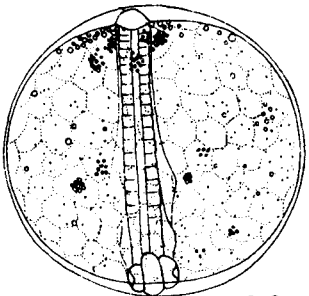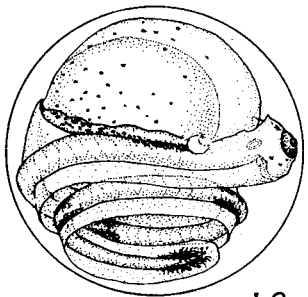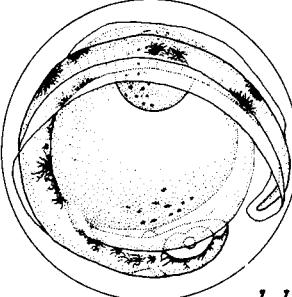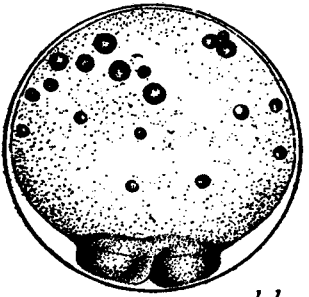
VARIETY OF PATTERNS IN PELAGIC MARINE FISH EGGS

		0 OIL GLOBULE	1 OIL GLOBULE	2 OR MORE OIL GLOBULES
SCULPTURED CHORION		*1.35* Synodus lucioceps	*1.72* Microstoma microstoma	*1.2* Myctophiform
SMOOTH CHORION	**WIDE PERIVITELLINE SPACE**	*5.5* Muraena helena	*1.7* Sardinops sagax	*2.43* Anguillid
	NARROW PERIVITELLINE SPACE — **SEGMENTED YOLK**	*1.35* Etrumeus acuminatus	*1.0* Trachurus symmetricus	*1.6* Soleid
	NARROW PERIVITELLINE SPACE — **UNSEGMENTED YOLK**	*1.9* Glyptocephalus zachirus	*1.1* Merluccius productus	*1.1* Prionotus carolinus

Perivitelline Space

In the majority of pelagic fish eggs the perivitelline space is narrow; however, eggs with a wide perivitelline space are the basic type among eels, are common among clupeiform fishes, and are encountered in stomiatoid fishes (Plate 2). All of these examples are "primitive" teleosts whose eggs have regularly segmented yolk. Fishes with homogeneous yolk seldom have a wide perivitelline space. A well-known exception is the flatfish genus *Hippoglossoides*, whose several species have pelagic eggs with a wide perivitelline space (Pertseva-Ostroumova 1955). The eggs of the striped bass, *Morone saxatilis*, also have a wide perivitelline space; however, this species enters estuaries or rivers to spawn, and the eggs are semi-buoyant.

When first spawned, even those pelagic fish eggs that ultimately develop a wide perivitelline space have little or no perivitelline space. In the Pacific sardine, *Sardinops caeruleus*, Miller (1952) found that the perivitelline space was small or nonexistant at time of extrusion from the female. The perivitelline space was almost completely formed within 2 hours after fertilization as a result of hydration. Egg diameter increased from 1.15 mm at fertilization to 1.64 mm after 2 hours, to the maximum diameter of 1.83 mm at 10 hours after fertilization. Since a fully formed perivitelline space requires some time to develop, its absence in recently spawned eggs can be misleading. In species that will ultimately develop a wide perivitelline space, it is helpful to give the diameter before and after hydration. Also in eggs with a wide perivitelline space, the diameter of the yolk mass is a useful measurement.

Oil Globule

For identifying pelagic marine fish eggs, perhaps no character is more important than the number of oil globules. Examples of species that lack oil globules in their yolk are known for many teleost orders, although for some of the orders, known examples are limited to one or a few species. Major families in which the eggs of all or many species lack an oil globule would include the Engraulidae, Synodontidae, Gadidae, and Pleuronectidae. Two other commonly occurring groups whose eggs lack an oil globule are the Trachipteroidei and Exocoetoidei.

Examples of pelagic eggs with multiple oil globules are known for at least seven orders. Multiple oil globules occur most frequently in anguilliform eels, bathylagid smelts, soleid and cynoglossid flatfishes, and in tetraodontiform fishes. The number of multiple oil globules can range from few (less than 10) to many (more than 50). The largest numbers occur in eggs of some soleid flatfishes. When numerous, oil globules tend to aggregate into clusters, and the pattern of distribution of the oil globules within the yolk mass can be useful in egg identification. In bathylagid smelts, the oil globules undergo remarkable migrations during embryonic development (Ahlstrom 1969).

The most common kind of pelagic fish egg is that with a single oil globule. This is true, for example, in most perciform families, in several families of flatfishes, and in many gadoids, stomiatoids, and clupeoids. A compilation of data from Mito (1961-63), Marinaro (1971), Robertson (1975), Russell (1976), and our California Cooperative Oceanic Fisheries Investigations (CalCOFI) area shows that for a total of 515 species, 24.5% lacked an oil globule, 60.1% had one oil globule, and 15.3% had multiple oil globules (Table 1). In eggs with a single oil globule, it usually lies at the vegetal pole opposite to the blastodisc and developing embryo. The single oil globules can range in size from < 0.10 mm to > 1.0 mm. The oil globule in formaldehyde-preserved pelagic eggs is usually colorless or faintly yellowish or reddish.

In eggs having a single oil globule, the position of the oil globule in the yolk sac can be of diagnostic value. The usual position of the oil globule is in the rear of the yolk sac; however, in a moderate number of families it is far forward in the yolk sac, as for example in labrids, most carangids, mullids, and lethrinids. In some genera the position of the oil globule can vary from species to species. Thus, two species of *Sphyraena* have the oil globule in a forward position (*S. pinguis* in Shojima et al. 1957; *S. borealis* in Houde 1972), and two species of *Sphyraena* have the oil globule in the rear of the yolk sac. (*S. sphyraena* in Vialli 1956; *S. argentea* in Orton 1955). In some species the oil globule is in an intermediate position or slightly forward. Several examples drawn from three families are serranids such as *Serranus cabrilla* (Raffaele 1888) and *Lateolabrax japonicus* (Mito 1963a); clupeids such as *Konosirus punctatus* (Uchida et al. 1958), *Harengula pensacolae* (Gorbunova and Zvyagina 1975) and *Brevoortia smithi* (Houde and Swanson 1975); and argentinids such as *Argentina silus* (Schmidt 1906) and *Nansenia oblita* (Sanzo 1931a).

Embryonic Characters

We have found it helpful to divide embryonic development in the egg into three stages: early (fertilization to blastopore closure), middle (from blastopore closure to the time that the separating tail begins to curve laterally away from the embryonic axis), and late (from the time that the tail is curved away from the embryonic axis to the time of hatching).

In eggs of some fishes the embryo is undergoing organogenesis prior to blastopore closure, whereas in others the embryo is relatively undifferentiated at closure of the blastopore. For example, in the Pacific hake, *Merluccius productus*, when the embryonic shield has enveloped approximately three-fourths of the yolk, the embryo has a discernible eye. Just before blastopore closure, 10 to 13 myomeres are visible behind the head of the developing embryo (Ahlstrom and Counts 1955). Similarly, in the jack mackerel, *Trachurus symmetricus*, the myomeres

TABLE 1
Frequency of Character Combinations in Pelagic Marine Fish Eggs.

| | Oil Globules | | | | | | All categories | |
| | 0 | | 1 | | 2 or more | | | |
	No.	%	No.	%	No.	%	No.	%
Ornamented chorion	23	4.5	18	3.5	11	2.1	52	10.1
Chorion smooth								
Wide perivitelline space	15	2.9	12	2.3	17	3.3	44	8.5
Segmented yolk, narrow perivitelline space	15	2.9	62	12.0	11	2.1	88	17.0
Homogeneous yolk, narrow perivitelline space	73	14.2	218	42.3	40	7.8	331	64.3
Total all categories	126	24.5	310	60.1	79	15.3	515	99.9

appear behind the head and the optic vesicles form shortly before blastopore closure (Ahlstrom and Ball 1954). In contrast, in argentinoid smelts the embryo is a simple undifferentiated ridge at blastopore closure.

In late-stage eggs a suite of characters can be used, including the shape of the developing embryo, its myomere count, the position of the anus on the body, and the nature of the finfold. Pigmentation usually begins forming on middle-stage eggs and reaches its fullest development on later stage eggs. In many kinds of eggs there is a sequence of changes in pigmentation during embryonic development. The pigment pattern may be confined to the embryo itself, or it can be developed over part or all of the yolk sac and may extend out into the finfolds. Also, it may be variously developed in relation to the oil globule if present. The melanophores originate from the neural crest region and usually first appear along the dorsal and dorso-lateral surfaces of the embryo. In many species the embryonic pigment at hatching is aligned along the dorsal margins of the body, often extending from the head to the end of the notochord.

For the majority of marine fishes with pelagic eggs, the yolk-sac stage is a period of rearrangement (migration) of melanophores from the predominant dorsal position on newly hatched larvae to their predominantly ventral position on late yolk-sac larvae. Some species, however, begin or even complete the migration and rearrangement of body melanophores before hatching. The mackerel, *Scomber japonicus*, furnishes an example where the downward movement of the dorso-lateral row of melanophores commences on late-stage embryos (Kramer 1960). Examples of species that reach a more advanced, although still intermediate, phase of rearrangement of melanophores on late-stage embryos are bonito, *Sarda lineolata* (Orton 1953); Pacific hake, *Merluccius productus* (Ahlstrom and Counts 1955); and cod, *Gadus morhua* (Fridgeirsson 1978). Several groups of fishes complete the rearrangement of pigment in the late-stage pelagic eggs, and the pattern is similar to that found in yolk-sac larvae and on into the preflexion larval stage. A few examples are the carangid, *Seriola quinqueradiata*

(Mito 1961b); stromateoids from several families (Ahlstrom et al. 1976); *Trachipterus* sp. (Mito 1961b); and the cynoglossid, *Areliscus trigrammus* (Fujita and Takita (1965). A variant of this is found in species that develop heavy pigment over the head and body of their embryos and retain such heavy pigmentation during the yolk-sac stage and larval period. Various flatfishes develop heavily pigmented embryos as, for example, in all species of *Pleuronichthys* (Sumida et al. 1979), in *Hypsopsetta* (Eldridge 1975), in *Scophthalmus rhombus* (Ehrenbaum 1905-1909), and in *Verasper variagatus* (Mito 1963b). Examples from other groups are *Coryphaena hippurus* (Mito 1961b), *Cololabis saira* (Hatanaka 1956), *Zeus faber* (Dehknik 1973), and *Mugil auratus* (Dehknik 1973).

Some pelagic eggs lack melanophores on late-stage embryos or at best have a few inconspicuous melanophores. Embryos and newly hatched larvae of engraulids lack melanophores. When melanophores become visible later in the yolk-sac stage, they already are ventral in position, lying along the gut and on the ventral margin of the tail. It is assumed that the pigment cells in Engraulidae migrate as in the Clupeidae but pigment formation is delayed until cells have reached more or less permanent locations. Other examples of fishes with this type of melanophore migration are two species of *Girella* (Orton 1953; Uchida et al. 1958); the Pacific halibut, *Hippoglossus stenolepis* (Thompson and Van Cleve 1936; Pertseva-Ostroumova 1961); the argentinid, *Argentina silus* (Schmidt 1906), and several synodontids (Mito 1961a).

Although larvae of some groups develop specialized larval characters such as elongated fin rays and head spination, such characters are seldom developed on embryos. A striking exception is the development of elongated elaborate dorsal and pelvic fin rays in embryos of trachipteroids. Another such character is the pair of appendages that develop during the embryonic period on the head of *Champsodon* spp. (Mito 1960, 1962).

The size and state of development at hatching is related to egg diameter for eggs with a narrow perivitelline space and to yolk size for those with a wide perivitelline space. The length of a larva at hatching is usually 2.5-3.0 times the diameter of the egg. Larvae hatching from small eggs are usually underdeveloped in that they lack a functional mouth, pigment in the eyes, and fins of any sort. Other organs are similarly underdeveloped. Larvae hatching from large eggs usually are much better developed. The eyes can be pigmented, the mouth formed, and the larval pectoral fins developed. In eggs of flying fishes, flexion of the caudal fin precedes hatching, and in some species of the group the other fins are well developed before hatching. An interesting exception to the correlation of large egg size and advanced development before hatching is found in *Argentina silus* (Schmidt 1906). This species has a large egg (ca 3.0-3.5 mm), an enormous oil

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globule (0.95-1.18 mm), and lacks a perivitelline space in early-stage eggs. At hatching, the yolk-sac larva of *S. silus* is as underdeveloped as in those species that hatch from eggs in the 0.6-1.0-mm size range. The eyes are unpigmented, the mouth undeveloped, and the pectoral fins lacking.

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THE FISHERY FOR NORTHERN ANCHOVY, *ENGRAULIS MORDAX,*
OFF CALIFORNIA AND BAJA CALIFORNIA IN 1976 AND 1977

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ABSTRACT
Anchovy landings for 1976 totaled 189,066 metric tons (208,407 tons) with 60% landed by American fishermen and 40% by Mexico. The 1977 landings amounted to 243,124 metric tons (267,995 tons) with 58% landed by Mexican boats and the remaining 42% by U.S. fishermen.

Age composition of the 1976 catch consisted largely of the 1973 year class for southern California samples, whereas the 1976 year class dominated Baja California samples. The 1976 year class dominated samples from both southern and Baja California during 1977.

Average fish sizes in 1976 were 106 mm standard length (Baja California) and 125 mm SL (California), whereas in 1977 the mean length of the Mexican fish increased to 113 mm SL although California-caught fish decreased in size to 120 mm SL. Sex ratios ranged during 1976 from 2.15 females to 1 male (Baja California) to 1.16 females per 1 male (southern California), whereas in 1977 the sex ratios were much closer to 1:1 in California and in Baja California.

RESUMEN
Las capturas de anchoveta para 1976 sumaron 189,066 toneladas métricas (208,407 toneladas), con el 60% de las capturas correspondiendo a los pescadoras norteamericanos, y el 40% a México. Las capturas de 1977 llegaron a 243,124 toneladas métricas (267,995 toneladas), con el 58% pescado por barcos mexicanos y el 42% restante, por pescadores de los EE.UU.

Para las muestras del sur de California, la generación de 1973 contribuía principalmente a la composición de la edad de los peces capturados en 1976, mientras que la generación de 1976 dominaba en las muestras de Baja California. La generación de 1976 dominó las muestras del sur de California y de Baja California durante 1977.

Los promedios de las tallas de los peces capturados en 1976 fueron de 106 mm de longitud normal (Baja California) y de 125 mm de longitud normal (California), mientras que en 1977 la longitud media del pez mexicano aumentó a 113 mm de longitud normal aunque el tamaño de los peces de California disminuyó a 120 mm de longitud normal. Las proporciones entre los sexos durante 1976 variaron de 2.15 hembras por 1 macho (Baja California) a 1.16 hembras por 1 macho (sur de California), mientras que en 1977 las proporciones entre los sexos eran mucho más cercanas a 1:1 en California y en Baja California.

INTRODUCTION
The anchovy resource off the west coast of California and Baja California has developed into a major fishery in recent years. Most of the catch was made between San Quintin, Baja California, to north of San Francisco, California (Figure 1). Major ports of landings are Ensenada, located in Baja California, and Monterey, Oxnard, and Terminal Island in California.

Since the anchovy resource is common to both the United States and Mexico, the Instituto Nacional de Pesca and the California Department of Fish and Game have entered into a cooperative program of monitoring the anchovy fisheries of each country. Chavez et al. (1977) have described the life history of the anchovy and the results of the fisheries during 1975. This report is the continuation of this cooperative study and summarizes the catch data for 1976 and 1977.

THE FISHERY FOR 1976
Anchovy landings for 1976 totaled 189,066 metric tons (208,407 tons), of which 113,320 mt (124,913 tons), or nearly 60%, were caught by American fisherman and 75,746 mt (83,495 tons) were landed by Mexican fishermen (Table 1).

A total of 106 vessels, representing 66 American and 40 Mexican boats, was involved in the anchovy fishery. The average capacity of the Mexican boat was considerably greater (116.7 metric tons [128 tons]) than the American boat (76.0 metric tons [84 tons]), although its size was slightly smaller (15.5 m [51 ft]) as compared to 19.0 m [62.7 ft], respectively). The slight increase in average capacity of Mexican boats was due to the addition of several large-capacity (296-mt [326-tons]) purse seiners (Table 2).

The American fleet, although numbering as high as 66 vessels, contained 45 boats that were considered full-time anchovy boats. A majority of these vessels participated in the anchovy reduction fishery, which accounts for 99% of all anchovies landed in California. Since the reduction fishery is regulated by a season and a quota (Chavez et al. 1977), the number of active fishing boats fluctuates throughout the year. Most of the fishing activity occurs in southern California, although a minor fishery occurred in central California. This fishery was influenced by other fisheries such as the herring fishery in San Francisco Bay, which occurred January through March, and by the
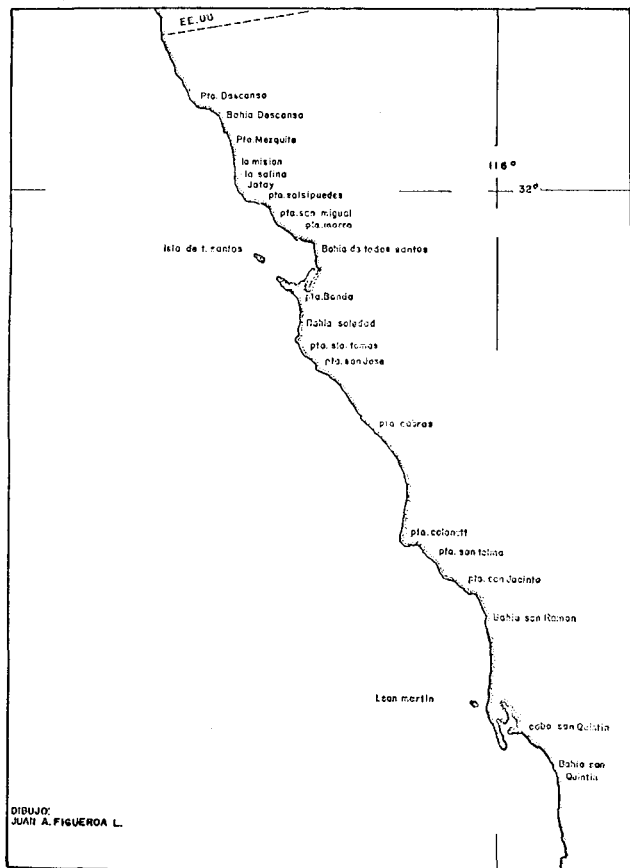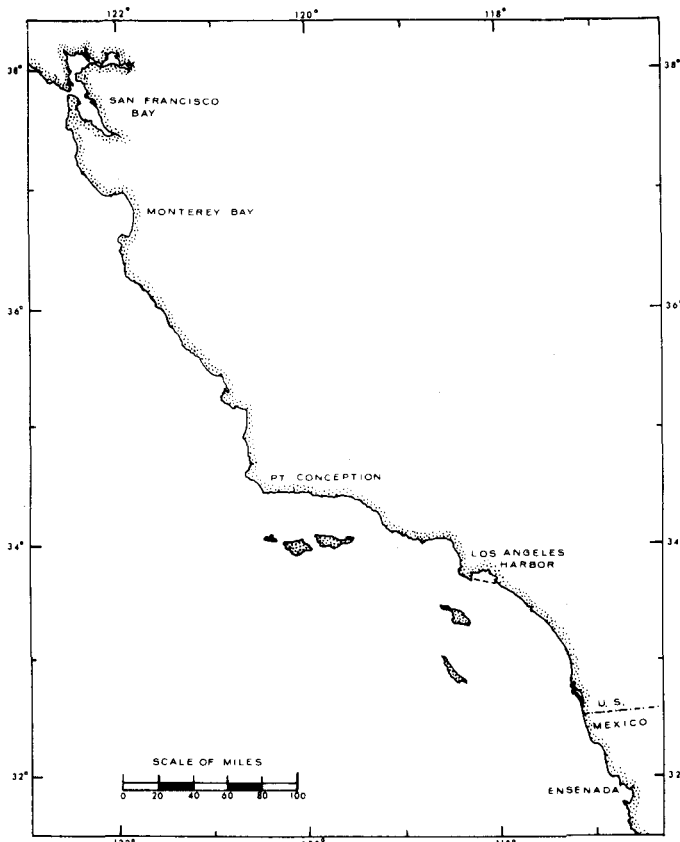
TABLE 1
Anchovy Landings for 1976.

Month	Weight (metric tons)		
	U.S.	Mexico	Total
January	18,009	85	18,094
February	1,549	119	1,668
March	10,597	49	10,646
April	16,225	1,055	17,280
May	1,648	1,437	3,085
June	115	3,753	3,868
July	174	12,836	13,010
August..........	425	5,097	5,522
September	6,833	15,000	21,833
October	10,037	15,943	25,980
November	27,234	14,297	41,531
December	20,474	6,075	26,549
Total	113,320	75,746	189,066
Short tons	124,913	83,495	208,407
%	59.9	40.1	100.0

mackerel and tuna fisheries in southern California, which occurred all year.

The Mexican fleet, which numbered a maximum of 40 boats, fluctuated between three boats during March and 30 boats in July, although in the fall and winter a major portion of the fleet became involved with the Gulf of California sardine fishery.

Monthly landings for the U.S. fishery were greatest during the fall and winter months with the smallest landings during the summer season (Table 1). The Mexican fishermen were most successful in summer and fall with winter months displaying the least amount, which reflects the effect of the sardine fishery (Table 1). The small amount of anchovies landed in U.S. waters during summer is due to the closure of the reduction fishery at this time. Mexico presently has no such regulation.

Major fishing grounds in southern California were the San Pedro Channel, Point Dume, Santa Monica Bank, and off Ventura. Fishing was best during the spring months in San Pedro Channel and off Huntington Beach, whereas fall catches occurred off Ventura and Santa Barbara. Central California landings occurred predominantly in Monterey Bay. A total of 2,312 boat trips were made in 1976, with as few as four trips in July to as many as 489 trips in November.

Primary Mexican fishing grounds were near Ensenada in February, May, and September, and the second most important areas were north of Ensenada: Playa del Rosarito, Punta Descanso, Las Salinas, Jatay, and Salsipuedes. Substantial catches were made south of Ensenada near Punta Cabras, Punta Colonett, Punta Piedras, Camalu, and Bahia San Ramon during July and August. The number of boat trips for 1976 totaled 1,391, ranging from five trips in January to 307 in October. Daily landings ranged from a maximum of 1,980 mt (2,182 tons) in October to 5.0 (5.5 tons) in November.

Figure 1. Top, anchovy fishing grounds of California; bottom, anchovy fishing grounds off Baja California.

Plant facilities in the U.S. remained the same as the previous year with four plants in southern California and two plants in central California. Processing capacity remained unchanged at 1,677 mt (1,850 tons) per day in the south and 200 mt (220 tons) in the north. Nine processing plants were located in Ensenada, which processed anchovies for canning (0.68%) and for reduction (99.32%).

Prices of anchovies ranged from $31 to $44.50/ton for U.S. fishermen, while Mexican fishermen received $17 to $30/ton for reduction and $24 to $28/ton for canning.

THE FISHERY FOR 1977

Landings in 1977 reached a record high of 243,124 metric tons (267,995 tons), of which 142,575 mt (157,160 tons), or nearly 58.6%, were caught by Mexico and 100,549 mt (110,835 tons) were caught by the U.S. (Table 3).

A dramatic change occurred in the dimensions of the Mexican fleet. In 1977, the average length of the vessel increased from 15.5 to 22.1 m (51 to 72 feet), and the catch capacity increased from 116.2 to 128 metric tons (129 to 141 tons; Table 2). This increase was due to the presence of 12 large-capacity 296-mt (326-ton) purse seiners. The American fleet on the contrary did not increase as much, as indicated by slight increases to 21.5 m (70 feet) and 90.7 mt (100 tons). Fleet size for both U.S. and Mexican fisheries totaled 41 vessels from Mexico and 45 boats from the U.S. (Table 2). The U.S. fleet size remained nearly constant during the fall, ranging between 35 to 45 vessels, but fewer boats were active during winter and spring (Table 2). This trend was the result of fishing effort towards jack mackerel and herring. The summer months saw little activity in anchovy fishing. Mexican fleet size fluctuated between 6 and 30 vessels/ month.

U.S. landings during January and February were considerably lower than the previous year as a result of the herring fishery interest in the northern zone and an excellent jack mackerel fishery in the south. Anchovy fishing did improve markedly in March, although catch success declined progressively throughout the spring. Summer monthly landings were minimal until August

when the reduction fishery was opened (Table 3). As it was noted the previous year, the fall months were most successful (Table 3). Total number of boat trips for the year was 2,015, ranging from five trips in July to 482 trips in October.

Mexican catches from January to May occurred south of Bahia Todos Santos (Camalu, Colonett, and Bahia San Ramon), and in the remaining months, the catch locations were in Bahia Todos Santos and nearby areas to the north (Punta Descanso, La Mision, La Salina, Salsipuedes, Punta Blanca, and Bahia Soledad). Number of boat trips totaled 2,032 with a low of 24 trips in February and a high of 407 trips in July. Daily landings ranged from 3.9 mt (4.3 tons) in February to 2,012 mt (2,218 tons) in July. Minor and occasional catches were made at Cedros Island, Bahia Tortugas, San Carlos, Isla Coronado, and Isla Margarita. Other species such as yellowtail (jurel), *Seriola dorsalis*; jack mackerel (charrito), *Trachurus symmetricus*; bonito, *Sarda chiliensis*; and Pacific mackerel (macarela), *Scomber japonicus*, were caught.

The southern California processing facilities increased their capacity from 1,677 to 1,877 mt (1,850 to 2,070 tons) per day. Mexican reduction capacities remained the same.

U.S. anchovy prices ranged from $34.50/ton to $58.75/ton with an average price of $41/ton. Mexican prices varied from $24 to $30/metric ton for reduction and $28 to $32/metric ton for canning.

FISHERY MONITORING

Methods and Materials

Sampling and aging methods utilized in both countries were described in detail by Chavez et al. (1977).

TABLE 2
U.S. and Mexican Fishing Vessel Information.

	U.S. 1976	U.S. 1977	Mexico 1976	Mexico 1977
Total number of boats	66	45	40	41
Mean vessel size				
Meters	19.0	21.5	15.5	22.1
Range	6-28	6-33	11-31	7-31
Mean catch capacity				
Metric tons	76.0	90.7	116.7	128
Range	5-181	10-208	14-296	12-296

TABLE 3
Anchovy Landings for 1977.

Month	Weight (metric tons) U.S.	Weight (metric tons) Mexico	Total
January	2,214	2,430	4,644
February	315	1,220	1,535
March	19,926	984	20,910
April	8,278	4,293	12,571
May	1,713	5,591	7,304
June	122	25,196	25,318
July	171	35,398	35,569
August	410	29,928	30,338
September	9,634	9,752	19,386
October	25,059	10,076	35,135
November	23,538	14,143	37,681
December	9,169	3,564	12,733
Total	100,549	142,575	243,124
Short tons	110,835	157,160	267,995
%	41.4	58.6	100.0
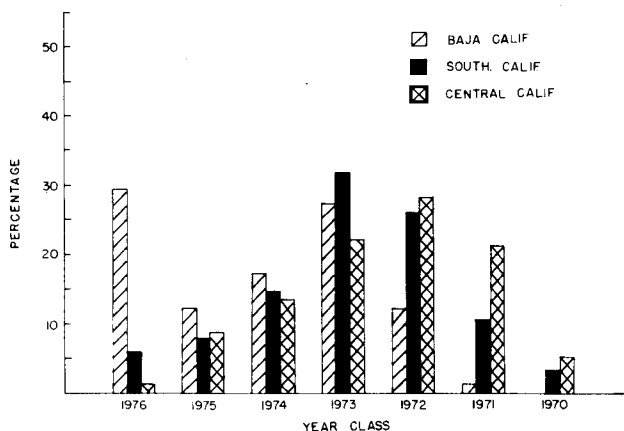
Figure 2. Age composition of anchovies caught off California and Baja California in 1976.

Results

Age Composition

Both southern California and Baja California samples during 1976 were characterized by large numbers of 1973 year class fish (32% and 27% respectively), although the Mexican catches were dominated by 1976 year class fish (Figure 2). This year class was nearly absent in California samples due to gear restrictions and a minimum size restriction. Older age groups were more prevalent in California samples than in Baja California samples.

Monthly age compositions differed between areas during the fall when Mexican samples consisted mainly of 1976 year class fish in contrast to the abundance of 1973 year class fish in U.S. samples (Figure 3).

In 1977, both California and Baja California age data indicated large percentages of young fish (Figure 4). Fish of the 1977 year class comprised over 50% of central California take, while the 1976 year class dominated the catch from southern and Baja California. Both California and Baja California age data revealed substantial numbers of the 1977 and 1976 cohorts throughout the year (Figure 5).

Length Composition

Baja California length data exhibited a bimodal distribution during 1976 with peaks near 85 and 115 mm (3.3 and 4.5 inches) standard length and an average length of 106 mm (4.2 inches) SL (Figure 6). Individuals smaller than 100 mm (4 inches) SL were present in all months and were extremely abundant in September through November (Figure 7). California anchovy lengths ranged from 80 to 160 mm (3.1 to 6.3 inches) SL with an average length of 125 mm (4.9 inches) SL (Figure 6). The total length distribution showed a pronounced mode at 130 mm (5.1 inches) SL and a minor mode at 100 mm (4 inches) SL (Figure 6). Monthly length distributions dis-
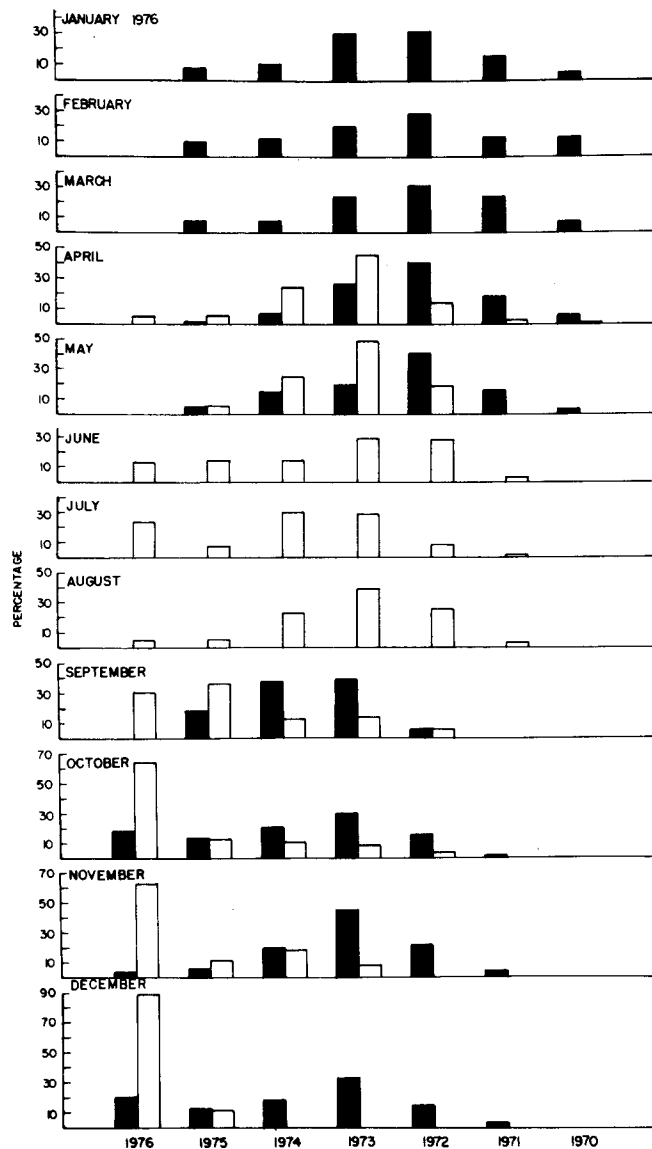
Figure 3. Monthly age composition by year class for 1976; solid bars, California; open bars, Baja California.

played a prominant mode near 125 mm (5 inches), although a small mode occurred near 95 mm (3.7 inches) SL (Figure 7).

During 1977, Mexican-caught anchovies averaged 113 mm (4.4 inches) SL with a range of 60 to 158 mm (2 to 5.3 inches) SL, whereas California data displayed unusual length distributions between central and southern California fish (Figure 6). Southern California length data were shown as a normal distribution with a mode of 120 mm (4.7 inches) SL, while central California data displayed a bimodal distribution.

Monthly length distributions for both countries were similar until August when the central California fishery was sampled (Figure 8). Normally, this region contains

135
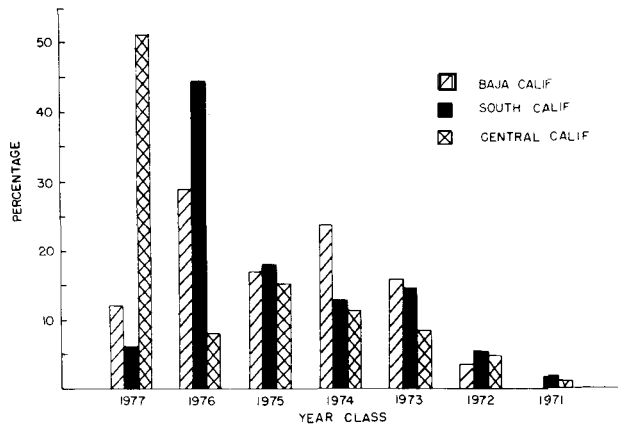
Figure 4. Age composition of anchovies caught off California and Baja California for 1977.
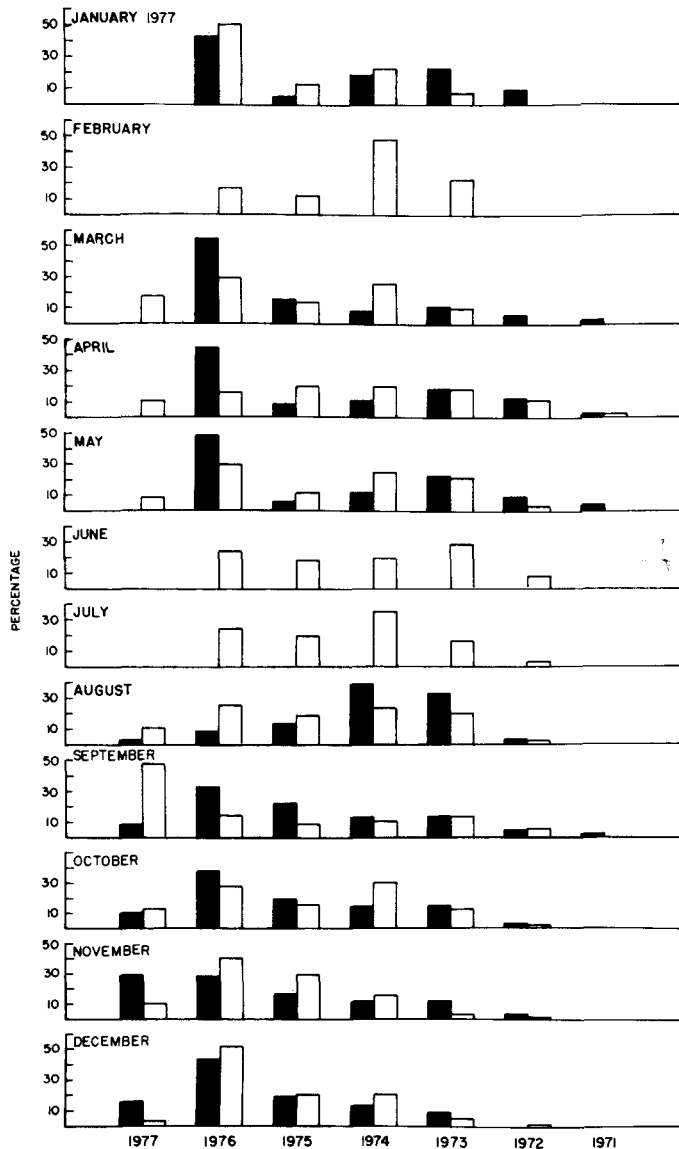
Figure 5. Monthly age composition by year class for 1977: solid bars, California; open bars, Baja California.

larger and older fish. Considerable length variations occurred between Baja California and California samples during September and December (Figure 8). An estimated 18% of the Mexican landings were fish smaller than 100 mm (3.9 inches) SL.

Sex Composition and Ratio

Sex composition of the catch during 1976 ranged from a female to male ratio of 1.16:1 in southern California to 2.15:1 in Baja California (Table 4). The Baja samples were dominated by females in all the months except December, whereas the southern California samples displayed a near 1:1 ratio in most of the months with an exception in May (Table 4). Central California samples indicated a nearly 2 to 1 female to male ratio, although only two months were sampled.

Anchovy sex ratios for California and Baja California were much closer to 1:1 during 1977 (Table 5). Baja California samples did contain slightly higher proportions of females than did the California samples (Table 5). One possible explanation for this decline in numbers of females could be the age structure of the catch, for significant numbers of young fish were caught during the year. Sunada (1976) stated that males were equal in proportion to females in younger age groups, whereas older age groups were dominated by females.
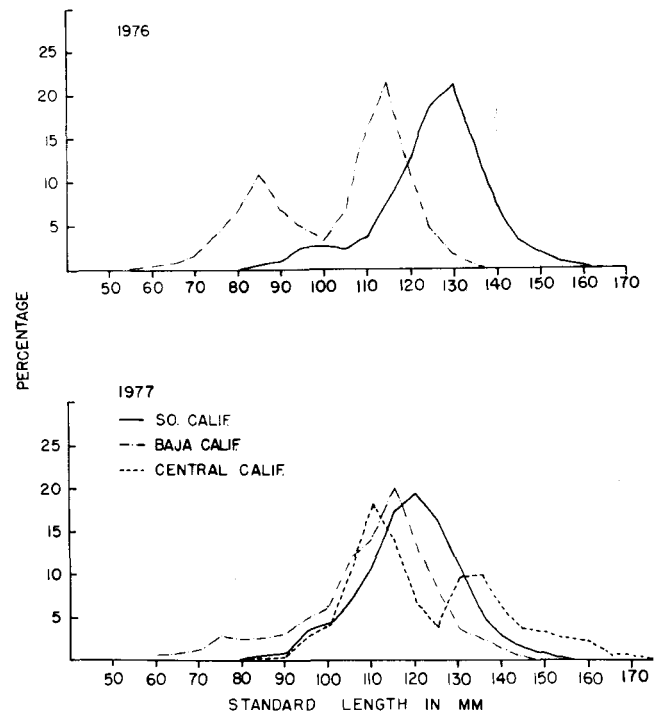
Figure 6. Annual anchovy length-frequency distribution for California and Baja California for 1976 and 1977.
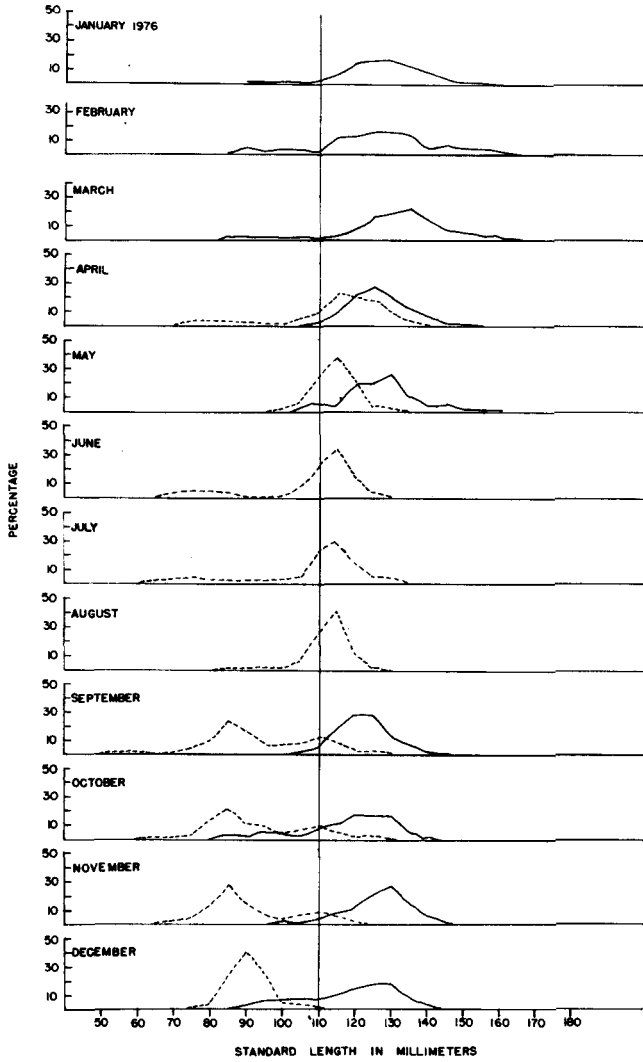
Figure 7. Length-frequency distribution of anchovies by month for 1976: dashed line, Baja California; solid line, California.
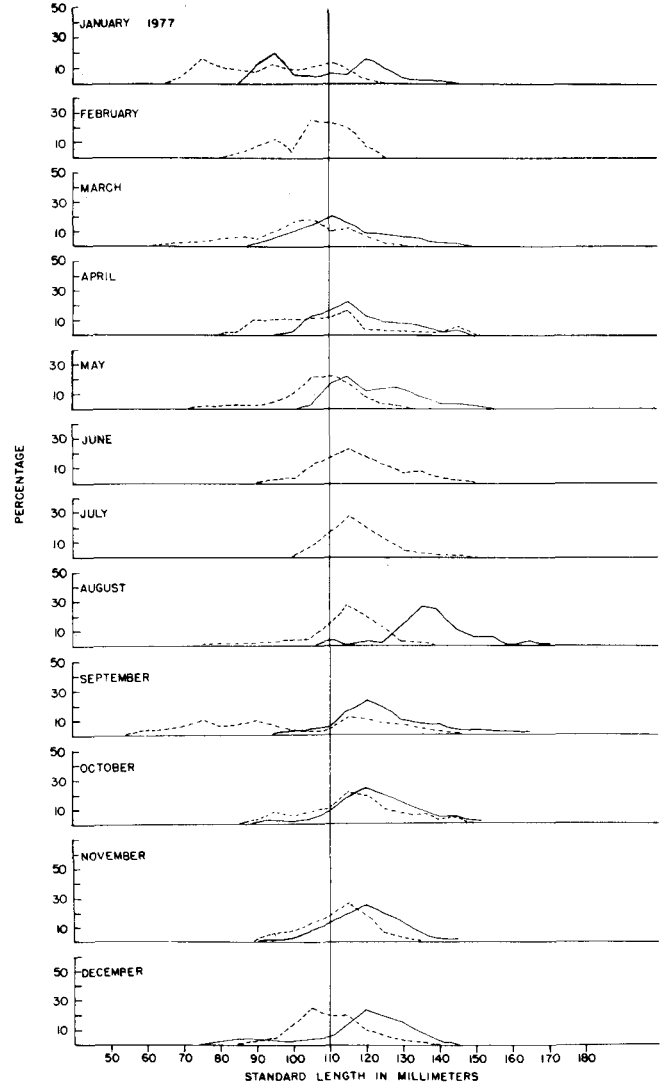
Figure 8. Length-frequency distribution of anchovies by month for 1977: dashed line, Baja California; solid line, California.

TABLE 4

Anchovy Sex Ratios for U.S. and Mexico for 1976.[1]

Month	Central California Male	Central California Female	Southern California Male	Southern California Female	Mexico Male	Mexico Female	Unknown
January	–	–	43.0	57.0	–	–	–
February	–	–	45.9	54.1	–	–	–
March	–	–	51.4	48.6	–	–	–
April	–	–	40.9	59.1	38.7	56.8	5.2
May	–	–	32.9	67.1	37.2	62.8	–
June	–	–	–	–	22.6	77.4	–
July	–	–	–	–	21.7	63.7	14.6
August	–	–	–	–	30.9	65.5	3.6
September ...	–	–	42.0	58.0	29.1	70.9	–
October	–	–	44.9	55.1	16.7	53.3	25.3
November ...	26.2	73.8	51.9	48.1	26.0	74.0	–
December ...	54.2	45.8	49.3	50.7	65.4	34.6	–
Percent	36.4	63.6	46.4	53.6	28.3	60.8	10.2
Ratio female:male	1.75:1		1.16:1		2.15:1		

[1]Percentage by numbers.

TABLE 5

Anchovy Sex Ratios for U.S. and Mexico for 1977.[1]

Month	Central California Male	Central California Female	Southern California Male	Southern California Female	Mexico Male	Mexico Female	Unknown
January	–	–	45.8	54.2	33.6	66.4	–
February	–	–	–	–	31.4	68.6	–
March	–	–	47.2	52.8	37.7	57.3	5.0
April	–	–	50.5	49.5	29.6	70.4	–
May	–	–	44.9	55.1	38.2	60.5	1.3
June	–	–	–	–	35.4	64.5	–
July	–	–	–	–	35.4	64.5	–
August	40.0	60.0	–	–	51.7	38.1	5.2
September ...	44.6	55.4	42.2	57.8	22.4	39.7	37.9
October	–	–	49.8	50.2	33.3	63.3	3.4
November ...	45.2	54.8	44.3	55.7	19.6	68.4	2.4
December ...	54.4	45.6	51.9	48.1	35.7	64.3	–
Percent	45.6	54.4	47.5	52.5	38.6	55.6	5.7
Ratio female:male	1.19:1		1.10:1		1.44:1		

[1]Percentage by numbers.

CONCLUSION

The anchovy fishery continued to expand in 1976 and 1977 with combined U.S. and Mexican landings of 189,066 metric tons (208,407 tons) in 1976 and 243,124 mt (267,995 tons) in 1977. Mexico increased her share of the catch from 40% in 1976 to 58% in 1977. Part of this trend can be attributed to the addition of 12 large purse seiners in the Mexican fleet. Fishing effort in both countries was influenced by the presence of more profitable species such as mackerel and herring.

Age structure of the sampled population during 1976 was dominated by the 1973 year class for California samples and by 1973 and 1976 cohorts in Baja California samples. The following year, age compositions from southern California and Baja California were quite similar, with 1976 year class dominating the catch. Central California samples contained unusually high percentages of young-of-the-year fish (1977 year class). Monthly age compositions differed between regions (U.S. and Mexico) during the fall of 1976, with Mexican landings dominated by young fish. During 1977, age structures of the two fisheries were more or less similar.

Mexican samples in 1976 exhibited a bimodal length distribution with peaks near 85 mm and 115 mm SL while California samples displayed a single mode near 130 mm SL. Length frequencies during the fall of 1976 showed distinct separation of size distribution between U.S. and Mexican catches. The lack of any size regulations in the Mexican fishery became obvious with the increased numbers of fish smaller than 100 mm SL. It is very possible these fish were from the southern stock with its slower growth rate. Both southern California and Baja California length data in 1977 displayed one mode while central California data exhibited two modes. Monthly length frequencies between countries were similar during the fall and winter with the exception of September. The majority of the fish were larger than 100 mm SL in all areas.

Anchovy sex ratios from the two countries showed greater numbers of females in the catch for both 1976 and 1977, although in 1977 the proportion of females, while still the majority, declined slightly.

The biological data from both countries indicate the fisheries to be harvesting primarily the central stock. As for the contribution of the southern stock, this is difficult to ascertain. Presently several studies are under way to more accurately determine the proportion of southern stock fish mixed with fish from the central stock.

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SEXUAL MATURITY, BATCH FECUNDITY, SPAWNING FREQUENCY, AND TEMPORAL PATTERN OF SPAWNING FOR THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, DURING THE 1979 SPAWNING SEASON

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ABSTRACT

Fifty percent of anchovy females reach sexual maturity by 96 mm standard length (95% confidence level 94-97 mm). Spawning batch fecundity, estimated from counts of hydrated eggs, was an exponential function of female weight. ($\ln Y = 4.2886 + 1.6281 \ln X$, where $Y =$ number of hydrated eggs and $X =$ female weight less ovary weight in grams). In the Los Angeles Bight the proportion of the population spawning/day (incidence of day-old post-ovulatory follicles) declined from 13.4% of the females in January-February to 10.0% in March-April and fell to 3.4% by June. Incidence of atresia in ovaries increased as the frequency of spawning declined. The percentage of females classed as post-spawning on the basis of the atretic condition of the ovary was 0.3% in January-February and 12% in March-April. Spawning of anchovy in Monterey Bay had nearly ended in March, and 71.9% of the females were classed as post-spawning.

The incidence of females with new post-ovulatory follicles and with hydrated eggs indicated that by sunset eggs were completely hydrated and spawning began; spawning reached a maximum between 2200-2300 hours and ended by 0200 hours. At 0600 hours females destined to spawn the next night began to hydrate eggs.

RESUMEN

El 50% de las anchovetas hembras alcanzan la madurez sexual al llegar a los 96 mm de longitud normal (nivel de confianza de 95%, 94-97 mm). La fecundidad del grupo desovante, calculado mediante recuento de óvulos hidratados, fue una función exponencial del peso de la hembra ($\ln Y = 4.2886 + 1.16281 \ln X$, donde $Y =$ el número de óvulos hidratados y $X =$ el peso de la hembra menos el peso del ovario en gramos). En la Bahía de Los Angeles la proporción de la población desovante diaria (incidencia de folículos post-ovulatorios de un día) disminuyó del 13.4% de las hembras durante enero-febrero al 10.0% en marzo-abril, y bajó al 3.4% en junio. La ocurrencia de atresia en los ovarios aumentó mientras que la frecuencia del desove disminuía. El porcentaje de hembras clasificadas como post-desovantes, a base de la condición atrética del ovario, fue 0.3% en enero-febrero y 12% en marzo-abril. El desove de anchoveta en la Bahía de Monterey casi había terminado en marzo, y 71.9% de las hembras fueron clasificadas como post-desovantes.

La presencia de hembras con nuevos folículos post-ovulatorios y con óvulos hidratados indicaba que, a la hora de la puesta del sol, los óvulos estaban completamente hidratados y se iniciaba el desove. El desove alcanzo un máximo entre las 2200-2300 horas y terminó a las 0200 horas. A las 0600 horas las hembras destinadas a desovar la siguiente noche empezaron a hidratar óvulos.

INTRODUCTION

To assess anchovy spawning biomass using the gonad-egg model of Parker (1980), spawning frequency and batch frequency must be estimated. This paper provides data on spawning frequencies and fecundity for the 1979 spawning season of the northern anchovy, *Engraulis mordax*. We also estimate the probability of sexual maturity of females as a function of length, examine the atretic state of the ovary using histological criteria, and reexamine the relation between the reproductive state of females and time of day. We combine our data with those of Hunter and Goldberg (1980) to establish general relationships between batch fecundity and weight and between time of day and spawning.

METHODS

Female anchovy were collected during two major survey periods in the Los Angeles Bight: January 26-February 16, 1979 (61 collections, total females = 619) and March 22-April 14, 1979 (48 collections, total females = 601). An additional set of three collections was taken June 9-19 in the Los Angeles Bight (33 females), and a set of five collections (150 females) was taken in Monterey Bay during March 20-22, 1979. Most of the fish were taken at night using a midwater trawl, but in January-February, 15 collections were from lampara nets set by commercial fishing vessels, and all the Monterey samples were from commercial vessels.

Our plan was to measure and sex a minimum of 25 fish per sample, weigh and preserve the first 10 mature females for histological examination, and all immature specimens until the quota of 10 mature females was obtained. In practice, the number of fish sexed remained constant, but the number of mature females preserved varied. In some cases, we increased the sample size of females to compensate for fewer samples, and in others a high incidence of immature females and a highly biased sex ratio reduced the number of mature females to less

than 10. In April 1979, we sampled a single area throughout one night to determine the consistency of spawning frequency within a single aggregation of schools. In this case we set the quota at 20 mature females/sample to increase the precision of the estimate. The variation in sample size of females has produced some statistical problems that have not been resolved. For this reason, error terms are not provided for spawning frequency estimates.

Batch fecundity was estimated for 32 females taken in January-February and 12 females taken in March-April by counting the number of hydrated eggs in a weighed sample of the gonad (Hunter and Goldberg 1980). The females used showed no evidence of recent spawning (no post-ovulatory follicles).

Many of the smaller females taken in January-February 1979 had small ovaries. Small females that had spawned within 24 hours could be confused with immature females if a judgement were made on the basis of ovary size alone. To avoid a histological examination of every immature ovary, we examined a subset of 160 females ≤ 12 g (body weight less ovary weight) to establish a weight criterion for immaturity. For these females we calculated the ratio of ovary weight/(body weight less ovary weight), grouped the data into eight ratio classes (N = 20 females per class), and calculated the percent of females in each class that were mature on the basis of histological criteria. Probit analysis (Finney 1952) was used to fit a line to the regression of maturity probability on $\log_{10}$ of the ratio of body weight/ovary weight (Figure 1). This analysis indicated that for females of 12 g or less, the probability of maturity was less than 5% when the gonad weight/body weight ratio ≤0.01. Henceforth, all females ≤12 g were considered immature if the ratio was 0.01 or less; all other females were examined histologically.

HISTOLOGICAL CLASSIFICATION

Spawning Frequency

For estimation of spawning frequency, females were examined histologically and classified into the five classes defined by Hunter and Goldberg (1980).

Hydrated. Ovaries with many hydrated eggs (eggs enlarged by fluid uptake just prior to ovulation) and no post-ovulatory follicles. Spawning considered to be imminent.

Age 0 day. New post-ovulatory follicles, showing no sign of degeneration. Hydrated eggs may occasionally be present. Elapsed time from spawning less than 24 hours.

Age 1 day. Regressing post-ovulatory follicles showing degeneration as described by Hunter and Goldberg (1980). Elapsed time from spawning equal to or greater than 24 hours but less than 48 hours.

Non-spawning (mature). Ovaries with many yolked oocytes; may contain post-ovulatory follicles in advanced
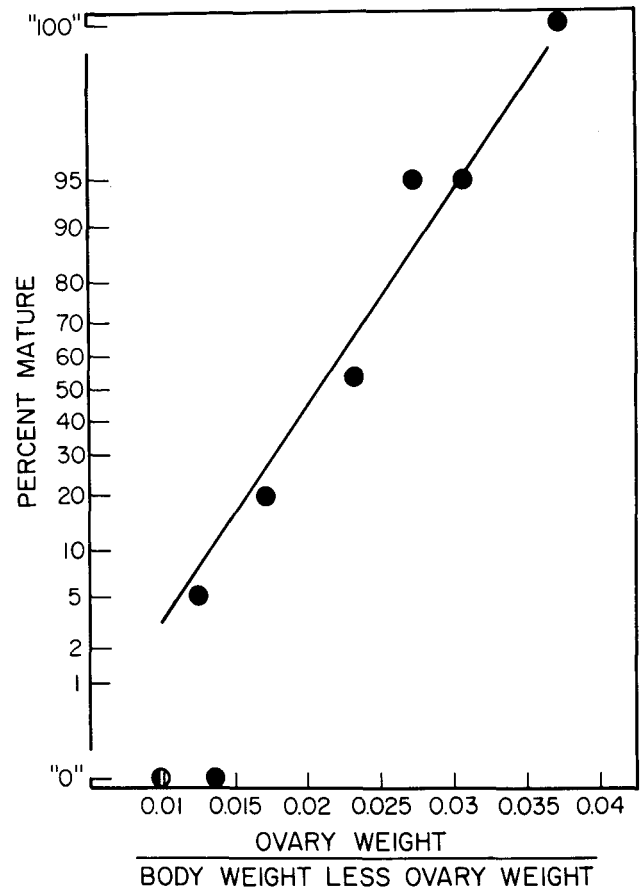
Figure 1. Percent of mature females (body weight ≤ 12 g) in eight classes of the ratio, ovary weight/(body weight less ovary weight);(N = 2 females/class): percentage plotted at the mean ratio within each class. Females taken in January-February 1979 in the Los Angeles Bight. Line fit using probit analysis; equation for line is Y = 21.52 + 9.837 X, where Y = % maturity in probits (Finney 1952) and X = $\log_{10}$ of the ratio.

stages of degeneration which cannot be readily distinguished from other atretic structures. May include females with highly atretic ovaries. Elapsed time from spawning 48 or more hours.

Immature. Few or no yolked oocytes. No atresia present in ovary other than late-stage corpora atretica. (A weight criterion was used to classify immaturity in some females ≤ 12 g; see methods section.)

We also determined the atretic condition of the ovaries of all mature female anchovy taken in 1979 including those with post-ovulatory follicles and hydrated eggs. This analysis provided an additional measure of the spawning potential of the population because rates of ovarian atresia would be expected to increase in ovaries as the end of spawning approaches and all yolked oocytes are resorbed. During the initial phase of the atretic process, the oocyte is resorbed and yolk globules are broken down and resorbed by hypertrophying granulosa cells of the follicle (the α stage of Bretschneider and Duyvené de Wit 1941; Lambert 1970). In the next stage (ß stage), all the yolk is gone, there remains a rather compact

structure with one or more cavities (corpora atretica); the tissue is composed of granulosa and theca cells with penetrating blood vessels. The degeneration of the granulosa and theca cells begins in this stage. In the third and fourth stages (stages γ and δ of Lambert 1970), regression of theca and granulosa cells continues thereby reducing the size of the follicle, and a yellow-brown pigment appears. This pigmented condition is characteristic of late-stage corpora atretica.

The incidence and extent of the above atretic oocyte stages in the ovary and the presence of yolked eggs were used as criteria for five classes of atretic ovarian condition (Table 1). All ovaries were assigned to one of the classes on the basis of the criteria given in the table. The presence of late corpora atretica was not used as a criterion because they may persist in the ovary for a long time and occur in ovaries regardless of the incidence of other atretic stages. The earliest atretic stage (α) was the most useful character because the size of the oocyte is still apparent.

We also include in the table the percentage of all mature females taken in 1979 that had post-ovulatory follicles (ages 0-1 day) combined with those with hydrated eggs. This percentage, defined as total spawning activity, decreased with an increase in atretic condition, indicating, as expected, that atretic condition of the ovary and spawning activity are correlated.

SEXUAL MATURITY

All females collected in February 1978 were mature (Hunter and Goldberg 1980); whereas only 64% of the females taken in January-February 1979 were mature, and 91% were mature in March-April 1979. Data for 1979 were grouped by 5-mm standard length (SL) classes, percent maturity calculated for each class (Table 2), and

the probability of maturity regressed on the $\log_{10}$ of the mean length of females in each class using probit analysis (Finney 1952). The estimated length at 50% maturity was the same for January-February, 96 mm (95% CI 94-97 mm) as for March-April, 96 mm (95% CI 94-98 mm). A good fit was obtained between probability of maturity and length in both sets (Figure 2).

The maturity lines for the two surveys in 1979 had different slopes because females 105-119 mm had a higher probability of maturity in March-April than they did in

TABLE 2

Percent Maturity of Female Northern Anchovy in the Los Angeles Bight by Length Class for February 1978, January-February 1979, and March-April 1979.

Length class (mm)	February 1978		January-February 1979		March-April 1979	
	N	% mature	N	% mature	N	% mature
71- 75	2	100	4	0		
76- 80	5	100	19	5		
81- 85	1	100	56	11		
86- 90	4	100	69	29	2	50
91- 95	3	100	80	48	7	86
96-100	6	100	70	56	46	67
101-105	8	100	58	76	120	80
106-110	17	100	39	82	134	94
111-115	47	100	46	87	117	96
116-120	53	100	33	94	59	100
121-125	36	100	31	94	48	100
126-130	24	100	50	100	40	100
131-135	35	100	44	100	19	100
136-140	25	100	13	100	15	100
141-145	18	100	5	100	3	100
146-150	9	100	1	100		
151-155	2	100	1	100		100
156-160					1	
Σ	295		619		611	

TABLE 1

Characters Used to Classify the Atretic Condition of Ovaries of Northern Anchovy[1] and the Total Spawning Activity within Atretic Ovary Classes.

Atretic ovary class	Total spawning activity[2]	Yolked oocytes present	Incidence of a stage[4] atresis in:			Incidence of ß stage atresia[4]	Other diagnostic characters
			Unyolked oocytes	Yoked oocytes[3]			
				Small	Large		
No atresia	0.36	+	0	0	0	0	
Minor atresia	0.21	+	*	*	0	+	
Early post-spawning	0.10	+	*	+	+	*	Less than 50% all yolked oocytes are in α stage atresia
Post-spawning	0	+	*	+	+	*	Greater than 50% all yolked oocytes are in α stage atresia.
Late post-spawning	0	0	*	0	0	+	

[1] + = present; 0 = absent; and * = may occur.
[2] Proportion of all mature females within each class having hydrated eggs or post-ovulatory follicles (ages 0 and 1). Combined data for January-February 1979 and March-April 1979 in Los Angeles Bight and March 1979 in Monterey Bay. Number of females in each of the five classes were: 592 (no atresia), 323, 92, 46, and 49 (late post-spawning).
[3] Distinction between atretic large and small yolked oocytes can be made only early in α stage of atresia when size differences are apparent, but yolked oocytes can be separated from unyolked throughout the α stage because of staining differences in hematoxylin and eosin preparations.
[4] α and ß stages of atresia are defined in text.
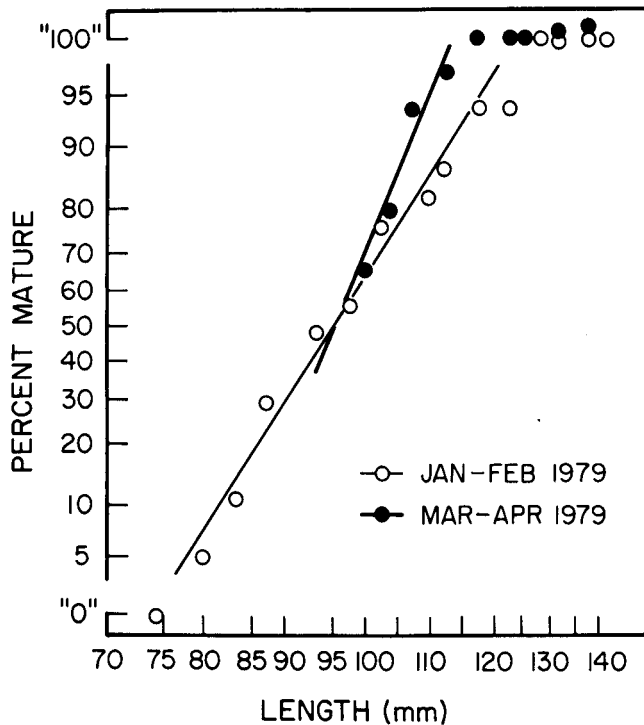
Figure 2. Percent maturity of female anchovy taken in Los Angeles Bight in January-February 1979 (open circles) and March-April 1979 (solid circles) as a function of standard length. Points are percent of females that were mature in each 5-mm class of length and are plotted at mean length within class. Equations for lines are: January-February, $Y = -29.793 + 17.572\ X$ and March-April, $Y = -48.30 + 26.899\ X$; where Y = % maturity in probits (Finney 1952) and X = log$_{10}$ standard length.

January-February 1979, whereas the probability of maturity for smaller females remained the same. The change in slope of the maturity line during 1979 and the difference in maturity between 1978 and 1979 could be caused by differences in sampling or statistical uncertainties. It could also be a measure of a real difference in the maturity-length relation as the spawning season progressed.

FECUNDITY

The spawning batch fecundity of female anchovy, on a unit weight basis, varied from 389 hydrated eggs/g female weight less ovary weight to 444 eggs/g, and the mean for all fecundity estimates was 421 ± 36 eggs/g (Table 3). MacGregor (1968) and Hunter and Goldberg (1980) concluded that for assessment work, the mean number of eggs per unit weight (relative fecundity) was sufficient and presented their data in that form. The existence of a larger data set (Table 4), based on hydrated eggs, permitted a reexamination of the fecundity weight relation. We regressed the number of hydrated eggs per female on female weight less ovary weight, using the combined data for 1978 and 1979. The geometric mean regression (Ricker 1973) yielded the equation $\ln Y = 4.183 + 1.620\ \ln X$, where Y = number hydrated eggs, X = female weight less ovary weight, $r^2 = 0.51$ and $s^2_{y \cdot x} = 0.1295$ (the 99% confidence intervals for the slope did not include 1; Figure 3, upper). The form of this relation was similar to the one between gonad weight and female weight for mature nonspawning females with eggs of 0.65 mm (major axis) in the most advanced mode (Hunter and Goldberg 1980). To compare the two equations, we estimated ovary weight using their equation, $\ln G = -4.213 + 1.069\ \ln W + .555\ D\ \ln W$ (G = ovary weight, W = female weight, and D = major egg axis [.65 mm]) and multiplied the estimated ovary weight by the mean number of advanced eggs per gram of ovary (8,630 ± 921; Hunter and Goldberg 1980). The two equations give similar results although based on different females and methods of calculation (Figure 3, lower). The regression equation appears to be a reliable method of estimating batch fecundity for females of the central subpopulation of northern anchovy and is more accurate than expressing fecundity on a unit weight basis. The error in using relative fecundity becomes substantial for females larger than 25 g (Figure 3, lower).

TABLE 3

Relative Batch Fecundity (Eggs per Unit Weight) for Females with Hydrated Eggs Taken in Each Survey and Calculated from Regression Equation for Batch Fecundity where X = Mean Weight of All Females Taken in Survey.

					Relative batch fecundity	
	Weight of all mature females (less ovary)		Mean for females with hydrated eggs		From regression equation, where X = mean weight of all females[3]	
Survey period	N	$X \pm 2SE$[2] g	N	$X \pm 2SE$[2] eggs/g (without ovary)	weight less ovary eggs/g	weight with ovary eggs/g
February 1978[1]	328	17.29±0.74	23	389±59	409	389
January-February 1979	394	16.40±0.67	32	444±57	396	376
March-April 1979	558	15.50±0.39	12	423±67	383	364
All data	952	15.87±0.30	67	421±36	388	369

[1]From Hunter and Goldberg (1980).

[2]±2 times standard error of mean.

[3]$\ln Y = 4.183 + 1.620\ \ln X$, where X = female weight less ovary and $\ln Y = 4.100 + 1.620\ \ln X$, where X = female weight with ovary. Estimate of total egg ($\ln Y$) increased by factor $\frac{1}{2}\ s^2_{y \cdot x} = 0.0647$ to correct for bias in taking antilog (Beauchamp and Olson 1973).

TABLE 4

Batch Fecundity of Northern Anchovy from Counts of Hydrated Eggs: Data for Three Surveys in the Los Angeles Bight.

Female weight less ovary (g)	Ovary weight (g)	Total hydrated eggs	Survey[1]	Female weight less ovary (g)	Ovary weight (g)	Total hydrated eggs	Survey[1]
9.3	1.171	3822	1	18.1	3.092	8978	3
9.3	1.406	2874	2	18.5	2.819	6420	2
9.8	1.202	3538	1	20.1	3.296	9447	1
10.8	1.190	2894	2	20.2	5.298	9595	2
10.8	2.109	6178	2	20.3	2.798	7714	2
11.7	1.485	3604	2	20.4	3.017	6181	1
11.9	1.202	5950	1	20.6	3.996	13266	1
11.9	1.704	4201	2	21.3	4.539	9159	2
12.5	1.038	4625	2	21.4	2.910	6292	2
12.7	1.697	4001	3	21.9	4.253	12461	1
12.9	2.155	6386	1	22.8	5.479	11902	2
13.1	1.995	4742	2	22.9	3.988	9366	1
13.1	1.586	4585	3	22.9	1.990	2794	2
13.4	1.888	4556	3	23.0	4.047	12742	2
13.7	1.575	6288	1	23.4	4.159	8354	2
14.2	3.083	8818	3	23.5	4.812	16662	1
14.6	1.287	3270	1	23.7	6.366	14196	2
14.7	1.352	3822	3	23.7	6.031	15310	2
14.9	1.523	4455	3	24.3	4.131	12515	2
15.2	2.473	5852	3	24.4	1.906	5392	1
15.3	2.114	5279	2	24.5	3.556	10217	2
15.4	0.835	3234	1	24.7	3.793	10621	2
16.0	2.210	4336	1	24.8	5.561	14037	3
16.0	1.235	4592	1	25.5	5.686	11577	1
16.0	2.586	7040	3	25.7	5.648	13955	2
16.1	2.058	4862	2	26.3	4.228	8548	2
16.4	2.750	8922	3	26.8	8.049	20797	2
16.6	2.622	5677	2	26.9	2.956	5972	1
16.6	5.624	13363	2	28.0	9.645	23044	2
17.2	3.275	7895	2	28.1	6.388	14668	2
17.2	2.148	7258	1	30.4	1.967	6292	1
17.3	2.473	5744	2	31.2	4.793	10577	1
17.3	3.883	7958	3	31.9	3.796	9251	1
17.9	2.369	8216	1				

[1] 1 = February 1978, $N = 23$;
2 = January-February 1979, $N = 32$;
3 = March-April 1979, $N = 12$.

We used counts of hydrated eggs to estimate spawning batch fecundity because it was a more rapid and more accurate method than counting the number of eggs in the most advanced mode (Hunter and Goldberg 1980). This method requires that fecundity be calculated in terms of female body weight, less gonad weight, because hydration of the ovary significantly alters the total weight of the female. On the other hand, to assess spawning biomass, fecundity must be expressed in terms of total weight. Our fecundity measurements can be converted to a total weight basis using the ratio of the two body weights for females without hydrated eggs (w/W, Table 5). This ratio was 0.95, and it varied little between seasons, regions, or years. The fecundity equation was re-estimated from the data in Table 4 using total female weight (female weight less ovary weight/0.95) as the independent variable. The

geometric mean regression (Ricker 1973) of numbers of hydrated eggs (Y) on total female weight (female weight less ovary/0.95; X) was $\ln Y = 4.100 + 1.620 \ln X$, where $r^2 = 0.51$, and $s^2_{y \cdot x} = 0.1295$.

We believe it is preferable to use the regression equation to estimate batch fecundity for assessment of spawning biomass rather than the average relative fecundity. In Table 3, we use the equation to estimate the relative batch fecundity for the mean of the weight of all mature females taken in each survey, and we compare these values to means calculated on a unit weight basis. Regression estimates of relative fecundity using the mean weight of females taken in a survey differ by 5-11% from the average relative fecundity for the same survey because of differences in the weights of hydrated females within the samples used for the unit weight averages.

FREQUENCY OF SPAWNING

Spawning frequency is best estimated from the incidence of day-old post-ovulatory follicles (day 1), because incidence of females with hydrated eggs or new post-ovulatory follicles are affected by the time of capture and sexual composition of the school (Hunter and Goldberg 1980). The ovaries of 13.4% of the mature females taken in January-February 1979 (Table 6) and 10.0% of those taken in March-April 1979 (Table 7) had day-old post-ovulatory follicles. Thus, on the average, female anchovy in the Los Angeles Bight spawned every 7-10 days during the three peak months of spawning in 1979. Only 3.5% of the 29 females taken in June 1979 in the Los Angeles Bight has post-ovulatory follicles. Although the sample size is small, these data indicate that the frequency of spawning had declined by June.

Incidence of day-old post-ovulatory follicles reported by Hunter and Goldberg (1980) were 15% for February 1978 and 14.2% for a small sample taken in March 1977. Thus, data for the peak spawning months in 1979 was in keeping with past results. As in the past study, no relation existed between incidence of day-old post-ovulatory follicles and size of the mature females, time of day, or locality within the Los Angeles Bight.

Ovaries of females taken in Monterey Bay in March 1979 were distinctly different: none contained day-old post-ovulatory follicles, and only two (1.3%) had new post-ovulatory follicles (day 0; Table 8). Thus, spawning had nearly ended in Monterey Bay by March, whereas it continued at a high level to the south in the Los Angeles Bight. Abundance of anchovy larvæ and eggs taken in the 1979 CalCOFI survey also indicated that spawning ended in Monterey by March but continued in the Los Angeles Bight and south along the Mexican coast (Stauffer and Parker 1980).

In a recent study Laroche and Richardson (in press) point out that the northern subpopulation of the northern anchovy off Oregon and Washington probably spawn fewer times than the central subpopulation we studied. They noted degeneration of oocytes in ovaries of females
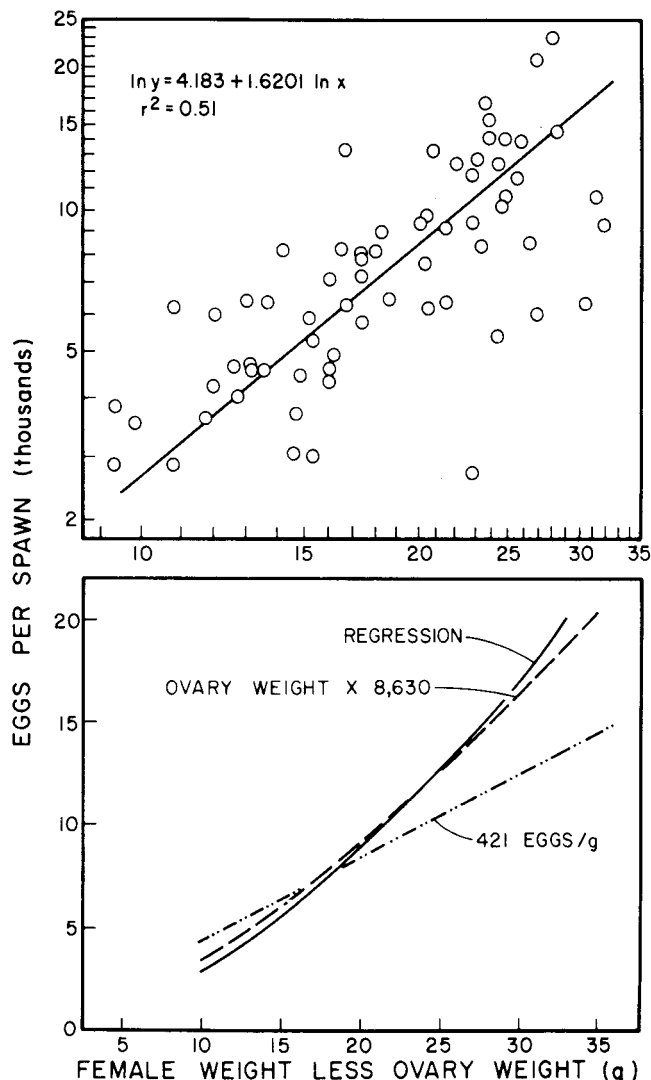
Figure 3. Batch fecundity of northern anchovy taken in the Los Angeles Bight, 1978-79. Upper panel: regression of ln total number hydrated eggs on ln female weight (less ovary weight). Lower panel: three methods of estimating batch fecundity are compared; solid line from regression in upper panel; dashed line, ovary weight (G) times mean number eggs (non-hydrated) in advanced mode (8630 ± 921) where $\ln G = -4.213 + 1.069 \ln W + D$ (0.555 $\ln W$). W = female weight (less ovary) and D = size of eggs (0.65 mm; from Hunter and Goldberg 1980), and dash-dot line is mean relative fecundity for 1978-79, 421 eggs/g female weight (less ovary).

TABLE 5
Mean Body Weight of Females[1] with (W) and without (w) the Ovary Included and Regression of W on w for Various Survey Periods and Regions.

| Survey and region | Total body weight (W) in g | | | Body weight less ovary (w) in g | | | $W = -a + bw$ where: | | |
	N	X	s	X	s	w/W	a	b	r²
February 1978 (Los Angeles Bight)	69[2]	20.2	8.05	19.2	7.45	0.950	.514	1.078	0.997
January-February 1979 (Los Angeles Bight)	355	17.1	7.15	16.2	6.64	0.947	.409	1.077	0.998
March-April 1979 (Los Angeles Bight)	536	16.2	5.10	15.5	4.70	0.957	.520	1.081	0.995
March 1979 (Monterey)	145	19.3	6.64	18.5	6.18	0.959	.516	1.073	0.997
All data combined	1099	17.2	6.36	16.4	5.90	0.954	.450	1.076	0.997

[1]Only sexually mature females included: females with hydrated eggs excluded.
[2]Gonad weight not available for all females examined.

TABLE 6
Reproductive State of Female Northern Anchovy Collected in the Los Angeles Bight in January-February 1979.

Collection number[1]	Month and day	Time of day (hours)	Number of females in various reproductive states				Total females	
				Post-ovulatory follicles		Mature no evidence of spawning		
			Hydrated eggs	0 day[2]	1 day		Mature	Immature
3040	2 10	18.03	–	2	1	5	8	3
3034	2 09	18.08	4	–	4	2	10	0
3025	2 07	18.12	3	–	3	4	10	0
3006	1 27	18.23	–	1	1	3	5	6
3017	2 03	18.27	1	–	1	8	10	0
3019	2 04	18.27	7	–	–	3	10	0
3000	1 26	18.37	–	–	–	1	1	12
3020	2 06	18.73	1	–	1	8	10	0
3012	1 29	18.88	–	–	–	2	2	5
3007	1 27	19.12	–	–	1	3	4	7
3046	2 13	19.17	–	–	1	7	8	1
3041	2 10	19.32	2	–	–	7	9	10
3018	2 03	19.48	5	–	1	4	10	0
3026	2 07	19.70	–	–	–	10	10	0
3001	1 26	20.05	–	–	–	2	2	8
3013	1 29	20.18	1	2	–	–	3	2
3035	2 09	20.27	2	1	–	6	9	0
3021	2 06	20.38	2	2	3	2	9	0
3042	2 10	20.63	3	–	–	6	9	3
3029	2 08	20.67	2	1	5	2	10	0
3008	1 27	20.93	–	–	1	2	3	12
3002	1 26	21.30	–	–	–	–	0	10
3036	2 09	21.62	2	–	2	6	10	0
3014	1 29	21.67	–	–	2	3	5	1
3022	2 06	21.82	–	5	1	4	10	0
3043	2 10	21.85	–	1	–	9	10	0
3030	2 08	22.27	1	1	–	8	10	0
3003	1 26	22.33	–	–	–	–	0	11
3009	1 27	22.45	–	–	–	1	1	16
3027	2 07	22.72	–	–	3	7	10	0
3037	2 09	23.02	–	–	–	3	3	0
3044	2 10	23.30	–	–	–	5	5	1
3015	1 29	23.55	–	3	–	7	10	0
3023	2 06	23.70	–	3	–	–	3	0
3010	1 27	23.75	–	–	–	6	6	7
3031	2 09	00.05	–	–	2	8	10	0
3028	2 08	00.12	–	1	3	6	10	0
3038	2 10	00.52	–	1	1	8	10	0
3004	1 27	00.72	–	–	–	–	0	14
3011	1 28	00.78	–	–	–	7	7	8
3045	2 11	00.95	–	2	–	–	2	0
3024	2 07	01.12	–	3	–	2	5	0
3032	2 09	01.63	–	1	4	5	10	0
3039	2 10	02.03	–	1	3	6	10	0
3016	1 30	02.90	–	1	–	1	2	2
3033	2 09	03.00	–	4	1	5	10	0
2006	2 05	03.42	–	1	1	8	10	0
2001	1 27	03.50	–	2	–	1	3	7
2005	2 02	04.00	–	–	–	7	7	3
2002	1 27	04.17	–	–	1	4	5	8
2004	1 30	04.50	1	–	1	3	5	5
2007	2 07	04.50	–	–	–	5	5	5
2010	2 16	04.50	–	, –	–	9	9	1
2003	1 27	05.00	–	–	–	2	2	11
2008	2 07	05.00	1	1	4	4	10	0
1002	2 08	05.00	–	–	–	2	2	9
2009	2 16	05.33	1	1	1	7	10	0
1004	2 12	05.50	–	1	–	7	8	2
1001	2 07	05.50	–	2	–	1	3	14
1003	2 08	06.00	–	–	–	3	3	11
1005	2 15	06.00	–	–	–	1	1	10
S			39	44	53	258	394	225
%			9.9	11.2	13.4	65.5	63.6	36.4

[1]Collection numbers in 1000 and 2000 series were commercial lampara sets; 3000 and 4000 were midwater trawl.
[2]Females with hydrated eggs and day 0 post-ovulatory follicles included in this class.

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TABLE 7
Reproductive State of Female Northern Anchovy Collected in the Los Angeles Bight in March-April 1979.

Collection number[1]	Month and day	Time of day (hours)	Hydrated eggs	Post-ovulatory follicles 0 day[2]	Post-ovulatory follicles 1 day	Mature no evidence of spawning	Total females Mature	Total females Immature
3064[3]	4 07	18.80	2	1	4	13	20	0
3054	4 03	18.92	1	–	1	8	10	0
3079	4 12	18.92	2	1	–	7	10	11
3082	4 13	18.92	–	–	4	6	10	–
4008	3 24	19.15	–	1	2	11	14	1
4001	3 22	19.25	–	–	–	11	11	0
3050	4 02	19.33	–	1	3	6	10	0
4004	3 23	19.57	3	1	1	9	14	1
3071	4 08	20.25	1	–	–	9	10	0
3055	4 03	20.35	–	–	3	7	10	0
3083	4 13	20.35	2	–	–	8	10	1
3058	4 05	20.43	–	–	2	8	10	0
3073	4 09	20.50	–	–	–	10	10	0
3065[3]	4 07	20.57	1	2	1	16	20	0
3047	4 01	20.60	–	–	3	7	10	0
3060	4 06	20.72	2	–	1	7	10	0
4009	3 24	21.30	5	8	–	1	14	1
3074	4 09	21.75	–	–	1	9	10	0
3072	4 08	21.78	–	1	–	9	10	0
3059	4 05	22.00	–	2	2	6	10	0
4005	3 23	22.05	5	3	2	5	15	0
3048	4 01	22.12	–	–	2	4	6	0
3066[3]	4 07	22.30	1	7	2	9	19	0
3061	4 06	22.50	1	2	1	6	10	0
4002	3 22	22.67	–	2	2	11	15	0
3057	4 04	22.83	–	1	–	7	8	2
3077	4 11	22.87	–	–	–	11	11	1
4010	3 24	23.42	–	2	2	10	14	1
3075	4 09	23.50	–	1	–	9	10	0
3067[3]	4 08	00.02	–	7	1	12	20	0
3062	4 07	00.03	–	1	1	8	10	0
4006	3 24	00.38	–	2	1	7	10	0
3051	4 03	00.48	–	–	3	7	10	0
3076	4 10	00.90	–	2	–	8	10	0
3080	4 13	01.10	–	–	1	4	5	18
3049	4 02	01.13	–	–	2	8	10	0
3078	4 12	01.57	–	–	–	10	10	0
3063	4 07	01.58	–	1	1	9	11	0
3068[3]	4 08	01.67	–	5	1	14	20	0
3084	4 14	02.98	–	4	–	5	9	1
4007	3 24	03.08	–	–	1	12	13	2
3069[3]	4 08	03.33	–	5	1	13	19	0
3081	4 13	03.42	–	–	1	9	10	0
3052	4 03	03.62	–	3	–	7	10	0
4003	3 23	03.65	–	1	1	9	11	2
3070[3]	4 08	04.92	–	4	2	13	18	1
2026	3 23	05.00	–	–	–	–	–	10
3053	4 03	05.05	–	–	–	10	10	0
Σ			26	71	56	405	558	53
%			4.7	12.7	10.0	72.6	91.3	8.7

[1]Collection numbers in 1000 and 2000 series were commercial lampara sets, 3000 and 4000 were midwater trawl.
[2]Female with hydrated eggs and day 0 post-ovulatory follicles included in this class.
[3]Collection is part of a 7-collection series taken in same locality on same night.

TABLE 8

Reproductive State of Female Northern Anchovy Collected in Monterey Bay, California, in March 1979.

Collection number	Month and day	Time of day (hours)	Hydrated eggs	Post-ovulatory follicles		Mature no evidence of spawning	Total mature females[1]
				0 day	1 day		
2014	3 21	02.30	–	1	–	29	30
2020	3 22	03.15	–	–	–	30	30
2017	3 21	03.45	–	–	–	30	30
2023	3 22	04.15	–	1	–	29	30
2011	3 20	05.00	–	–	–	30	30
Σ			0	2	0	148	150
%				1.3		98.7	100

[1]All females judged sexually mature, but many ovaries in post-spawning condition (see Table 9).

taken in the peak month of July and spawning in the northern subpopulation occurs only from mid-June to mid-August. We examined a small sample of 25 females taken in four research trawl catches taken off Oregon July 18-21, 1977. Ovaries of ten of these females (40%) had new post-ovulatory follicles and four (16%) had day-old post-ovulatory follicles. Twenty-three of the ovaries from these females (92%) exhibited no or only minor atresia, but the ovary from one female was in the early post-spawning condition and that from another in the late post-spawning condition. The latter female had clearly completed spawning for the season. On the basis of this evidence we suggest that the spawning frequency during peak periods of spawning is about the same for the northern as for the central sotck (about once a week), but the northern stock may be limited to about four spawnings per year because of the short duration of the spawning season.

INCIDENCE OF ATRESIA

In January-February 1979, when the frequency of spawning was the highest (13.4%), only 0.3% of the mature females were classed as post-spawning on the basis of ovarian atresia, whereas in March-April 1979, when spawning frequency had declined to 10.0%, 14% of the mature females were classed in one of the three post-spawning stages and 5% clearly were incapable of further spawning (Table 9). In Monterey during March, little spawning occurred, and 71.9% of the females were classed in one of the three post-spawning stages. Thus the incidence of ovarian atresia was inversely correlated with the frequency of spawning, and this indicates that the decrease in the frequency of spawning during the season may be caused by a cessation of spawning. In other words, the interval between spawning may be a biological rhythm having a period of about a week, and the change in the observed spawning frequency may be caused by cessation of spawning by some females in the population rather than changes in the interval between spawning in individual females.

TABLE 9

Incidence of Atretic Classes of Ovaries in Mature Female Northern Anchovy Taken in the Los Angeles Bight and Monterey Bay in 1979.

Region and month	N[1]	Percentage of Females[2]				
		No atresia	Minor atresia	Early post-spawning	Post-spawning	Late post spawning
Los Angeles Bight January-February	394	64.4	35.3	0.3	0	0
Los Angeles Bight March-April	558	57.7	28.3	9.0	1.4	3.6
Monterey Bay March	149	10.8	17.3	27.3	25.3	19.3

[1]All mature females.
[2]Stages of atresia defined in methods.

TEMPORAL PATTERN OF SPAWNING

The seven trawl samples taken during a single night in the same locality (March-April 1979, Table 6) provide an illustration of the temporal pattern of spawning within a single group of schools. The percent of females with hydrated eggs decreased from 10% at sunset to zero by midnight, whereas the number of females with new post-ovulatory follicles increased sharply at 2100 hours and varied between 25 and 35% throughout the rest of the night (Figure 4, upper). The incidence of new post-ovulatory follicles in this series was consistently higher than the mean of all collections taken in March-April 1979 (13%, Table 6). Thus, on this particular night, more spawning may have occurred in this group of schools than was typical for all schools in the Los Angeles Bight in March-April. The frequency of day-old post-ovulatory follicles ranged from 5 to 20% but did not vary with time of day; the mean was 9%, close to the average (10%) for the March-April survey period as a whole.

The temporal pattern of spawning for all surveys combined (February 1978, January-February 1979, and March-April 1979) was similar to the one for a single night. Percent of females with hydrated eggs declined
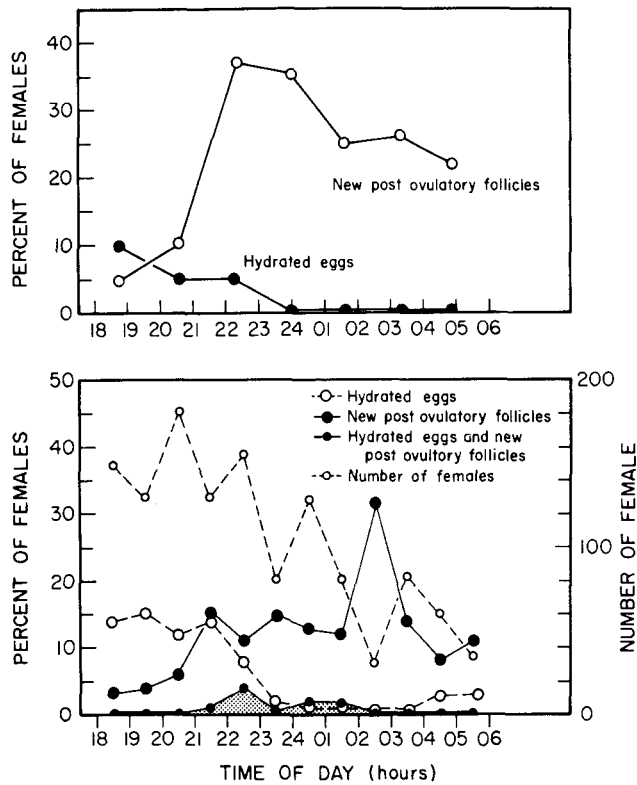
Figure 4. Percent of females in various reproductive stages as a function of time of day. Upper panel: percent of females with only hydrated eggs and females with new post-ovulatory follicles. Samples of 18-20 females taken over a single night at the same locality in the Los Angeles Bight in April 1979. Lower panel: percent of females with only hydrated eggs, only new post-ovulatory follicles, and with both hydrated eggs and new post-ovulatory follicles (shaded area), as a function of time of day. Data are from surveys in the Los Angeles Bight (1978-79). Number of females in each hour class (upper dashed lines) ranged from 35-183.

from about 14% at sunset to 0 at 0100 hours. The occurrence of females with new post-ovulatory follicles increased sharply at 2100 hours and varied between 10-15% throughout the rest of the night (Figure 4, lower). These combined data reveal two additional patterns not resolved in smaller sample sizes: a reappearance of females with hydrated eggs around 0500-0600 hours and the occurrence of females with both hydrated eggs and new post-ovulatory follicles. The reappearance of females with hydrated eggs indicates that hydration for the next night of spawning began in the early morning. The process probably continued throughout the day, resulting in females being ready to spawn at sunset. This view is supported by the fact that our histological examination of hydrated ovaries collected between 0500-0600 hours indicated that they were in the early stages of hydration (characterized by the disappearance of the nuclear membrane, diffused nuclear elements lying in one pole of the eggs, and only partial fusion of yolk globules into the large plate-like bodies).

The best indicator of the time of spawning may be the occurrence of females with both hydrated eggs and new

post-ovulatory follicles, because these females were caught while spawning. Their low frequency in the collections indicates that spawning was completed rapidly, and the time of occurrence indicates that the period of maximum spawning occurred between 2100 and 0200 hours, with a peak between 2200 and 2300 hours (Figure 4, lower, shaded area).

On the basis of these results, nightly pattern of spawning in anchovy can be divided into three periods: early spawning period (1800 to 2100 hours), some spawning occurs but the ovaries of most reproductively active females are in the hydrated state; maximum spawning (2100-0200 hours), most females spawn (females with hydrated eggs decline to 0 and females with new post-ovulatory follicles reach the maximum number for the night); and post-spawning (0200-0600 hours), little or no spawning occurs and females destined to spawn the next night begin hydration.

DISCUSSION

This study provided the first quantitative estimate of the size threshold for sexual maturity in female northern anchovy. Clark and Phillips (1952) reported that only a few females mature at 90-100 mm SL, about 30% mature at 100-200 mm, and 50% at 130 mm, whereas Brewer (1978) and Hunter and Goldberg (1980) found significant numbers of mature females less than 90 mm. The present study provided functions from which the probability of maturity can be estimated for any length. The slope of maturity line changed somewhat over the spawning season, but the length at 50% probability of maturity remained the same.

Data collected on the occurrence of female anchovy with hydrated eggs and post-ovulatory follicles in the Los Angeles Bight were similar to those presented by Hunter and Goldberg (1980) for February 1978. The mean interval between spawnings was about 7 days in their study, and it ranged from 7-10 days during the peak spawning months in the present study. The larger number of observations in the present study, combined with past data of Hunter and Goldberg (1980) allowed us to calculate a weight function for batch fecundity and enabled us to describe in greater detail the temporal pattern of spawning behavior.

This paper has provided the reproductive data needed for biomass assessment using the model of Parker (1980). It also indicates needed refinements for future surveys and alternate sampling procedures. That the spawning frequency in Monterey Bay was distinctly different from that of the Los Angeles Bight emphasizes the importance of obtaining samples representative of the entire central subpopulation. Error terms need to be developed for spawning frequency estimates when sample sizes are highly variable. In addition to the incidence of day-old

post-ovulatory follicles, the incidence of females with new post-ovulatory follicles or hydrated eggs could be used as a measure of spawning frequency, if appropriate weights were developed for the time of sampling. If anchovy could be sampled during the day, it might be possible to use females with hydrated eggs alone as the measure of spawning frequency. This is an attractive alternative to use of post-ovulatory follicles because it would cost less, as histological examination would not be required.

ACKNOWLEDGMENTS

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THE RELATION BETWEEN THE DISTRIBUTION OF ZOOPLANKTON PREDATORS AND ANCHOVY LARVAE

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ABSTRACT

Monthly CalCOFI cruises of 1954, 1956, and 1958 were analyzed for abundance of populations of species of Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. Data were also noted on other abundant zooplankters in the samples (copepods, euphausiids, decapod larvae, pteropods, heteropods, polychætes, salps, doliolids, and pyrosomes). Information was grouped into three categories of abundance of anchovy larvae per standard haul (more than 241 anchovy larvae, from 1 to 240, and absence of larvae). In general, concentration of predators was inversely related to aggregations of anchovy larvae. Absence of anchovy larvae coincided with prochordates, decapod larvae, pteropods, heteropods, and polychætes, and abundance of anchovy larvae concurred with abundance of copepods and/or euphausiids. This habitat can be designated "anchovy water."

Gut content analysis indicated that predatory pressure on fish larvae was weaker when there was abundance of other food animals, e.g. copepods and euphausiids in the waters, as shown by the plankton collections.

RESUMEN

Las poblaciones de especies de Quetognatos, Sifonóforos, Condróforos, Medusas y Ctenóforos han sido analizadas en las colecciones de plancton obtenidas durante los cruceros mensuales de CalCOFI en 1954, 1956 y 1958. Conjuntamente se anotaron datos sobre la abundancia de otros zooplanctones presentes en esas muestras de plancton (Copépodos, Eufáusidos, larvas de Decápodos, Pterópodos, Heterópodos, Poliquetos, Salpas, Doliolos y Pirosomas). La información obtenida sobre la abundancia de las especies correspondientes, se ha agrupado en tres categorías, en relación con la cantidad de larvas de anchoa en cada arrastre (más de 241 larvas, desde 1 hasta 240, y ausencia de larvas). En general, la concentración de depredadores y larvas de anchoa aparecía en relación inversa. Se observó con frecuencia, que en las zonas de surgencia no aparecían larvas de anchoa. La ausencia de larvas de anchoa coincidía con la presencia de Procordados, larvas de Decápodos, Pterópodos, Heterópodos, y Poliquetos, y la abundancia de larvas de anchoa concurría con gran cantidad de Copépodos y Eufáusidos. Este hábitat podría denominarse "agua de anchoa."

Los análisis del contenido estomacal de los depreda-

dores y las correspondientes muestras de plancton han demostrado que cuando abundaban en el plancton copépodos y eufáusidos, los depredadores ingerían menos larvas de peces.

INTRODUCTION

Mortality of pelagic marine fish larvae can result from a variety of causes, both biotic and abiotic. Among the more important biotic causes are starvation, predation, parasites, and disease; among the abiotic causes are storms, currents, ultraviolet radiation, temperature, salinity, oxygen, and pollution. It was the consensus of participants in a Colloquium on Larval Fish Mortality Studies, held in La Jolla during January of 1975, "that the major causes of larval mortality are starvation and predation, and that these may interact" (Hunter 1976). It was noted in the report that most research emphasis had been placed on starvation and relatively little work existed on predation. Observations on predation of invertebrate plankton organisms on fish larvae appear in Lebour (1922, 1923, 1925), Bigelow (1926), Fraser (1969), Dekhnik et al. (1970), and others, as discussed in Alvariño (1976, 1977).

Several recent laboratory studies have dealt with invertebrate predation on newly hatched larvae of the northern anchovy: copepods as predators (Lillelund and Lasker 1971) or the euphausiid *Euphausia pacifica* in Theilacker and Lasker (1974). These predators are most effective on the relatively passive yolk-sac larvae of the anchovy and less so on actively swimming larger anchovy larvae. The principal planktonic predators on large anchovy appear to be Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. Predation by these zooplankters has been observed frequently by planktologists, who find fish larvae in various stages of digestion inside the guts of these predators. Despite such observations, no one has attempted a thorough analysis of such predation on fish larvae.

It is the purpose of this contribution to study the relation between occurrence and abundance of anchovy larvae (*Engraulis mordax*) to the other elements in the plankton, with emphasis on potential predators, and also to characterize the assemblages of plankters in relation to anchovy larva abundance. The monthly CalCOFI collections made off California and Baja California in 1954, 1956, and 1958 were selected for this study. These three

years were respectively, slightly colder, colder, and warmer than the long-term average for the California Current region. One reason for reanalyzing field collections of plankton rather than doing experimental studies in the laboratory on Chætognatha, Siphonophoræ, Chondrophopæ, Medusæ, and Ctenophora as predators is that these organisms are difficult subjects for experiments. They lack the capacity for food reserve storage, for example, hence must feed continuously to avoid starvation. The reason for limiting the study to anchovy larvae while ignoring occurrence and abundance of anchovy eggs is that the eggs are less exposed to predation by these predators, which respond primarily to movement.

METHODS

The plankton collections analyzed were from the monthly cruises of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) for 1954, 1956, and 1958. The area covered was the California Current region off California and Baja California, with usual coverage between San Francisco, off central California, to Cape San Lazaro, off southern Baja California (CalCOFI lines 60 to 137). The plankton was collected with a bridled net, 1 m in diameter at the mouth, about 5 m in length, constructed of heavy-duty bolting grit gauze of 50xxx mesh. The nets were equipped with flow meters to measure the volume of water strained during each tow. The hauls were made obliquely from about 140 m to the surface, depth of water permitting.

The total plankton sample was analyzed for the five groups of predators: Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. It should be pointed out that Ctenophora are often destroyed by preservation, hence the numbers recorded are underestimates of their true abundance in the collections. In all five groups, specimens present in each sample were identifed to species and counted by species. Only occasionally, when a species occurred in large numbers, were counts made on an aliquot of the total sample. Numbers of each species were standardized to the number in 1,000 m^3 of water strained. In addition, the size of each specimen in mm was recorded, together with stage of sexual maturity and/or stage of life cycle. Also, the number of specimens with food in the stomachs was noted, and partially digested organisms were identified. It is supposed that many of these predators fill their guts while in the plankton net, hence presumed newly ingested organisms were not considered. Table 5, which is not included in this report, but is available from the author upon request, detailed the assemblages of plankton at selected locations in the anchovy larvae realm, with absence of anchovy and highest concentration of anchovy larvae, for the monthly cruises of 1954, 1956, 1958. Also in this Table appear for each selected station the abundance of each of the species of

Chætognatha, Siphonophoræ, Medusæ, Ctenophora; the presence of copepods, euphausiids, pteropods, heteropods, decapoda larvae, polychætes, tunicates; and information on the volume of water strained per haul.

During the analysis of the collections of the three years, it was observed that approximately 36% of the chætognaths had food in their stomachs, and all specimens of the two largest species, *Sagitta hexaptera* and *S. scrippsae*, contained food in many collections. Some chætognath stomachs contained prey not present in the corresponding plankton samples.

Data also were taken on the relative abundance of the various constituent groups in each sample. The groups included, in addition to the five groups of predators discussed above, were copepods, euphausiids, decapod larvae, pteropods, heteropods, polychætes, salps, doliolids, and pyrosomes. The determinations were based on dominance of a group or groups in the collections analyzed.

Although initially it was proposed to analyze all samples taken during the three years, 1954, 1956, and 1968, this soon proved to be too large a task. Instead, emphasis was placed on the areas that contained anchovy larvae in some abundance, in order to determine areal and temporal coverages that would bear most directly on the problem of predator-anchovy interactions. The collections used in the following analyses were 849 for 1954, 316 for 1956, and 899 for 1958.

Anchovy abundance was divided into three categories on the basis of abundance in the tows: high, low, and zero. The standard haul values of anchovy larvae in the high category corresponded to 241 larvae or more per haul. The standard haul value is the estimated number of anchovy larvae under 10 m^2 of sea surface. The count of low abundance included all positive hauls with counts lower than 241 larvae per standard haul. Inasmuch as the average CalCOFI haul sampled to about 140 m depth, the actual volume of water involved under 10 m^2 of sea surface is approximately 1,400 m^3. Although the number of anchovy larvae is not ordinarily expressed as the number in 1,000 m^3 water strained, the unit of volume used for zooplankters would be about 10/14 that of anchovy larvae on the average, or approximately 172 larvae or more for the high category of anchovy larvae abundance.

KINDS AND ABUNDANCE OF PREDATORY SPECIES IN THE FIVE CATEGORIES BEING STUDIED

A list of the species encountered by category, number of individuals taken and number of positive hauls (occurrences) of each species by year, and information on size and depth distribution of each species is contained in Table 1. The information included in this table, such as the kinds and abundance of the species of chætognaths,

TABLE 1
Abundance of Predatory Species (Frequency, in Parentheses) with Information on Size and Depth Distribution.

Species	Total number (and frequency) 1954 (849 hauls)	1956 (316 hauls)	1958 (899 hauls)	~Maximum size (mm)	Nect.	cm complete animal	Depth distribution
Eukrohnia bathypelagic, Alvariño 1962 ...		34(1)		23			Upper 100 m during upwelling
E. hamata (Möbius) 1875		43(1)		43			Upper 100m during upwelling
Krohnitta pacifica (Aida) 1897	464(20)		943(40)	8			Upper 100 m
K. subtilis (Grassi) 1881	5402(144)	2186(29)	5735(242)	16			Upper 100 m to surface
Pterosagitta draco (Krohn) 1895	5189(175)	1761(43)	13531(350)	10			Upper 100 m to surface
Sagitta bedoti Beraneck 1895	528(5)		2797(12)	15			Upper 100 m to surface
S. bierii Alvariño 1961	785319(712)	235853(210)	481090(700)	17			Upper 100 m to surface
S. bipunctata Quoy and Gaimard 1827 ...	10870(244)	2969(43)	32665(384)	18.5			Upper 100 m to surface
S. decipiens Fowler 1905	3446(12)	3184(35)	1744(46)	16			Upper 100 m during upwelling
S. enflata Grassi 1881	366890(511)	43618(135)	831089(794)	25-30			Upper 100 m to surface
S. euneritica Alvariño 1961	2052102(616)	592934(284)	983727(485)	15.5			Upper 100 m to surface
S. hexaptera d'Orbigny 1834	10941(422)	2599(157)	14009(477)	40-60			Upper 100 m to surface
S. maxima (Conant) 1896		184(12)		>90			Upper 100 m during upwelling
S. minima Grassi 1881	250862(625)	44374(217)	300710(662)	10			Upper 100 m to surface
S. neglecta Aida 1897	606(12)		466(13)	8			Upper 100m to surface
S. pacifica Tokioka 1940	8664(84)	3137(26)	25187(256)	14			Upper 100 m to surface
S. pseudoserratodentata Tokioka 1936	40940(248)	6301(36)	92194(420)	10			Upper 100 m to surface
S. pulchra Doncaster 1903			23(1)	24			Upper 100 m to surface
S. regularis Aida 1897	1996(22)		5065(54)	6			Upper 100 m to surface
S. robusta Doncaster 1903	179(6)		1539(24)	12			Upper 100 m to surface
S. scrippsae Alvariño 1962	52289(443)	13903(169)	11192(169)	60			Upper 100 m to surface
S. zetesios Fowler 1905		24(1)		43			Upper 100 m during upwelling
Agalma okeni Eschscholtz 1825	25(5)	37(13)	58(18)		20	>100	Surface and depth
Nanomia cara Agassiz 1865		5(1)			>51	>100	Surface and depth
Stephanomia bijuga (Delle Chiaje) 1841 ...	552(59)	1157(101)	210(43)		15	>100	Surface and depth
Bargmannia elongata Totton 1954		82(5)	11(1)		30	>100	Surface and depth
Physophora hydrostatica Forskal 1775		56(15)	19(6)		8	12	Surface and depth
Erenna richardi Bedot 1904			3(1)		40	>100	Surface and depth
Epibula ritteriana Haeckel 1888	15(2)	3(1)				6	Surface
Rosacea cymbiformis 1841 Chiaje	6(2)	11(2)	3(1)		350	many	Surface and depth
R. plicata Quoy and Gaimard 1827	6(2)	12(2)			200	many	Surface and depth
Nectodroma dubia Quoy and Gaimard 1834	3(1)	88(4)	6(2)		85	many	Upper 100 m
N. reticulata Bigelow 1911		2(1)			55	many	Upper 100 m
Nectopyramis thetis Bigelow 1911			3(1)		40	many	Upper 100 m and depth
Lilyopsis rosea Chun			6(2)		120	many	Upper 100 m and depth
Amphicaryon acaule Chun 1888	6(2)	9(2)			>15	many	Upper 100 m and depth
A. ernesti Totton 1954	18(4)	9(1)	6(1)		>15	many	Upper 100 m and depth
Hippopodius hippopus Forskal 1776	3(1)	20(6)	18(6)		19	many	Surface and depth
Vogtia kuruae Alvariño 1967		3(1)			20	many	Surface and depth
V. spinosa Kefferstein and Ehlers 1861 ...		40(2)			20	many	Surface and depth
Chelophyes appendiculata Eschscholtz 1829	15819(145)	7079(160)	14628(154)		10	2	Upper 100 m to surface
C. contorta (Lens and Riemsdijk) 1908	83(3)	7(1)	2622(20)		7	14	Upper 100 m to surface
Dimophyes arctica Chun 1897		23(2)			13		Upper 100 m to surface
Diphyes bojani (Eschscholtz) 1829		12(3)	562(150)		15	3	Upper 100 m to surface
D. dispar Chamisso and Eysenhardt 1821	19802(89)	614(9)	150(6)		20	4	Upper 100 m to surface
Diphyopsis mitra Huxley 1859	79(3)	105(5)	2243(22)		10	2	Upper 100 m to surface
Muggiaea atlantica Cunningham 1892	25117(123)	29565(165)	11495(95)		7		Surface
Eudoxia macra Totton 1954	916(8)	366(12)	808(12)		4		Surface
Eudoxoides spiralis Bigelow 1911	1008(15)	617(12)	16690(64)		7		Upper 100 m to surface
Sphaeronectes sp.	29(2)	135(6)	155(8)		8		Upper 100 m to surface
Lensia campanella Moser 1925			279(4)		6	1	Upper 100 m to surface
L. challengeri Totton 1954	14366(69)	17862(99)	7236(77)		9	1.7	Upper 100 m to surface
L. conoidea Kefferstein and Ehlers 1861	53(3)	495(30)	267(12)		20	4	Upper 100 m and depth
L. grimaldii Leloup 1933		4(1)			7	1.3	Upper 100 m
L. hotspur Totton 1954	1273(11)	855(35)	1711(31)		5	0.9	Upper 100 m to surface
L. meteori Leloup 1934			14(1)		5		Upper 100 m
L. multicristata Moser 1925	61(4)	730(36)	498(23)		17	3.5	Upper 100 m and depth
L. subtilis Chun 1886			115(3)		12	2.2	Surface
L. subtiloides (Lens and Van Riemsdijk) 1908			31(2)		5	1	Surface
Chuniphyes multidentata Lens and van Riemsdijk 1908	2(1)	4(1)	37(2)		40	7.6	Upper 100 m and depth
Sulculeolaria biloba Sars 1846		12(2)	29(2)		20	4	Surface and depth
S. chuni Lens and van Riemsdijk 1908	34(1)	3(1)	113(4)		8	1.5	Upper 100 m

TABLE 1 (CONTINUED)
Abundance of Predatory Species (Frequency, in Parentheses) with Information on Size and Depth Distribution.[1]

| Species | Total number (and frequency) | | | ~ Maximum size | | | Depth distribution |
	1954 (849 hauls)	1956 (316 hauls)	1958 (899 hauls)	(mm)	Nect.	cm complete animal	
S. monoica Chun 1888	94(1)	45(6)	94(7)		10	2	Surface and depth
S. quadrivalvis Blainville 1834	86(4)	65(7)	796(29)		20	3.7	Upper 100 m to surface
Abyla bicarinata Moser 1925		6(2)			10	2	Upper 100 m
A. brownia Sears 1953		41(2)					Upper 100 m to surface
A. haeckeli Lens and van Riemsdijk 1908		9(2)	53(7)		9	1.8	Upper 100 m to surface
Abylopsis eschscholtzi Huxley 1859			26(3)		8	1.3	Upper 100 m to surface
A. tetragona Otto 1823	165(3)	3(1)	3(1)		20	4.3	Upper 100 m to surface
Bassia bassensis Quoy and Gaimard 1834		92(2)	88(2)		7	1.3	Upper 100 m to surface
Velella velella Linne 1758		4(2)				10.4	Surface
				μm (height ×width)			
Euphysora furcata Kramp 1948	6(1)		13(3)	8×6.5			Surface
Annatiara affinis (Hartlaub) 1913		3(1)		23			Upper 100 m during upwelling
Leuckartiara octona (Fleming) 1823			82(4)	20			Upper 100 m to surface
L. zacae Bigelow 1940	840(32)	326(36)	806(22)	21×18			Upper 100 m to surface
Octotiara russelli Kramp 1953		3(1)		7			Surface
Bythotiara murrayi Gunther 1903		3(1)		20			Upper 100 m during upwelling
Calycopsis nematophora Bigelow 1913		2(1)		30			Upper 100 m to surface
C. simulans (Bigelow) 1903			52(1)	30×22			Upper 100 m to surface
Sibogita geometrica Maas 1905	7(1)			38×20			Upper 100 m
Melicertum georgicum Agassiz 1862			7300(1)	20			Upper 100 m to surface
Mitrocoma discoidea Torrey 1909	10(1)			45			Surface
Obelia spp.	6(1)	147(3)		6			Upper 100 m to surface
Phialidium gregarium (L. Agassiz) 1862	97(2)			12			Surface
Eirene hexanemalis (Goette) 1886			3(1)	18			Surface
Phialopsis diegensis Torrey 1909	655(13)	78(12)	153(8)	10×30			Upper 100 m
Gossea brachymera Bigelow 1909			21(3)	20			Surface
Liriope tetraphylla (Chamisso and Eysenhardt) 1821	39853(119)	16035(148)	21548(99)	30			Upper 100 m to surface
Aglaura hemistoma Péron and Lesueur 1809	3892(14)	3157(11)	33144(58)	6×4			Upper 100 m to surface
Colobonema sericeum Vanhoffen 1902			11(1)	45×35			Upper 100 m and deep waters
Rhopalonema velatum Gegenbaur 1856	5709(57)	2883(60)	9913(78)	10			Upper 100 m to surface
Aegina citrea Eschscholtz 1829	134(50)	1032(17)	82(9)	50			Surface and deep water
Aeginura beebei Bigelow 1940			3(1)	18×100			Upper 100 m
A. grimaldii Maas 1904	186(5)	329(9)	225(9)	45			Upper 100 m and deep water
Solmundella bitentaculata (Quoy and (Gaimard) 1822		240(4)	9(1)	12			Upper 100 m to surface
Pegantha clara R.P. Bigelow 1909		14(2)	6(1)	25×55			Upper 100 m
P. laevis H.B. Bigelow 1909		3(1)		40			Upper 100 m
Solmaris corona (Keferstein and Ehlers)1861	8(2)	108(8)		>15			Upper 100 m and surface
S. rhodoloma (Brandt) 1838	13800(1)			7			Surface
Cunina globosa Eschscholtz 1829		6(1)		18			Surface
C. tenella (Bigelow) 1909		3(1)		7			Surface
Atolla wyvillei Haeckel 1880			6(2)	150			Upper 100 m during upwelling
Atorella vanhoeffeni Bigelow 1909		7(2)		7			Upper 100 m during upwelling
Periphylla periphylla (Péron and Lesueur) 1809	3(1)		4(1)	200			Upper 100 m during upwelling
Pelagia colorata Russell 1964		2(1)		450			Surface
Bolinopsis sp.		10(2)	116(1)	122			Surface
Pleurobrachia sp.	182(2)	765(2)	121(1)	30, tentacles 20 times longer			Surface
Mertensia ovuum (Fabricius) 1780		3(1)		55, tentacles 5 times longer			Surface
Beroe sp.	1397(55)	443(44)	632(29)	>90			Surface

[1] Size and depth distribution from Alvariño unpublished and published information.

siphonophores, chondrophores, medusæ, and ctenophores in the California Current is not available elsewhere.

Chaetognatha

Altogether 22 species of Chætognatha were observed in the collections analyzed. Not all of the species were taken in a given year; rather, 17 species were found in 1954 collections, 16 in 1956, and 18 in 1958. Only 12 species were taken in all three years. The species occurring in greatest abundance were *Sagitta euneritica* (maximum size 15.5 mm), *S. bierii* (maximum size 17 mm), and *S. enflata* (maximum size 25-30 mm). Of these, *S. enflata* is the most voracious predator of fish larvae. The size of chætognaths obtained ranged from 6 to more than

90 mm in length. The predatory potential of an individual chætognath is roughly proportional to its size; the predatory potential of the species is related to both size and abundance.

Siphonophorae

During the three years, 48 species of siphonophores were observed, with the largest complement of species; 40 taken in 1956, 37 in 1958, and only 26 in 1954. Specimens of siphonophores ranged in size from 5 mm total length for nectophores of some species of Diphyidæ in the polygastric phase, to several meters in total length in various species of Agalmidæ and related families. Undoubtedly, the siphonophores in the family Agalmidæ are among the most successful predators inasmuch as they can move swiftly through the waters and can act as living nets in capturing other plankters. The only commonly occurring agalmid in CalCOFI collections was *Stephanomia bijuga*; this could be one of the primary predators on fish larvae. Several siphonophores in the family Diphyidæ are common to abundant, including *Chelophyes appendiculata, Muggiaea atlantica, Lensia challengeri, L. hotspur,* and *Diphyes dispar.* The latter species was commonly taken only in 1954; among diphyid siphonophores it is a relatively large species, consequently it has the potential to be an effective predator on fish larvae. *M. atlantica,* the most abundant diphyid, particularly in inshore waters, is a small species that would be an effective predator only on small anchovy larvae. *C. appendiculata,* also among the most common diphyid siphonophores, is large, hence perhaps a more effective predator on fish larvae.

Chondrophorae

Only a single species was observed, *Velella velella,* and this only in two hauls made in 1956.

Medusae

The total number of species of Medusæ taken during the three years was 34, with 15 species in 1954, 20 in 1956, and 19 in 1958. The distribution of Medusæ is more erratic than that of Chætognatha or Siphonophoræ. Only seven species were common to the three years; of these the most abundant species, both with regard to abundance and to frequency of occurrence, were *Liriope tetraphylla* and *Rhopalonema velatum.*

Ctenophora

Ctenophores except *Beroë* sp. were infrequently taken. Although there were 128 occurrences of *Beroë* sp. recorded during the three years, there were only five occurrences of *Pleurobrachia* sp., three of *Bolinopsis* sp., and one of *Mertensia ovum.* Even so, the number of specimens of *Pleurobrachia* or *Bolinopsis* in the samples in which they did occur could be quite large (i.e. over 100 individuals per sample). Most ctenophores occur at or

near the surface; hence, their predation would be limited to this zone. *Beroë* is known to feed on other Ctenophora, but the other ctenphores are known to be voracious predators on zooplankton including fish larvae (Chun 1880; Kamshilov 1960; Kamshilov et al. 1958; Horridge 1965; Lebour 1922, 1923; Mayer 1912; Miller 1974; Swanberg 1974). As mentioned earlier, Ctenophora tend to fragment and disintegrate on preservation and could easily be overlooked.

ABUNDANCE OF THREE GROUPS OF PREDATORS IN RELATION TO ABUNDANCE OF ANCHOVY LARVAE

Variations in the composition of species of all groups were observed in all years. Tropical species were taken in 1958, the year with warmer than average temperatures. The highest variability occurred in the Medusæ, which show erratic distribution both in time and space.

Information on the abundance of Chætognatha, Siphonophoræ, and Medusæ is summarized for 3-month intervals for the three years, 1954, 1956, and 1958, in Table 2. Yearly abundance values are summarized in Table 3 and illustrated in Figure 1.

Monthly average abundance of plankton predators are compared to the monthly percentage concentration of anchovy larvae (from Ahlstrom 1967) for all three years in Figure 2.

Chaetognatha

Little or no relation appeared between abundance of anchovy larvae and abundance of chætognaths. This applies both for abundance of total chætognaths versus anchovy larvae and for *Sagitta enflata,* a common species known to be a prime predator on fish larvae. The only prime predator species to show an inverse abundance relation with anchovy larvae, i.e. fewer present when anchovy larvae were abundant, was *Sagitta hexaptera.* However, it should be noted that the two most abundant chætognaths, *S. euneritica* and *S. bierii* are not considered important predators on fish larvae, because of their size, and the abundance is mainly made up of young specimens, too small to feed on anchovy larvae.

Siphonophorae

During two of the three years, 1954 and 1958, lowest abundance of siphonophores occurred in hauls with high abundance (> 241/haul) of anchovy larvae. The inverse relation was most marked in the warmest year, 1958, when only 12 siphonophores/1,000 m³ on the average were taken in hauls with anchovy larvae counts exceeding 241 larvae/standard haul, 33 siphonophores/haul on the average for low abundance of anchovy larvae (1 to 241/standard haul), and 101 siphonophores in hauls with 0 anchovy larvae.

However, in 1956, siphonophores were more abun-

TABLE 2

Part I. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with High Number of Anchovy Larvae
(i.e. > 241 Larvae per Standard Haul) in 1954, 1956, 1958.

Cruises	Predators Number hauls	Chaetognatha Number species	Chaetognatha Total count	Chaetognatha Average count	Siphonophorae Number species	Siphonophorae Total count	Siphonophorae Average count	Medusae Number species	Medusae Total count	Medusae Average count	Average all categories
5401-5403	41	12	139,906	3,412	8	2,024	49	3	175	4	3,465
5404-5406	22	11	116,767	5,308	4	319	14	3	56	3	5,378
5407	3	4	24,304	8,101	2	28	9	3	153	51	8,161
5412	3	5	12,522	4,174	1	25	8	0	0	0	4,182
Yearly total	69	13	293,499	4,254	9	2,396	35	4	384	6	4,295
5601-5603	15	12	35,869	2,391	11	2,093	140	5	930	62	2,593
5604-5606	18	7	66,909	3,717	8	5,042	280	4	872	48	4,045
5607-5608	8	7	15,228	1,904	4	1,741	218	1	1,035	129	2,251
5610-5612	–	–			–			–			–
Yearly total	41	12	118,006	2,878	15	8,876	216	6	2,837	69	3,163
5801-5803	53	15	149,975	2,830	8	652	12	7	151	3	2,845
5804-5806	48	13	409,398	8,529	8	536	11	4	103	2	8,542
5807	4	7	35,522	8,888	2	31	8	0	0	0	8,896
5810-5812	–	–			–			–			–
Yearly total	105	16	594,895	5,666	12	1,219	12	9	254	2	5,680

Part 2. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with Low Concentration of Anchovy Larvae
(i.e. 1 to 241 Specimens per Standard Haul) in 1954, 1956, 1958.

Cruises	Predators Number hauls	Chaetognatha Number species	Chaetognatha Total count	Chaetognatha Average count	Siphonophorae Number species	Siphonophorae Total count	Siphonophorae Average count	Medusae Number species	Medusae Total count	Medusae Average count	Average all categories
5401-5403	91	14	206,977	2,274	10	14,525	159	4	986	10	2,443
5404-5406	135	14	741,944	5,495	16	18,025	133	8	11,622	86	5,714
5407-5409	74	13	745,777	10,078	8	3,508	47	8	4,761	64	10,189
5410-5412	34	13	110,430	3,259	8	1,693	49	5	2,721	80	3,388
Yearly total	334	16	1,805,128	5,405	23	37,751	113	12	20,090	60	5,578
5601-5603	57	14	253,326	4,444	17	8,321	146	9	1,482	26	4,616
5604-5606	39	9	115,795	2,969	10	6,381	163	5	3,220	82	3,214
5607-5608	20	12	60,705	3,035	12	6,642	332	6	2,128	106	3,475
5610-5612	10	10	25,121	2,512	10	1,664	166	2	968	96	2,774
Yearly total	126	14	454,947	3,611	24	23,008	183	11	7,798	62	3,856
5801-5803	116	13	474,664	4,091	20	3,883	33	8	1,755	15	4,139
5804-5806	143	16	682,198	4,770	17	5,390	37	8	2,774	19	4,826
5807	26	10	126,351	4,859	6	214	8	2	634	24	4,891
5810-5812	13	15	33,753	2,596	3	312	24	3	303	23	2,643
Yearly totaL	298	17	1,316,966	4,419	25	9,799	33	11	5,466	18	4,470

Part 3. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with Absence of Anchovy Larvae in 1954, 1956, 1958.

Cruises	Predators Number hauls	Chaetognatha Number species	Chaetognatha Total count	Chaetognatha Average count	Siphonophorae Number species	Siphonophorae Total count	Siphonophorae Average count	Medusae Number species	Medusae Total count	Medusae Average count	Average all categories
5401-5403	94	17	238,679	2,539	13	9,075	97	4	2,490	26	2,662
5404-5406	210	15	592,525	2,822	16	17,253	82	6	19,512	93	2,997
5407-5408	75	13	449,014	5,986	9	6,760	90	7	5,076	68	6,144
5410-5412	67	16	217,842	3,251	10	6,386	95	6	17,654	263	3,609
Yearly total	446	17	1,498,060	3,359	21	39,474	89	10	44,732	100	3,548
5601-5603	46	12	113,954	2,477	28	5,606	122	8	5,389	117	2,716
5604-5606	44	14	75,215	1,709	20	11,939	271	11	4,570	104	2,084
5607-5609	26	13	131,240	5,048	15	9,049	348	9	1,632	63	5,459
5610-5612	33	13	59,742	1,810	18	1,805	55	9	2,155	65	1,930
Yearly total	149	15	380,151	2,551	37	28,399	191	17	13,746	92	2,834
5801-5803	129	18	241,677	1,873	22	11,374	88	10	4,186	32	1,993
5804-5806	211	16	436,361	2,068	29	30,844	146	11	42,592	201	2,415
5807	55	12	80,724	1,467	15	3,734	67	5	8,899	161	1,695
5810	101	16	133,053	1,317	12	4,116	40	4	11,984	118	1,475
Yearly total	496	18	891,815	1,798	32	50,068	101	14	67,661	136	2,035

dant in all types of hauls than in the other two years and were equally abundant in hauls with > 241 anchovy, < 241 anchovy larvae, and 0 anchovy larvae.

One of the siphonophores that is probably an effective predator on fish larvae is the diphyid *Chelophyes appendiculata*. This species had a striking inverse relation to abundance of anchovy in all three years. Another diphyid species, *Diphyes dispar*, was commonly taken only in

TABLE 3

Yearly Abundance of Chaetognatha, Siphonophorae, and Medusae in the Three Categories of Anchovy Hauls: High, Low, and Zero Abundance.

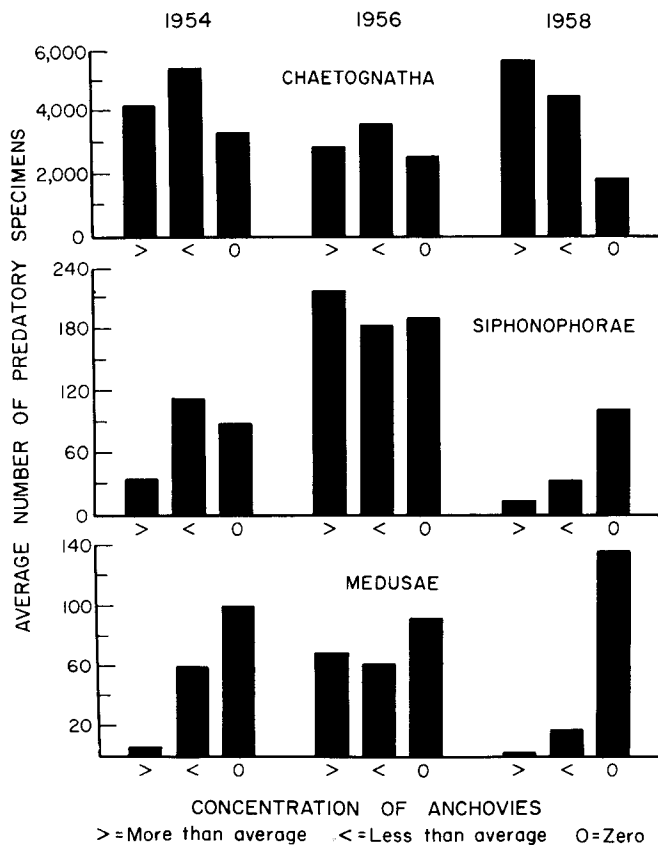| Anchovy abundance | Number hauls | Chaetognatha | | | | Siphonophorae | | | | Medusae | | | | Average count 3 plankters |
		Number species	Total specimens	Average count/haul		Number species	Total specimens	Average count/haul		Number species	Total specimens	Average count/haul		
1954														
High, > 241	69	13	293,499	4,254		9	2,396	35		4	384	6		4,295
Low, < 241	334	16	1,805,128	5,405		23	37,751	113		12	20,090	60		5,578
Zero anchovy	446	17	1,498,060	3,359		21	39,474	89		10	44,732	100		3,548
1956														
High, >241	41	12	118,006	2,878		15	8,876	216		6	2,837	69		3,163
Low, < 241	126	14	454,947	3,611		24	23,008	183		11	7,798	62		3,856
Zero anchovy	149	15	380,151	2,551		37	28,399	191		17	13,746	92		2,834
1958														
High, > 241	105	16	594,895	5,666		12	1,219	12		9	254	2		5,680
Low, < 241	298	17	1,316,966	4,419		25	9,799	33		11	5,463	18		4,470
Zero Anchovy	496	18	891,815	1,798		32	50,068	101		14	67,661	136		2,035

Figure 1. Yearly abundance of predators (Chaetognatha, Siphonophorae, Medusae) and concentration of anchovy larvae (high = more than 241 larvae per standard haul, low = less than 241 anchovy larvae per standard haul, zero = absence of anchovy larvae).

1954; in fact, 96.3% of the total specimens of this species were obtained during this year, 3% in 1956, and less than 1% in 1958. In the 1954 collections, there was also a marked inverse relation between abundance of this species and of anchovy larvae. The agalmid, *Stephanomia bijuga*, was the only one in this family taken in any abundance; it was least common in hauls containing high counts of anchovy larvae.

Medusae

During 1954 and 1958, abundance of medusæ showed a striking inverse relation with abundance of anchovy larvae. However, as also shown above for siphonophores, this relation breaks down in 1956. In this year, one species of medusæ, *Liriope tetraphylla*, contributed 85% of the specimens of medusæ in hauls with high anchovy counts, 74% in hauls with low anchovy counts, and 67% in zero count hauls. This is a moderately large species attaining a width across the umbrella of 30 mm, hence undoubtedly an effective predator on fish larvae.

RELATION OF UPWELLING AND ANCHOVY LARVAE

Sagitta decipiens has been used as an indicator of upwelling (Alvariño 1965; Nair 1977; Nair and Rao 1973; and others). During the three years studied, *S. decipiens* was taken in 93 of 2064 hauls, or in 4.5% of the hauls. During 1954 it was taken in only 12 hauls, or in 1.4%; in 1956 it was taken in 35 hauls or in 11.1% of the hauls; in 1958 it was taken in 46 hauls or in 5.1% of the hauls.
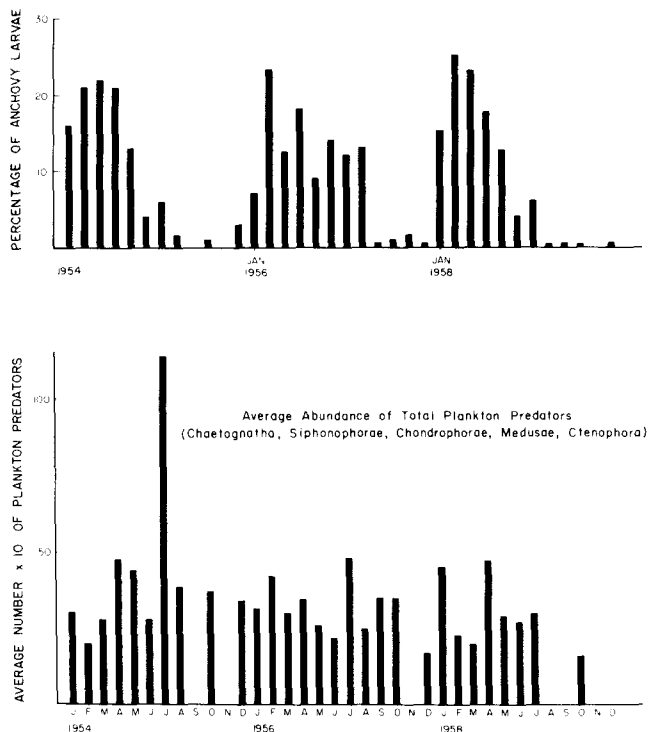
Figure 2. Monthly average of abundance of plankton predators, compared with Ahlstrom (1967) monthly percentages of anchovy larvæ for 1954, 1956, and 1958.

Hence, based on *S. decipiens* as an indicator of up-welling, this phenomenon was most intense in 1956, intermediate in 1958, and low in 1954, which agrees with Bakun (1973) and Wyllie (1966). Occurrences are probably preferable to actual counts of specimens because of the influence on counts of few large hauls. In fact, 36.2% of the total specimens taken in all three years were obtained at a single station in April of 1954. This may have been an indication of intense upwelling at that station, but it certainly biases results based on counts. Based on numbers taken, the average abundance per haul was 10.0 in 1956, 4.1 in 1954, and 1.9 in 1958. However, for stations other than that in 5404, the average count per haul was 0.5 specimens for 1954.

Sagitta decipiens occurred in 2.8% of the hauls with large concentrations of anchovy larvae, in 4.35 % of the hauls with low counts of anchovy larvae, and in 4.95% of the hauls with zero anchovy abundance. This could be interpreted as an indication that large concentrations of anchovy larvae occur infrequently in upwelling areas.

Based on occurrence by quarters (seasons) of the year, there were 3.6% positive hauls in winter, 4.5% in spring, 4.1% in summer, and 6.1% in the fall. Occurrences in 1956 contributed substantially to the fall total, inasmuch as 11 of 43 hauls taken in these months in 1956 contained *Sagitta decipiens* (i.e. it occurred in over 25% of the hauls). This appears to be the period of most widespread

upwelling encountered during the three years. During 1958, upwelling as indicated by the occurrences of *S. decipiens* was most widespread during the spring months.

RELATION OF PLANKTON ASSEMBLAGES TO ANCHOVY LARVAE

To obtain information on the plankton assemblages associated with high and zero abundance of anchovy larvae, several stations with high and zero abundances of anchovy larvae were selected from each monthly cruise within the main anchovy spawning areas. The number of stations thus chosen from 1954 survey cruises was 27 with high anchovy abundance and 33 with zero anchovy abundance; for 1956 the number of corresponding stations was 30 and 36, and for 1958, it was 19 and 33.

During 1954, 14 of the 27 stations with high concentrations of anchovy larvae were dominated by copepods, 11 by copepods and euphausiids, and 2 by euphausiids and pteropods. In contrast, 17 of the 33 stations with zero abundance of anchovy larvae contained predominantly salps; 4 stations were dominated by salps and doliolids; 4 others were mostly decapod larvae; 1 each were dominated by pteropods, by heteropods, by polychætes, by euphausiids, and by euphausiids and decapods; and the other 3 had a mixture of constituent organisms.

During 1956, 22 of the 30 collections from stations with high abundance of anchovy larvae were dominated by copepods, 5 by copepods and euphausiids, 2 by euphausiids, and 1 by copepods, euphausiids, and pteropods. The selected stations from 1956 that lacked anchovy larvae had 23 of 36 composed mostly by pyrosomes; 1 had a mixture of pyrosomes and salps; 3 contained mainly salps; 4 were dominated by megalopa larvae; 2 included mostly pyrosomes and the euphausiid *Euphausia pacifica*, and 1 had salps with *E. pacifica*; and 2 had a mixture of constituents. Pyrosomes were markedly more abundant in 1956 than in the other two years.

During 1958, 16 of the 19 collections from stations with high counts of anchovy larvae were dominated by copepods, and 1 each with copepods and euphausiids, with copepods and pteropods, and with a mixture of constituents. The dominant constituents of the 33 stations that lacked anchovy larvae were salps in 16, megalopa larvae in 2, doliolids in 1, doliolids and salps in 1, pteropods in 1, copepods in 1, and a miscellaneous array of constituents without a dominant group in 11.

The dominant plankton constituents in hauls with large concentrations of anchovy larvae were markedly different from the constituents in hauls with zero anchovy larvae (Figure 3). In the former, the dominant constituents in most hauls were copepods, followed by euphausiids alone or copepods and euphausiids, and less frequently with pteropods together with euphausiids and/or copepods.

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Areas in which these constituents dominate could be called "anchovy water." Hauls from areas lacking anchovy had only an occasional sample with copepods or euphausiids as the dominant constituent, and the majority of the samples were dominated by jelly-like organisms, by salps, or salps and doliolids in 1954 and 1958 and by pyrosomes in 1956. In "anchovy water," the organisms needed for food for anchovy larvae, particularly copepods, were abundant. In areas lacking anchovy larvae, organisms needed for food by anchovy larvae were scarce.

Most Abundant Large Predators and High and Zero Concentration of Anchovy Larvae

Invertebrate predators in the three main groups (Chætognatha, Siphonophoræ, and Medusæ) were present in many of the hauls containing large numbers of anchovy larvae, as well as in the hauls lacking anchovy larvae during these three years, 1954, 1956, and 1958. In fact, two species, the chætognath, *Sagitta euneritica*, and the siphonophore, *Muggiaea atlantica*, occurred in larger numbers in anchovy-rich hauls than in hauls lacking anchovy larvae. Both species are small in size. Abundance of *S. euneritica* is usually contributed by young specimens, not observed to prey on anchovy larvae.

The species considered to have the highest potential as predators because of size and abundance are the chætognaths, *Sagitta enflata*, *S. hexaptera*, and *S. scrippsae*; the siphonophores, *Stephanomia bijuga, Chelophyes appendiculata*, and *Diphyes dispar*; and the medusæ *Liriope tetraphylla, Rhopalonema velatum*, and *Aglaura hemistoma*, (Table 4). These species are present in fewer of the anchovy-rich hauls in all instances and occur in lesser abundance in most comparisons (i.e. 18 out of 21).

The species showing the greatest difference between anchovy-rich and anchovy-lacking stations are *Sagitta hexaptera, Chelophyes appendiculata, Rhopalonema velatum,* and *Aglaura hemistoma. S. hexaptera* occurred

twice as often in hauls lacking anchovy larvae as in anchovy-rich hauls, and for the other three species the disproportion between occurrences and numbers in anchovy-lacking versus anchovy-rich hauls is even more marked. The siphonophore, *Stephanomia bijuga*, also occurred most frequently and in large numbers in hauls lacking anchovy rather than in anchovy-rich hauls in all three years.

Although the medusa, *Liriope tertaphylla*, and markedly more abundant in hauls lacking anchovy larvae in 1954 and 1958 than in anchovy-rich hauls, it was present in about the same percentage of hauls of the two categories in 1956 and was more abundant on the average in anchovy-rich hauls during that year. As noted previously, the siphonophore *Diphyes dispar* was commonly taken during 1954, when it occurred more frequently and in larger numbers in collections lacking anchovy larvae. The other two chætognaths were taken in greater abundance in anchovy-rich hauls than in hauls lacking anchovy larvae in one of the three years, in 1956 for *Sagitta enflata* and in 1954 of *S. scrippsae*, but even for these the frequency of occurrences was higher in hauls lacking anchovy larvae in all three years.

SUMMARY

In summary, the numbers and kinds of plankton carnivores, potential predators on fish larvae, have been studied for five groups, Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora, for three CalCOFI years, 1954, 1956, and 1958. Altogether, 22 species of Chætognatha, 48 species of Siphonophoræ, 1 Chondrophoræ, 34 Medusæ, and 5 Ctenophora were recorded. For each of these species, abundance and number of occurrences are given in Table 1 for each of the years.

Collections studied could be grouped into three categories with respect to anchovy larvae: anchovy rich (more than 241 larvae per standard haul), anchovy poor (1 to

TABLE 4
Most Abundant Large Species of Predators Occurring with the Highest and with Zero Concentrations of Anchovy Larvae.

Anchovy larvae abundance	1954				1956				1958			
	High		Zero		High		Zero		High		Zero	
Sps. abundance Species	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.
Sagitta enflata	56	491.3	73	1,093.7	43	191.8	47	121.6	74	271.6	82	308.4
S. hexaptera	22	5.5	55	16.1	27	1.8	53	62.0	26	15.5	52	42.2
S. scrippsae	33	48.1	52	19.2	20	3.2	33	17.4	16	6.5	27	9.9
Stephanomia bijuga	7	0.2	27	0.8	13	1.2	22	2.0	11	0.2	27	1.8
Chelophyes appendiculata	33	10.0	76	89.3	17	5.0	47	7.6	32	2.6	67	46.2
Diphyes dispar	22	14.7	48	44.1	0	0	0	0	0	0	3	0.4
Liriope tetraphylla	22	20.9	64	253.6	37	96.5	42	41.8	21	6.8	58	89.4
Rhopalonema velatum	7	0.6	46	30.3	7	0.3	28	4.1	5	0.3	33	18.2
Aglaura hemistoma	0	0	12	40.2	0	0	3	1.1	5	0.2	18	51.7

[1]Average from all localities occupied, including those where species were present and absent.

240 larvae per standard haul), and anchovy lacking (zero anchovy larvae per standard haul). An inverse relation between abundance of anchovy larvae and abundance of predators was found for most siphonophores and medusæ, but the relation numerically is less well defined for chætognaths.

An unanticipated finding was that anchovy larvae occur in abundance primarily in hauls dominated by Copepoda and/or Euphausiidæ and never in hauls dominated by pelagic prochordates (salps or pyrosomes). The habitat of

1954

the former association can be characterized as "anchovy water."

In the introduction it was pointed out that the major causes of larval mortality are starvation and predation and that these may interact. This investigation, which studied the distribution and abundance of predatory and other planktonic organisms in relation to abundance of anchovy larvae, helps to confirm that statement.

One of the characteristics of "anchovy water" is the presence of potential food for anchovy larvae in some abundance. Another characteristic is that potential predators among chætognaths, siphonophores, and medusæ occur usually in lesser abundance than in hauls lacking anchovy larvae. In anchovy waters these potential predators have a greater range of prey to feed upon and, as evidenced by gut contents, prey primarily on copepods.

The best way to reduce mortality from starvation is for the anchovy larvae to be in waters with an adequate food supply. The best way to reduce mortality from predation is for anchovy larvae to be in waters where potential predators are in reduced abundance. This favorable combination of factors has been shown for "anchovy water."

ACKNOWLEDGMENTS

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1956

1958
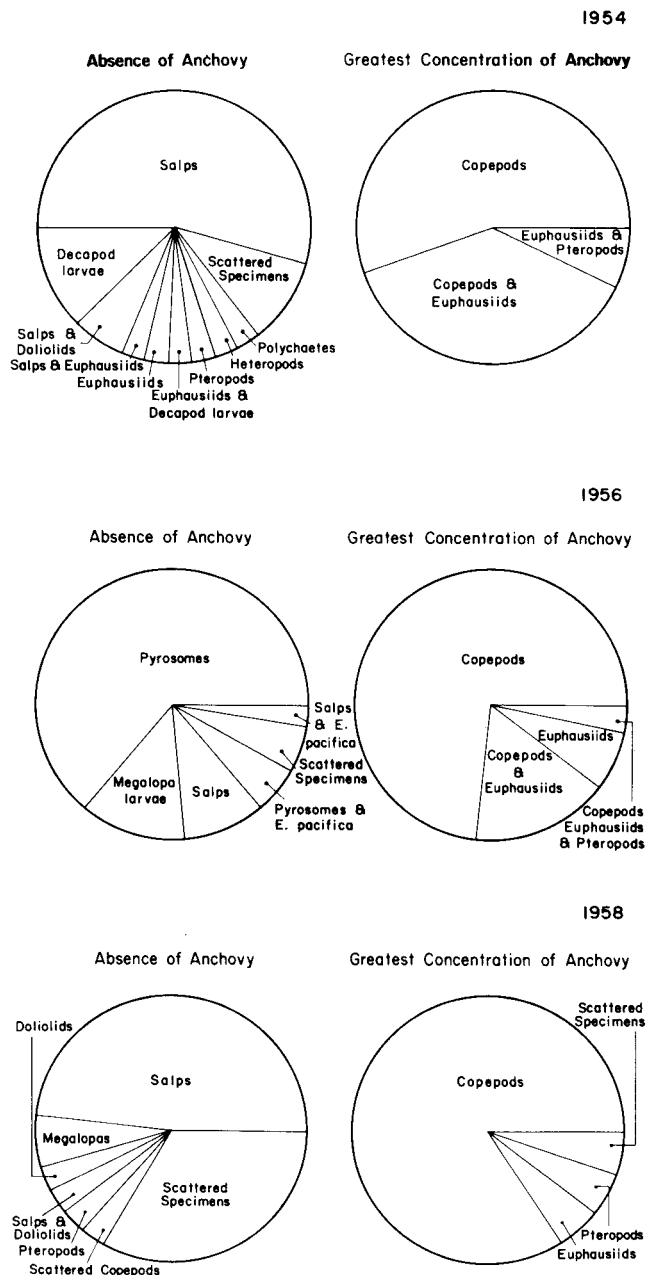
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FOOD AND FEEDING OF PACIFIC HAKE LARVAE, *MERLUCCIUS PRODUCTUS*, OFF SOUTHERN CALIFORNIA AND NORTHERN BAJA CALIFORNIA

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ABSTRACT

The diet of larval Pacific hake, *Merluccius productus*, consisted primarily of copepod eggs and calanoid copepod adults, copepodites, and nauplii, based on an examination of material collected in March 1975 off southern California and northern Baja California. In spite of a large mouth, Pacific hake larvae ingested a broad size range of prey, with a concentration of food particles 70-200 μm in width. First-feeding Pacific hake larvae fed upon a wide range of prey (50 to about 400 μm prey width), and the range in prey sizes changed little with larval length from 3.0-10.7 mm. Although copepod eggs, nauplii, and copepodites were a significant portion of the diet in numbers of prey, adult copepods contributed about 74% of prey volume.

Observations of feeding incidence in relation to time of capture revealed a slow rate of gut evacuation. Larvae began feeding at about 1000 hours, and the number of prey items found in the gut increased during the day, reached a maximum after sunset, and thereafter decreased gradually. The comparatively large mouth, slow evacuation rate, and ability to feed on copepod stages from egg to adult seem to form an adaptive strategy for success in the relatively deep and cold strata inhabited by Pacific hake larvae.

RESUMEN

El examen del material colectado en marzo de 1975 en las costas del sur de California y del norte de Baja California indicaría que la dieta de las larvas de merluza del Pacífico, *Merluccius productus*, consiste principalmente de huevecillos de copépodos y adultos copépodos calanoides, copepoditos, y nauplios. Las larvas de merluza del Pacífico, a pesar de tener una boca muy grande, ingirieron presas de muy variados tamaños, con una concentración de partículas de comida que alcanzaba de 70-200μm de anchura. Las larvas de merluza del Pacífico se alimentaban primero de una amplia calidad de presas (de 50 a 400μm anchura de presa), y la amplitud de tamaños de presas cambió poco con las larvas de longitudes de entre 3.0 a 10.7 mm. Aunque los huevecillos de copépodos, nauplios, y copepoditos formaron una parte significativa de la dieta en cuanto a su frecuencia como presa, los copépodos adultos formaron aproximadamente 74% del volumen de la presa.

Observaciones sobre las incidencias del alimento en relación con el tiempo de captura presentaron una pro-

porción muy baja de evacuaciones intestinales. Las larvas empezaron a comer alrededor de las 1000 horas, y el número de presas encontradas en el intestino aumentó durante el día, alcanzando un máximo después de la puesta del sol, y disminuyendo después gradualmente. La boca comparativamente grande, una baja proporción de evacuaciones, y la habilidad de alimentarse de todas las fases de desarrollo de los copépodos, desde huevecillo hasta adulto, forman conjuntamente una estrategia de adaptación perfecta al complejo faunístico de los estratos relativamente profundos y fríos habitados por las larvas de merluza del Pacífico.

INTRODUCTION

Pacific hake[1] larvae (*Merluccius productus*) are the second most abundant pelagic fish larvae in the California Current, being surpassed only by larvae of the northern anchovy, *Engraulis mordax* (Ahlstrom 1965; MacGregor 1966). A hake fishery exists off the California-Washington coast, exploited primarily by foreign trawlers (Grinols and Tillman 1970; Pacific Fishery Management Council 1979). Information is available on larval development and distribution and on adult spawning and feeding of *M. productus* (Ahlstrom and Counts 1955; Ahlstrom 1959, 1969; Kramer and Smith 1970; Smith and Richardson 1977; Bailey 1980; Best 1963; Alton and Nelson 1970). In contrast, little is known of the feeding habits of Pacific hake larvae, although studies have been undertaken for larvae of *Merluccius merluccius hubbsi* in the South Atlantic (de Ciechomski and Weiss 1974) and for other kinds of gadoid larvae and juveniles (Marak 1960; Sysoeva and Degtereva 1965; Bainbridge and McKay 1968; Arntz 1974). The present report analyzes data obtained on gut contents, mouth size, and feeding incidence of Pacific hake larvae.

METHODS AND MATERIALS

A total of 298 larvae, 3.0-10.7 mm in length, from 18 formaldehyde-preserved samples taken during the March 1975 CalCOFI cruise aboard the R/V *David Starr Jordan* were examined. Stations represented cover a region 33° 25' to 29°02' N by 115°18' to 120°54.5' W, roughly off San Pedro, California, to south of Punta Baja, Baja California. All samples were collected with a 505-μm

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[1] The common name "pacific hake" has been replaced by "Pacific whiting" for *Merluccius productus* by the marketing and fishing industry, however, the former name is retained in this work.

mesh, 1-m aperture plankton net, towed obliquely from an approximate depth of 210 m to the surface. When samples contained more than 100 hake larvae, sub-samples of 25 were randomly selected over a representative size range for dissection.

Body lengths (measured from the tip of the snout to the tip of the notochord) were recorded from the specimen on a glass slide under a stereomicroscope. In order to hold the larva in position for mouth width measurements, a plexiglass plate was etched with a size gradient of grooves, and the larva was placed along its dorsal body edge in the appropriate sized groove with its upper and lower jaws held open at about 90° for the measurement.

The entire gut was removed intact from each specimen and was placed in a drop of glycerin on a glass depression slide (see Arthur 1976). Using probes tipped with pig's eyelashes, the mid- and hindgut walls were carefully slit open, and prey organisms teased out. A drop of lactic acid pigmented with Chlorazol Black E saturated in 70% ethanol was added to the gylcerin to stain crustacean cuticle (Judkins and Fleminger 1972), greatly improving the visibility of the prey and facilitating their enumeration and measurement (maximum width). Identifications of food particles were made to the lowest taxa possible with the aid of a compound microscope.

Food volume index was calculated for each food particle by treating copepod eggs as spheres, and nauplii, copepodites, and adults as ellipsoids. The ellipsoidal length for nauplii was generalized as twice the width, and for copepodites and adults, 2.5 times the width. Thus, the general volumetric equation, $V = 4/3 \pi abc$, where a, b, and c are diameters along the three axes, could be used to calculate a food volume index for the principal food components. Singular cases of oddly shaped food items, such as fish and polychaete larvae, were measured and treated individually for volume computations.

RESULTS

Composition of Food

Copepod eggs, calanoid adults, copepodites, and nauplii were the principal components of ingested material (Table 1). The copepods *Clausocalanus, Paracalanus, Calocalanus*, and the cyclopoid *Oithona* occurred the most frequently. The rather low diversity of food organisms indicates that hake larvae may feed selectively. This problem could not be investigated because the samples were from oblique integrated tows. No significant variations in the composition of diet were indicated in day versus night or inshore versus offshore samples.

One case of cannibalism (common in adults, Best 1963) occurred, in which two yolk-sac larvae were preyed upon by a 5.5-mm hake larva. The two larvae were partially digested in the midgut of the predator hake larva, providing evidence against the possibility of net feeding.

Size of Food

Pacific hake larvae fed on a wide size range of food particles (Figure 1), ingesting prey almost as large as their maximum mouth width (Figure 2) soon after yolk absorption. Larvae ingested an abundance of copepod eggs, nauplii, and copepodites as well as larger organisms such as adult copepods at larval lengths up to 8 mm (Figure 1). However, examination of the cumulative frequency distribution of numbers and volume of prey types (Table 2) reveals that adult copepods constitute the bulk (ca. 74%) of prey volume, and copepod eggs less than 1%. Of 27 yolk-containing larvae examined, 7 had begun feeding before yolk depletion.

TABLE 1
Food Composition of Pacific Hake Larvae.

Food item	3.0-3.9 No.	3.0-3.9 %	4.0-4.9 No.	4.0-4.9 %	5.0-5.9 No.	5.0-5.9 %	6.0-6.9 No.	6.0-6.9 %	7.0-7.9 No.	7.0-7.9 %	8.0-10.9 No.	8.0-10.9 %
Copepod adults:												
Clausocalanus spp.	25		51		38		23		8			
Paracalanus spp.	19		39		21		6					
Calocalanus spp.	5		10		17		16		3			
Calanus spp.			1						2			
Mecynocera clausi			6		10		4					
Oithona spp.	2		13		32		10		6		4	
Calanoid-unidentifiable	6		9		14		20		7		1	
Disintegrated	5		7		8		2				3	
Total adults	62	17.7	136	22.0	140	20.4	81	37.3	26	37.7	8	88.9
Copepodites:												
Calanus spp.	1		5		5		5		1			
Oithona spp.	2		13		7		2					
Calanoid (most are *Paracalanus/Clausocalanus*)	72		84		99		10		4			
Cyclopoid	2		5		6		18		1			
Disintegrated	14		31		15				2			
Total copepodites	91	26.0	138	22.3	132	19.2	35	16.1	8	11.6		
Copepod nauplii:												
Calanoid	102		98		141		39		5			
Cyclopoid	29		20		16							
Disintegrated	1		2									
Total nauplii	132	37.7	120	19.4	157	22.8	39	18.0	5	7.2		
Copepod eggs, single	58		214		251		62		29			
Copepod eggs, clusters	1		5		4							
Total copepod eggs	59	16.8	219	35.4	255	37.1	62	28.6	29	42.0		
Unidentified invertebrate eggs	2	0.6	5	0.8								
Polychaete larva					1	0.1						
Hake yolk-sac larvae					2	0.3						
Mollusc larva											1	11.9
Unidentified crustacean fragment	3	0.9	1	0.2					1	1.4		
Unidentified particles	1	0.3			1		0.1					
TOTAL NUMBER FOOD ITEMS	350		619		688		217		69		9	
Number larvae examined (Σ=298)	86		113		72		16		8		3	
Number larvae empty (Σ=90)	29[1]		38		18		3		1		1	

[1] 20 with yolk
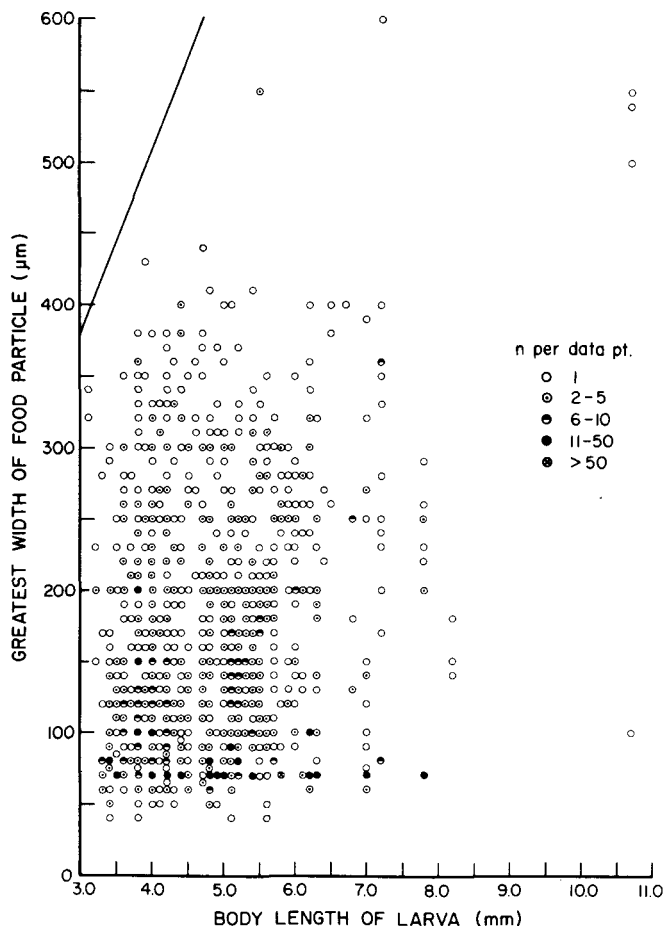
Figure 1. Food size of 208 Pacific hake larvae. Diagonal line indicates maximum mouth width.

Figure 2. Mouth width of Pacific hake larvae. The correlation with body length is $r = 0{,}93$.

Feeding Incidence

Feeding incidence is defined by Arthur (1976) as the percentage of larvae containing at least one food item in the gut for a given sample. This term refers to presence of food in the gut and does not necessarily reflect recent feeding activity. Analysis of feeding incidence of Pacific hake larvae at time of capture (Figure 3) shows presumptive diurnal feeding activity followed by a slow digestion rate with complete gut evacuation occurring between 0600 and 0800 hours PST. That evacuation rates are slow was supported by the extent of digestion and decomposition of prey organisms in larval hake stomachs; food

TABLE 2
Cumulative Frequency Distribution of Numbers and Volume for Major Prey Types Found in *M. productus* Larvae.

Prey	Range max. width (μm)	Mean food volume ($10^6 \mu m^3$)	Standard deviation ($10^6 \mu m^3$)	Frenquency	Frequency $\times$ volume (10^9 um^3)	% of total volume
Copepod eggs	50-100	0.364	0.083	674	0.24534	0.7
Copepod nauplii	40-300	4.013	5.148	441	1.76973	5.3
Copepodites	80-450	14.698	24.308	393	5.77631	17.4
Adult copepods	110-600	57.418	54.850	426	24.46007	73.8
Other	40-550	49.401	107.783	18	0.88922	2.7
					$\Sigma = 33.14067$	

items from specimens collected between 0400 and 0930 hours showed progressive disintegration over the time range, whereas larvae captured after 1000 hours contained prey in the freshest condition, indicative of first feeding in their diurnal feeding rhythm.

Plots of the mean number of prey and mean food volume index for larvae per sample (Figure 4) are dissimilar in shape. The number curve indicates an increasing accumulation of prey after 1000 hours towards a peak after sunset, whereas the volume index curve is variable and does not show such a trend.

DISCUSSION

Much attention has been given to feeding of marine fish larvae as a factor in larval survival and its effect on population dynamics of fishes. May (1974) and Hunter (1976; in press) provide excellent reviews and discussion of gut content studies in the literature. De Ciechomski and Weiss (1974) showed that hake larvae (*Merluccius merluccius hubbsi*) off Argentina have a very high incidence of feeding (94% during spring) that contrasted sharply with the low feeding incidence (28%) of anchovy (*Engraulis anchoita*) larvae. Feeding incidence is as
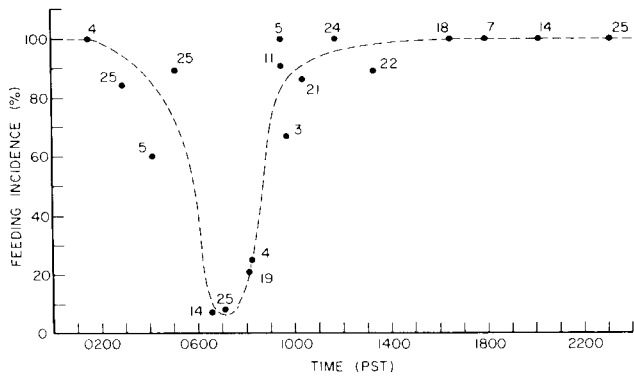
Figure 3. Feeding incidence of Pacific hake larvae in relation to time of capture. Values of data points indicate sample size of larvae. Feeding yolk-sac larvae were excluded from percentage calculations.
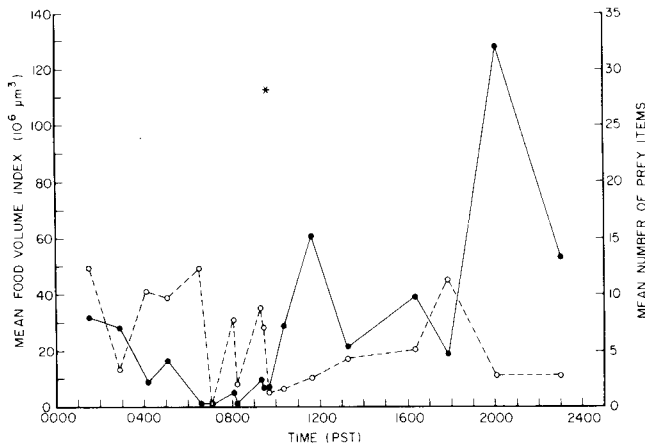

Figure 4. Mean food volume index (dashed line) and mean number of prey (solid line) of hake larvae. Asterisk indicates volume for small sample at 0944 hours when it includes a 7.2-mm hake larva that preyed on a single, unusually large copepod, which was the largest prey encountered in this study.

great or greater for small samples of Pacific hake larvae (up to 100%), but feeding incidence for larvae of the northern anchovy (*Engraulis mordax*) averages less than 10% (Arthur 1976). This disparity in the feeding incidence of two dominant spring ichthyoplankters off California and off Argentina is partly explained by defecation by larvae at time of capture and preservation, especially those with straight guts as found in clupeoid larvae (see Arthur 1976). Hake larvae, however, have folds and a pronounced loop in the gut, which would aid in food retention during capture.

According to de Ciechomski and Weiss (1974), larvae of *M. merluccius hubbsi* feed almost exclusively on copepodites and adult copepods, with calanoids dominating the diet. Average prey width increases from about 500 μm at first feeding to 800 μm at 8-mm larval length. Copepods, particularly calanoids, also dominate the diet of Pacific hake larvae; however, copepod eggs and nauplii

constitute about half of the diet items throughout the size range studied (Table 1). Despite their high incidence in the diet, these small-sized prey items contribute only about 6% of the total food volume of prey (Table 2). Hake larvae may be dependent on the successful capture of copepodites and adult copepods to provide the required nutritive level for survival and growth.

First-feeding Pacific hake larvae are capable of feeding on a large size range of prey (50- to about 400-μm prey width), and the propensity to exploit prey organisms throughout this size range persists even in the largest larvae examined in our study. In contrast, clupeoid larvae tend to have relatively small and restricted prey size ranges that are more closely correlated with mouth size (Arthur 1976). Larvae of jack mackerel (*Trachurus symmetricus*) are intermediate between clupeoids and Pacific hake with respect to prey size range. According to Arthur (1976), first-feeding jack mackeral larvae contain prey items in the 50- to 200-μm size range (mostly copepodites and adult copepods). Maximum prey size increases with larval size (to about 400 μm at 7-mm larval length), and larvae tend to exploit prey over a wide size range, although to a lesser extent than do larvae of Pacific hake. Availability of prey organisms is an important factor contributing to prey sizes consumed. Examination of the spawning periods and the distribution and abundance of major prey items in the region would be helpful in understanding these observations on larval feeding.

In *M. productus* larvae, the number of prey items in the gut increases during the day, reaches a maximum after sunset, decreases during the night, and reaches a minimum at dawn (Figure 4). Bainbridge and McKay (1968) showed a similar sequence for cod (*Gadus morhua*) larvae in the north Atlantic, where the number of identifiable copepod nauplii peaked after sunset. Their data for redfish (*Sebastes marinus*) larvae show a pre-sunset peak for number of nauplii in the gut. Arthur (1976) showed a gradual increase in feeding incidence in Pacific sardine (*Sardinops sagax*) during the day, reaching a peak before sunset, followed by a gradual decline during the night. Last (1978) found that the number of prey items of three species of flatfish larvae (plaice, flounder, and sole) reached a peak after sunset, whereas a fourth species, the dab, reached a pre-sunset peak. The disparity between the curves for mean volume and mean number of prey in hake larvae could be due to a longer digestion rate for large prey such as adult copepods, which would be retained in the gut longer and would be reflected in the variable peaks in mean volume despite a low number of prey organisms (Figure 4). The curve for number of prey may then reflect greater temporal sensitivity to feeding activity on smaller prey such as copepod eggs and nauplii.

Since marine fish larvae, including hake, are primarily

visual feeders (see review by Hunter, in press), the post-sunset feeding peak shown by hake and some other species is intriguing. One would expect that feeding success would diminish markedly at sunset, providing they do not switch over to another sensory modality at dusk. Initial speculation that hake larvae, unlike most fish larvae, develop rods in their retina early in life, thereby allowing greater visual perception in diminishing light, proved unfounded. A lack of rod development in hake larvae through 8 mm and the formation of rods in a 13.4-mm larva were observed in histological sections of the eye (O'Connell, personal communication). The development of rods in hake larvae between 8 and 13.4 mm indicates that they are similar to anchovy larvae (O'Connell in press), which initiate retinal rod formation at 10-12 mm and which are visual feeders and probably representative of most pelagic fish larvae. Another explanation may be that possible vertical migration of prey after sunset increases the probability of encounters for feeding success. A further possibility is that the general metabolic level of hake larvae declines at sunset, producing a decline in gut evacuation rate and consequently an apparent post-sunset feeding peak. Perhaps the post-sunset feeding peak may result from a combination of these suggested causes.

Adult and juvenile Pacific hake are considered to be opportunistic feeders owing to the variety and availability of their prey organisms (Best 1963; Alton and Nelson 1970). In addition to a host of invertebrates and fish species, adult hake stomachs have contained smaller hake (Best 1963). The propensity to cannibalize is expressed early in ontogeny. The finding of cannibalism by a small hake larva in this study raises the possibility that this could be an important mortality factor when patches of yolk-sac larvae are spatially contemporary with larger larvae and juveniles. If cannibalism is a characteristic of hake larvae, one could speculate that the comparatively short spawning period of this species, late January to late March (Smith and Richardson 1977), enhances survival by reducing size heterogeneity within the larval population and consequently reducing the proportion of potential cannibals. It would be of interest to investigate further the degree of cannibalism by Pacific hake larvae, whether opportunistic or deliberate, and to determine its role in the ecology and density-dependent dynamics of hake populations.

ACKNOWLEDGMENTS

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RECENT CHANGES IN THE DISTRIBUTION OF HAKE LARVAE: CAUSES AND CONSEQUENCES

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ABSTRACT

In the mid-1960's hake larvae decreased in abundance off the coast of Baja California and increased off central California. The hypothesis that this shift resulted from intensive fishing pressure is difficult to test with the available data. A simulation model indicates that fishing is a likely explanation. Hake larvae in central California are distributed farther offshore compared to Baja California. The offshore distribution of larvae is correlated to indices of Ekman transport.

RESUMEN

A mediados de 1960 la abundancia de larvas de merluza disminuyó fuera de las costas de Baja California y aumentó frente a la zona central de California. La hipótesis de que este cambio se debía a la acción de una pesquería intensiva es difícil de probar con los datos disponibles. Un modelo simulado indica que la acción de la pesquería pudiera resultar una explicación probable. Las larvas de la merluza de California central están distribuidas más lejos de la costa que las de Baja California. Existe una correlación entre la distribución de larvas fuera de la costa y los índices de transporte Ekman.

INTRODUCTION

Starting in the mid-1960's and persisting through 1979, hake larvae became much less abundant off Baja California and more abundant off central California (Figure 1). An intensive hake fishery beginning in 1966 coincides with the redistribution of the larvae; an explanation related to environmental conditions seems unlikely since there is no evidence for a persistent change of temperature in the spawning region (Johnson et al. 1978). Environmental conditions differ between Baja and central California, and the shift in larval distribution could affect their survival and thus influence the pattern of recruitment.

Where and when hake spawn has been examined from the distribution of the smallest size class of larvae (2-3 mm) from the CalCOFI surveys. Spawning occurs primarily from January to March throughout the Los Angeles Bight and over the continental slope outside of the Bight region (Table 1). Prior to the mid-1960's the distribution of larvae was closely related to temperature (Figure 2). In cold years most larvae were spawned off Baja

California; however, larvae have been sparse in that area during recent cold years, including 1968, 1972, and 1975.

HYPOTHETICAL EFFECTS OF A FISHERY ON THE DISTRIBUTION OF LARVAE

Smith (1975) first related the change in larval hake distribution to the beginning of an intensive fishery in the Pacific Northwest. He hypothesized that the increasing cline in length of adult hake which is observed northward in summer (Alverson and Larkins 1969) reverses itself southward in winter and that large fish, now depleted by the fishery, once spawned farther south. Spawning in the northern end of the spawning range could be intensified due to advanced maturity of young fish after exploitation, as has been observed for other stocks. Spawning hake have been difficult to locate to test this hypothesis; however, a limited amount of support comes from three winter trawl surveys. Of four areas examined, the greatest proportion of large fish (greater than 55 cm) occurred in 1976 at 28-29°N. In the same year at 30-32°N, a smaller proportion of the large fish occurred. An alternative to the length cline explanation is that hake are multiple spawners (they have more than one mode of eggs in the ovaries; MacGregor 1966), and large fish are more likely to develop multiple broods. Thus, as spawning schools progress south, the percentage of eggs contributed by large fish increases because smaller adults are not developing further broods. A test of these two hypotheses may come in the next 1-3 years as the abundant 1973 year class becomes older; we may expect more spawning off Baja California in cold years than has recently been observed.

Assuming that large females are responsible for larvae located off Baja California, I have used a modified yield per recruit model (Gunderson 1977) to analyze the effect of a fishery on the age structure and theoretical distribution of eggs in a population. The variables are fishing mortality (F) and age of recruitment, varied by changing the vulnerability coefficient (V_i). The model calculates age-group fecundity,

$E_i = N_i m_i$, where $N_i - 1 \exp{-(V_i - 1 F + M)}$; mean biomass,

$B_i = ((N_i W_i)/(V_i F + M)) (1 - \exp{-(V_i F + M)})$; and yield,

$Y_i = F V_i B_i$.

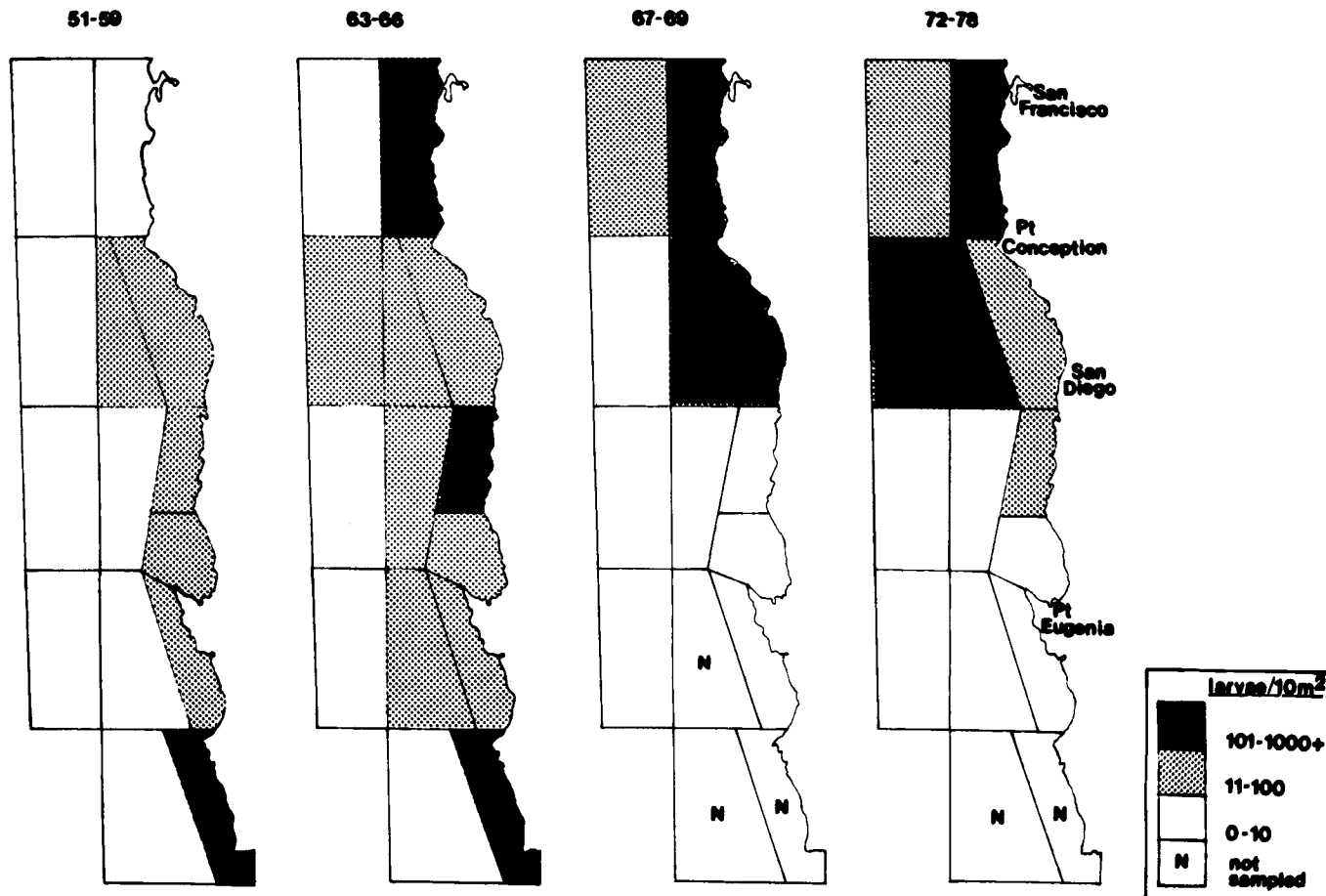**51-59** **63-66** **67-69** **72-78**

Figure 1. Historical changes in the distribution of Pacific hake larvae in January surveys.

TABLE 1
The Distribution of Eggs and Larvae in Relation to the Continental Slope.[1]

	Over slope		Not over slope (inshore or offshore)	
Larvae	37937	90.6	3922	9.4
Eggs	34639	92.7	2717	7.3

[1]Analysis of eggs is from the January 1955 survey; analysis of larvae, 2.0-2.7 mm length, is from the 1963-69 surveys.

TABLE 2
Catches of Large Mature Hake During the Spawning Season.

Survey	Latitudes °N	% Larger than 55 cm
Poseidon 1976	28-29	33
Cobb 1964	29-30	14
Poseidon 1976	30-32	12
Cobb 1965	32-33	12
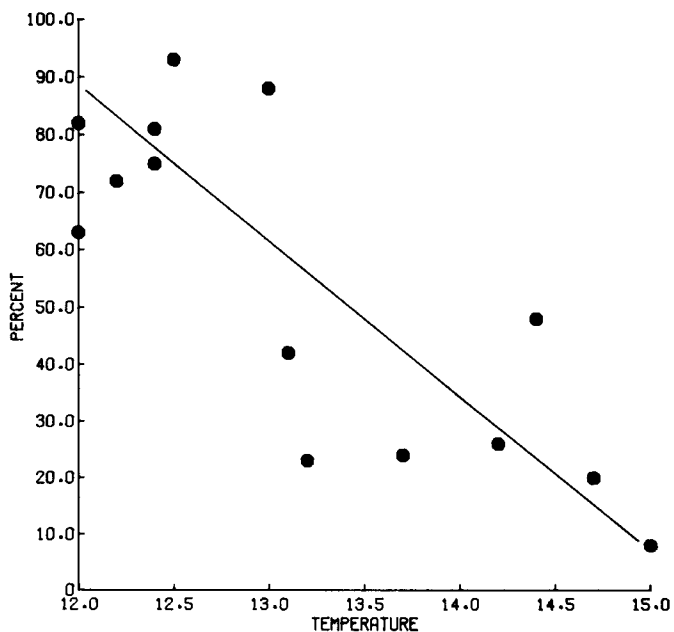
Figure 2. Percent of larvae south of CalCOFI line 100, as an index of the north-south distribution, versus the January temperature at 50 m in the Los Angeles Bight.

Average weight (W_i) and fecundity (m_i) for each age class (i) are estimated from Dark (1975) and MacGregor (1966). The natural morality coefficient $M = 0.35$ was estimated as a middle value from a range of published values (Pacific Fishery Management Council 1979).

In the simulated virgin population ($F = 0.0$), 34% of eggs are spawned by fish greater than 55 cm. Making a simplifying assumption that large fish, 55 cm and greater, are spawning off Baja California, this number compares to the pre-fishery distribution of larvae, when 45% of hake larvae occurred of Baja California. After fishing pressure is applied, the proportion of eggs contributed by large adults declines (Figure 3). With $F = 0.40$, only 7% of all eggs are contributed by fish greater than 55 cm. At this moderate fishing intensity, which probably approximates the actual fishery (calculated from the catch equation with $M = 0.35$, average exploited biomass $= 7 \times 10^5$ metric tons and the average yield $= 2 \times 10^5$ metric tons), the abundance of eggs produced by large females greater than 55 cm decreases 87% from the virgin population. Assuming that these large fish were spawning off Baja California, this decrease in eggs compares closely to the actual observed 93% decrease in abundance of larvae off the coast of northern and central Baja California since 1967.

CONSEQUENCES

What effect might the redistribution of larvae have on recruitment? Transport of larvae from favorable juvenile nursery grounds could be one of the important factors establishing recruitment strength. Bakun's (1973) upwelling indices have been used here as an indirect measure of offshore advection. The three strongest year classes of hake in recent history, 1961, 1970, and 1973, were spawned in three Januarys of the strongest onshore transport in central California since 1950 (Bailey in preparation), suggesting that larvae transported far seaward of the continental shelf and slope may not find conditions suitable for survival as juveniles.

CalCOFI larval survey data from 1950-72 in the region between CalCOFI lines 70-80 were analyzed to see whether transport of larvae is also correlated to the upwelling indices. The mean distance of hake larvae offshore was calculated as Σ|(Number $\times$ Distance)/Σ Number. Two very large catches (greater than 10,000 larva/10 m²) of the smallest size class of larvae were excluded from the calculations. The mean distance of larvae offshore in January and February surveys is positively correlated to the January upwelling index ($r = 0.70$, significant at the 99% confidence level, $n = 17$;· Table 3, Figure 4). Furthermore, larvae in January 1961 and March 1970, which grew into strong year classes, were located relatively inshore compared to other years.
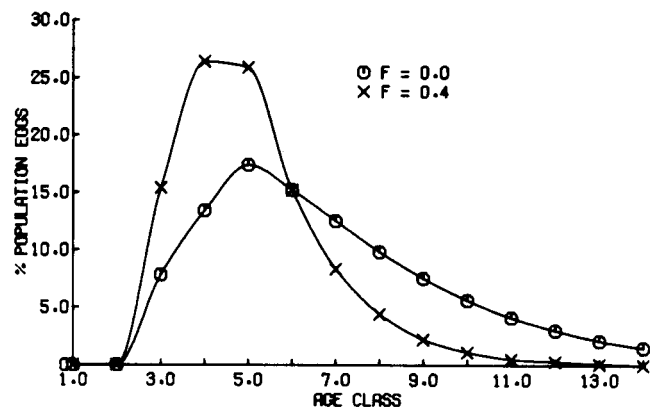
Does the change in the distribution of larvae affect

Figure 3. The theoretical percentage of eggs contributed by each age class in simulated populations for the current fishery and the virgin population.

TABLE 3
January-February and March Mean Distances of Larvae Offshore.[1]

Year	Distance Jan.-Feb. lines 70-80	Distance Jan.-Feb. lines 107-17	March Distance lines 70-80	Jan. Upwell Index 36°N	Jan. Upwell Index 30°N
1950	124	33	118	35	60
1951	120	25	115	41	112
1952	nl	40	82	5	24
1953	81	53	96	11	56
1954	40	102	nl	14	77
1955	112	10	88	15	81
1956	40	64	100	3	72
1957	nl	8	95	4	20
1958	69	40	87	−4	105
1959	12	29	ns	12	99
1960	10	20	ns	1	45
1961	1	5	ns	−15	33
1963	39	38	ns	6	9
1964	34	38	ns	23	69
1965	3	24	ns	7	44
1966	53	19	ns	4	44
1968	22	ns	ns	−3	32
1969	33	37	ns	−3	8
1970	ns	ns	50	−17	33
1972	53	39	78	15	69
mean	50	35			
variance	1554	514			

ns = not sampled
nl = no larvae

[1]Calculations used a 40 nautical-mile grid.

their transport offshore? Larvae averaged 15 miles farther offshore in the above northern region (CalCOFI lines 70-80, approximate Latitudes 35-36°N) than in a southern region (lines 107-117, approximately Latitudes 29-30°N) in years when both areas were surveyed (Table 3). Furthermore, the average width of the continental shelf is 20 miles in the northern region and 29 miles in the southern region; relatively, larvae are even farther from suitable nursery area in the north than in the south. Perhaps even more important, the variability in mean distance offshore between years is much greater in the northern region than in the southern region.
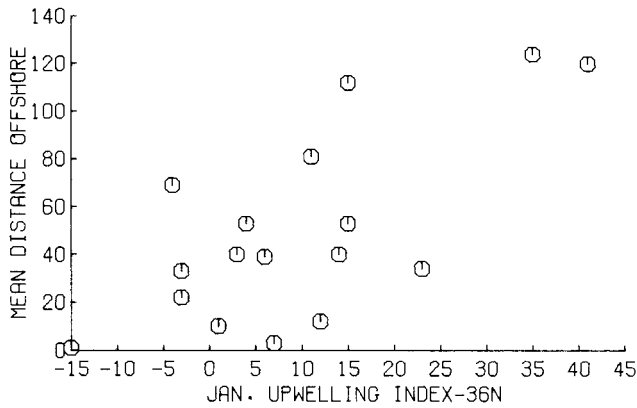
Figure 4. January upwelling index at 36°N versus the mean distance of larvae offshore in January-February surveys between CalCOFI lines 70-80.
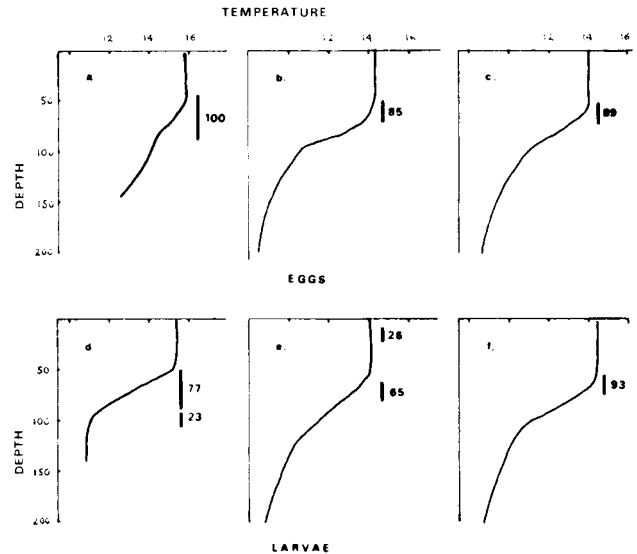

Figure 5. The vertical distribution of hake eggs and larvae less than 5-mm length compared to the temperature profile. Numbers beside bars are the percent found within that depth interval: a) Cruise 5504, Station 107.80, $n = 15$; b) 5403, 94.80N, $n = 102$; c) 5403, 94.80D, $n = 99$; d) 5504, 120.50, $n = 35$; e) 5403, 94.80D, $n = 687$; f) 5403, 94.80N, $n = 1656$.

In the southern region the mean distance of hake offshore is not correlated to a southern upwelling index (at 30°N, $r = 0.12$) or to the distance of larvae offshore in the north ($r = 0.08$). The region off Baja California, at least from Punta Baja to Punta Eugenia, is one where negative wind stress curl, associated with downwelling, extends from seaward to the coast (Bakun and Nelson 1977). As a result of downwelling, the thermocline is deepened in this region. The depth of hake eggs and larvae appears to be closely associated with the depth of the thermocline zone (Figure 5), thus when the thermocline is deep, as off Baja California, eggs and larvae are below the Ekman layer and are protected from transport offshore.

Larvae in central California appear to be more affected by wind stress transport than are larvae off Baja California. Because relatively more larvae are now spawned in the north than previously, recruitment of hake may be more variable due to an increased dependence of year-class strength on an environmental variable, i.e. wind stress. However, the change in the distribution of larvae has not affected the ability of the hake population to spawn strong year classes, as evidenced in 1970 and 1973. Intensive fishing pressure increases a stock's sensitivity to environmental conditions. Low-fecundity species may respond eventually to this increased sensitivity by stock collapse (Smith 1978). How an increase in sensitivity to environmental conditions, i.e. recruitment variability, may affect the production of high-fecundity stocks, such as hake, is at present unknown and is probably best approached as a question by simulation studies.

CONCLUSIONS

A shift in the distribution of hake larvae coincides with the beginning of an intensive fishery for large adults off the Oregon-Washington coast. No evidence currently exists to indicate that changes in the ocean environment are connected to the redistribution. A simple model of the hake fishery suggests that fishing pressure can explain the redistribution of larvae if large adults are mostly responsible for spawning in the southern end of the range. More information on spawning adults is necessary to critically examine this hypothesis. This data has been unavailable in the past due to difficulty in locating schools of spawning hake; however, with recent findings on where and when hake spawn, future surveys may be more successful.

Correlations between indices of Ekman transport, larval distribution, and adult year-class strength suggest that advection of larvae offshore may be an important influence on recruitment. Larvae in the northern end of the hake spawning range appear to be more vulnerable to transport offshore than in the southern end of the range. Consequently, a shift in the distribution of larvae towards the north, under the influence of the fishery, could increase the dependence of year-class strength on favorable advection.

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DESCRIPTION OF THE LARVAE AND EARLY JUVENILES OF THE PACIFIC BUTTERFISH, *PEPRILUS SIMILLIMUS* (FAMILY STROMATEIDAE)

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ABSTRACT

Larvae of the stromateid fish, *Peprilus simillimus*, are relatively common in nearshore samples of California Cooperative Oceanic Fisheries Investigation (CalCOFI) plankton samples taken off central California to Baja California. This paper describes the larvae of *P. simillimus* from hatching to juvenile and presents criteria for distinguishing early-stage larvae of this species from those of similar-appearing species, in particular the white croaker, *Genyonemus lineatus*. Analysis of *P. simillimus* larvae from CalCOFI survey cruises of 1975 showed a near-coast distribution with areas of concentration in the Southern California Bight and Bahia Sebastian Viscaino, where the shelf is relatively broad.

RESUMEN

Las larvas de *Peprilus simillimus* son bastante comunes en las muestras de plancton colectadas en la zona nerítica durante el programa CalCOFI (California Cooperative Oceanic Fisheries Investigations), desde California central hasta Baja California. En este trabajo se describen las fases larvales de *P. simillimus*, desde su eclosión del huevo hasta la fase juvenil, y se presentan los criterios básicos para distinguir los primeros estados larvales de esta especie y de otras especies similares, en particular *Genyonemus lineatus* (roncador blanco). Las larvas de *P. simillimus* colectadas durante los cruceros de CalCOFI en 1975, presentaron una distribución nerítica, y se concentraron principalmente en la Bahía del Sur de California y la Bahía Sebastián Vizcaino, donde la plataforma continental es más ancha que en el resto del litoral.

INTRODUCTION

The stromateid fish, *Peprilus simillimus,* is one of four eastern Pacific species of *Peprilus* and is the only one found north of Mexico (Horn 1970). It ranges from Bahia Magdalena, Baja California (ca. 24°N), north to British Columbia (ca. 55°N; Miller and Lea 1972). Marketed as Pacific butterfish or Pacific pompano, it is the subject of a minor fishery with a recent peak of 182,000 pounds in 1971 (Oliphant 1973).

Juveniles and adults of *P. simillimus* are found associated with nearshore soft-bottom habitats, and the larvae occur in coastal CalCOFI stations from Point Concep-

tion, California, to Bahia Magdalena, Baja California (Horn 1970).

The early larval stages of *P. simillimus* can be confused with those of some other species, particularly the white croaker, *Genyonemus lineatus*. The purpose of this paper is to describe the development of *P. simillimus* from hatching to juvenile, to provide criteria for distinguishing the early larval stages from those of similar-appearing species, and to summarize the distribution of the larvae in CalCOFI samples from 1975.

METHODS AND MATERIALS

A life history series was assembled consisting of newly hatched larvae to fully transformed juveniles. Most of the larvae were obtained from the CalCOFI ichthyoplankton collections. Other larval and juvenile material was obtained from Scripps Institution of Oceanography (Food Chain Research Group), SIO Fish Collection, and the Los Angeles County Museum. A few specimens were reared incidentally with other species at the Southwest Fisheries Center, La Jolla.

A series was established for the study of morphological development, morphometrics and pigment formation, using the techniques and terminology of Ahlstrom et al. (1976). A second series was cleared in KOH-glycerine and stained with Alizarin Red-S to study the development of meristic characters.

Terminology of specimen length follows that described in Moser and Ahlstrom (1978). Standard length is defined as the distance between the tip of the snout and the posterior edge of the hypural plate. In larvae that have not completed notochord flexion, that is, before the edge of the hypural plate becomes vertical, the body length is measured from the snout to the tip of the notochord.

DESCRIPTION

Literature

Larvae of two Atlantic species have been described, *P. paru* by Pearson (1941) and *P. triacanthus* by several workers (summarized in Martin and Drewry 1978).

Distinguishing Features

P. simillimus hatch at 1.8-2.0 mm, undergo notochord flexion at about 4.8-6.2 mm, and begin to transform into juveniles at about 20 mm. Our smallest fully transformed juvenile is 27.9 mm.

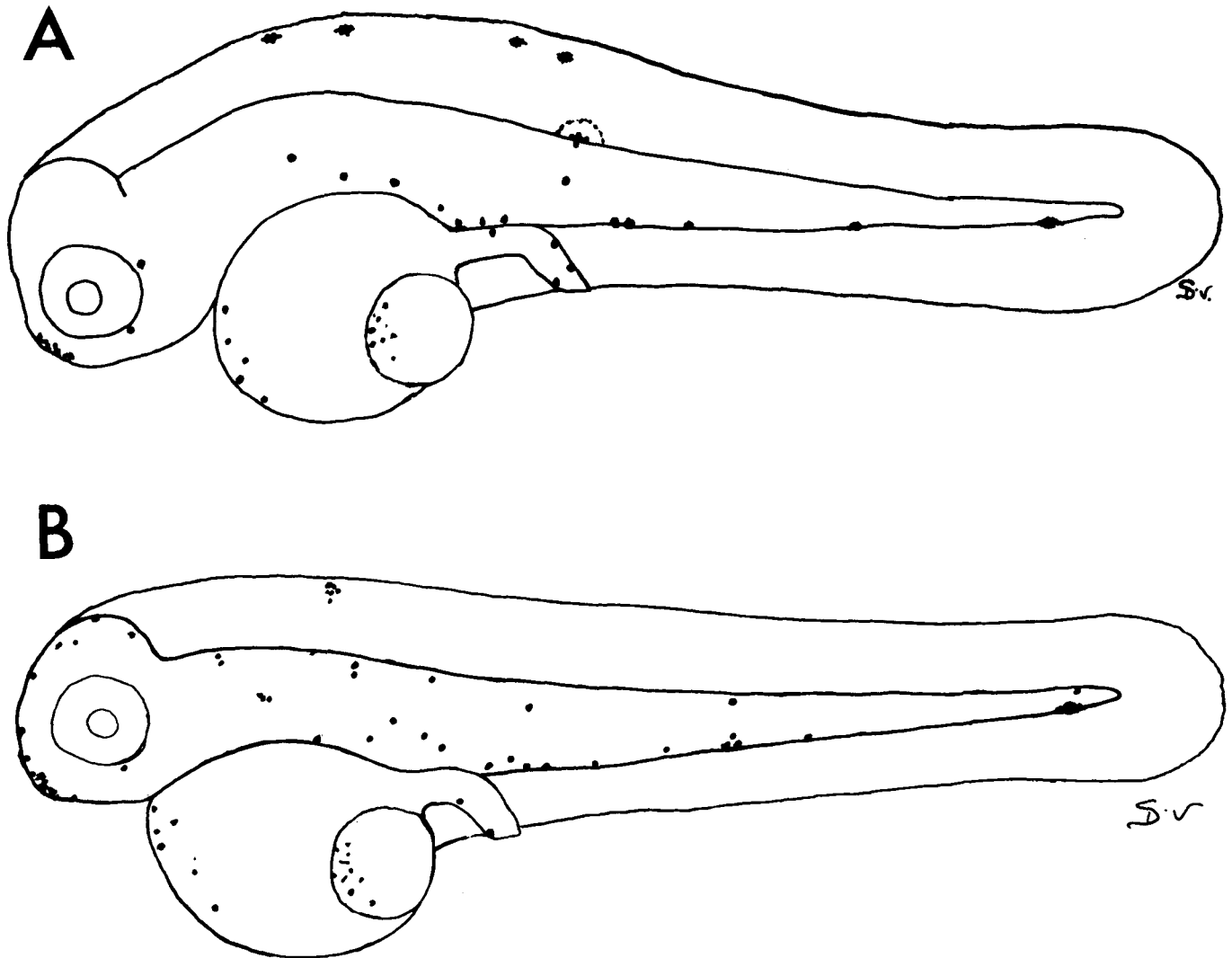Yolk-sac larvae have scattered melanophores along

Figure 1. Yolk-sac larvae of A. *Peprilus similimus* (2.0 mm) and B. the white croaker, *Genyonemus lineatus* (2.1 mm).

the ventral region of the head and body and are characterized by a prominent median dorsal melanophore located slightly posterior to a vertical from the anus. This serves to distinguish them from the yolk-sac larvae of the white croaker, *G. lineatus*, which lack pigment in this area (Figure 1). At the completion of yolk absorption, the larvae have a prominent zone of large melanophores on the trunk above the gut and a median ventral series extending from the cleithrum to the anus (Figure 2). The latter series helps to distinguish early larvae of *P. similimus* from those of the spotted turbot, *Pleuronichthys ritteri*, which lack the median ventral series. In larger *P. similimus* larvae, the deep head and body form, and the lateral zone of large melanophores, which gradually expands to cover the entire body, are distinguishing features (Figure 3).

Morphology

Newly hatched larvae have a robust body form, a sizable yolk-sac with a posteriorly located oil globule (ca. 0.2-mm diameter), a moderately long gut (snout to anus distance/body length = ca. 0.50 mm), an incomplete mouth, and unpigmented eyes. At a length of 2.2 mm the yolk is absorbed, the mouth is formed, the eyes are becoming pigmented, and the gut is beginning to coil. Notochord flexion occurs in the larval length range of 5.0-7.0 mm (Table 1). Morphometric proportions are summarized in Table 2. The most conspicuous trend is the twofold increase in relative body depth during ontogenesis. Other more subtle ontogenetic trends are a relative shortening of snout-to-anus length, an increase in relative head length, and a decrease in relative eye size.

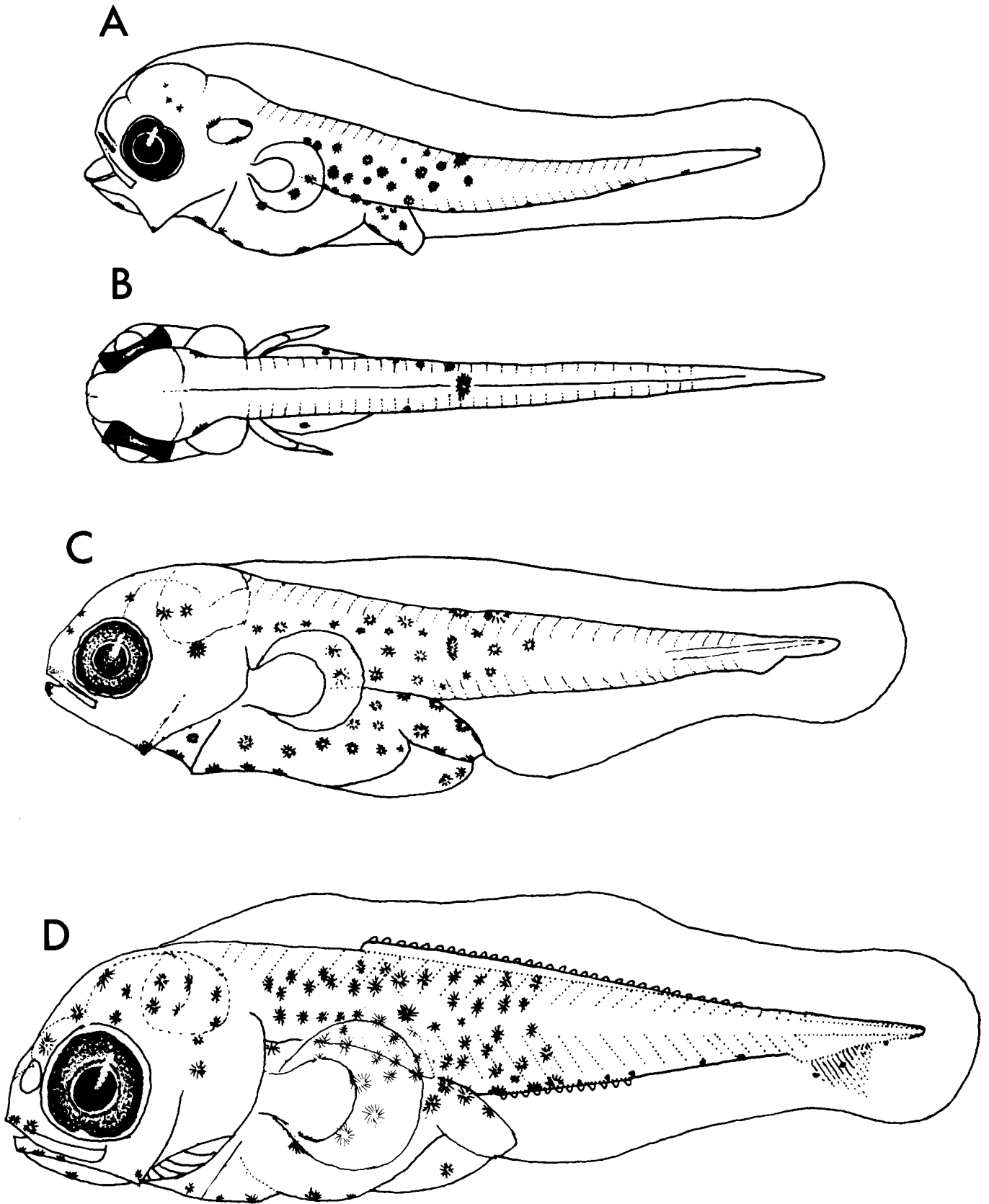Small spines develop on the preopercular margin.

Figure 2. Developmental stages of *Peprilus simillimus*: A) 2.4 mm; B) 2.4 mm, dorsal view; C) 4.1 mm; D) 4.7 mm.
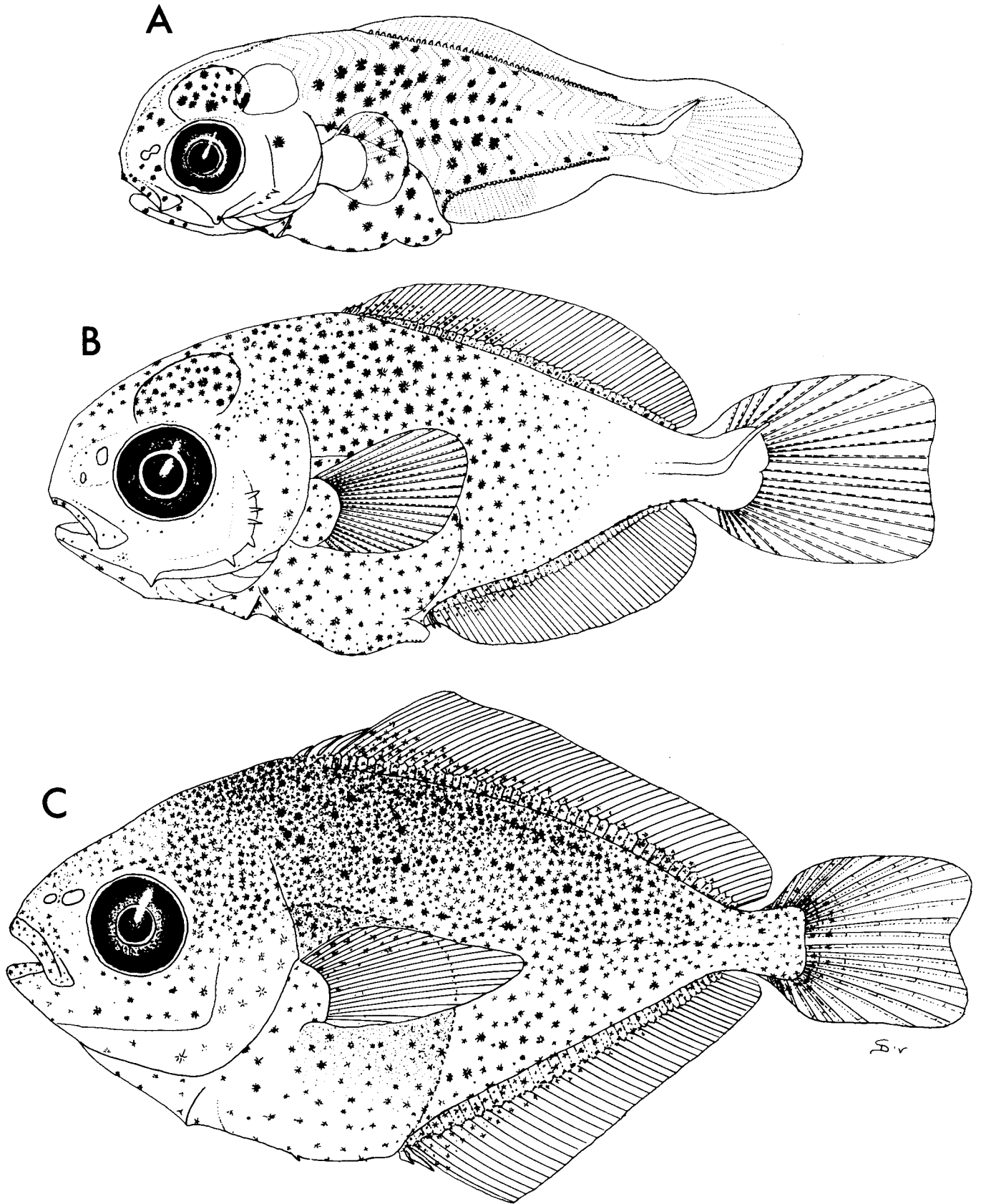
Figure 3. Developmental stages of *Peprilus simillimus*: A) 6.5 mm; B) 10.8 mm; C) transforming specimen, 21.3 mm.

TABLE 1

Measurements in mm of Developmental Series of *Peprilus simillimus*.[1]

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to dorsal fin origin	Snout to anal fin origin	Snout to pelvic fin origin
7505-120.26	1.9	1.0	0.27	0.18	0.08	0.48	–	–	–
7505-120.26	2.3	1.1	0.39	0.22	0.12	0.52	–	–	–
7505-120.24	2.6	1.4	0.54	0.23	0.12	0.58	–	–	–
7803-90.27.6	3.3	1.9	0.83	0.36	0.16	0.98	–	–	–
7803-90.27.6	3.9	2.2	0.98	0.40	0.18	1.1	–	–	–
7803-87.36	4.2	2.5	1.0	0.44	0.23	1.4	–	–	–
7510-120.25	4.8	2.6	1.3	0.49	0.31	1.4	–	2.5	–
6204-130.30	5.4	3.0	1.5	0.56	0.29	1.5	–	2.9	–
6902-127.34	5.5	3.0	1.5	0.56	0.35	1.6	–	3.0	–
7803-93.29	5.8	3.3	1.7	0.64	0.39	1.8	–	3.2	–
7511-83.44.7	6.0	3.2	1.7	0.64	0.39	1.8	–	3.2	–
7801-87.32.7	6.2	3.4	1.7	0.66	0.33	1.8	–	3.2	–
7803-80.60	5.9	3.4	1.8	0.72	0.40	2.0	–	3.1	–
7511-83.55	6.9	4.2	2.4	0.92	0.56	2.8	–	4.1	–
SCBS-4-103	7.5	4.3	2.7	0.96	0.58	2.9	3.0	4.3	–
7606-Los Angeles Bight, CA	8.9	4.7	2.9	1.2	0.80	3.7	3.7	5.0	–
6204-133.25	9.2	4.8	3.1	1.2	0.76	3.7	3.7	4.8	–
6707-117.30	10.2	5.5	3.6	1.4	0.84	4.6	4.2	5.5	4.0
5707-137.35	12.0	5.6	4.4	1.4	1.2	5.4	5.0	6.0	damaged
TC50-sta. 28	13.0	6.0	4.8	1.7	1.3	6.5	5.2	7.0	4.6
7803-73.50	15.2	7.3	5.5	2.2	1.1	6.8	5.4	7.6	6.2
7510-117.30	18.0	7.4	5.8	2.4	1.2	8.5	6.8	8.3	7.2
7510-117.30	19.6	9.4	6.0	2.3	1.4	9.4	7.4	9.1	6.9
7808-MWT22	21.3	9.9	6.7	3.0	1.9	10.3	7.4	10.4	8.0
6402-140.30	23.0	10.5	7.5	3.0	1.9	11.7	9.2	10.5	9.2
LACM 9659-7 Mex. Cedros Isl.	27.9[2]	12.9	9.6	3.2	1.5	14.0	9.8	13.4	11.0
SIO H52-221	28.6	14.1	10.0	3.2	2.2	13.4	11.2	13.7	12.1
SWFC reared	33.6[2]	14.3	12.2	4.8	2.2	17.8	13.3	16.8	12.4
LACM 9659-7, Mex. Cedros Isl.	36.0[2]	17.0	12.0	4.9	2.1	17.0	12.0	17.4	14.5
C6208-Cobb 55-18	45.9[2]	19.9	13.9	4.4	3.1	22.5	16.2	20.5	15.0
SIO 60 409.42A	47.0[2]	19.0	15.8	5.3	3.6	20.6	15.9	18.2	17.3

[1] Specimens between dashed lines are undergoing notochord flexion.
[2] Juvenile.

TABLE 2

Body Proportions of Larval and Juvenile *Peprilus simillimus*.[1]

Body proportion	N	Snout to anus / body length	Head length / body length	Eye diameter / head length	Snout length / head length	Body depth at pectoral fin base / body length	Snout to dorsal fin / body length	Snout to anal fin / body length	Snout to pelvic spine / body length
Preflexion ...	7	54.4±3.9 (49-60)	22.0±4.8 (14-27)	46.8±9.4 (38-64)	23.4±4.5 (18-30)	25.2±4.5 (22-33)	–	–	–
Flexion	6	55.4±1.06 (54-57)	28.8±1.5 (28-31)	37.6±1.0 (36-39)	21.4±1.6 (19-23)	29.8±2.3 (27-34)	–	53.5±0.6 (53-54)	–
Postflexion ...	10	51.5±5.6 (41-61)	35.0±1.8 (32-38)	37.2±2.9 (32-41)	23.5±2.2 (21-27)	43.5±3.6 (38-50)	39.9±1.8 (36-42)	53.0±4.0 (46-59)	38.9±2.1 (35-41)
Transforming	4	47.4±1.63 (46-49)	32.4±1.9 (31-35)	38.6±5.0 (32-44)	25.0±2.7 (22-29)	48.5±1.7 (47-51)	38.0±2.3 (35-40)	47.2±1.4 (46-49)	38.8±3.1 (32-42)
Juvenile	5	43.9±2.76 (40-47)	33.6±2.2 (30-36)	35.7±4.1 (32-41)	19.2±3.2 (16-23)	48.6±3.4 (44-53)	35.4±2.5 (33-40)	46.0±4.5 (39-50)	37.2±2.9 (33-39)

[1] Values are expressed as percent of body or head length (mean, standard deviation, and range).

TABLE 3
Meristics of Cleared and Stained Larvae of *Peprilus simillimus*.[1]

Size (mm)	Dorsal fin	Anal fin	Pectoral fin	Pelvic spine	Caudal fin	Vertebrae	Branchiostegal rays	Gill rakers
4.2	–	–	–	–	–	–	2	–
4.8	–	–	–	–	–	–	–	–
5.8	–	–	–	–	3+2	–	5	–
6.2	16	16	10	–	0+9+8+1	–	6	–
6.5	19	16	9	–	0+8+8+1	–	6	4
7.1	36	37	13	–	3+9+8+3	–	6	6
7.8	I, 35	0, 32	13	–	2+9+8+2	–	6	8
9.7	II, 46	II, 42	17	damaged	5+9+8+4	13+17=30	6	10
10.5	III, 43	II, 38	19	spine bud	5+9+8+5	13+17=30	6	5
12.0	III, 44	II, 39	18	✓	6+9+8+6	13+17=30	6	0+14
12.4	II, 45	II, 40	19	✓	5+9+8+4	13+17=30	6	0+11
13.9	III, 45	II, 42	21	✓	7+9+8+6	13+17=30	6	0+11
15.0	III, 46	II, 42	19	✓	6+9+8+6	13+17=30	6	0+12
17.0	III, 46	II, 42	19	✓	7+9+8+6	13+17=30	6	1+13
18.8	III, 44	II, 40	20	✓	7½+9+8+7	13+17=30	6	3+13
20.0	III, 46	III, 40	21	✓	6+9+8+6	13+17=30	6	3+11

[1]Specimens between dashed lines are undergoing notochord flexion. Check indicates presence of pelvic spine.

They begin to form at about 6.5-mm length and become incorporated into the preopercular bone by about 14-mm length. The number of observed spines ranged from one in the small sizes to as many as nine seen in a 12-mm specimen.

Fin Formation and Internal Structures

The caudal, pectoral, dorsal, and anal fin rays begin to ossify towards the end of the notochord flexion phase (Table 3). The adult complement of 9+8 principal caudal rays is ossifying before notochord flexion is complete. The full ray complements are ossifying in the pectoral (19-23), dorsal (II-IV, 41-48), and anal (II-III, 35-44) fins at about 10.0-mm length. Pelvic fins are represented by a single minute spine projecting from near the distal end of the pelvic bone. The pelvic bone begins to ossify at about 9.5-mm length and the pelvic spine at about 10 mm. Ossification of the vertebral column begins after the completion of notochord flexion, and the full complement of 29-31 vertebrae is ossifying by about 10.0-mm length. The stellate teeth of the pharyngeal sacs begin ossifying at about 7.1-mm length, and most are present by about 9.7-mm. The three predorsal bones begin to ossify at about 9.7-mm length. These interdigitate with the neural spines such that they precede the first, second, and third neural spines. Scales on the lateral line begin forming at about 19-mm length, marking the beginning of transformation. The smallest completely scaled specimen seen was 27.9 mm.

Pigmentation

Yolk-sac larvae have melanophores on the snout, around the eyes, on the anterior region of the yolk-sac, on the anterior surface of the oil globule, just above the gut on each side, along the ventral midline from the anus to the notochord tip, and at the margin of the dorsal finfold above the trunk (Figure 1). A characteristic median dorsal pigment structure, on about the 16th myomere, can be seen in the earliest stages and persists through larval development. This structure is composed of 1-6 pigment clumps and in yolk-sac larvae is usually slightly above the dorsum in the finfold. It is associated with an opaque zone in the surrounding finfold and may be a large melanophore or a complex of small ones.

After yolk absorption, melanophores fill in around the dorsal spot and down the side of the trunk and gut towards the head so that the anterior half of the trunk is fairly well pigmented by about 3.0-mm length. The head, nape, and dorsum are bare of pigment (Figure 1). A median ventral line of pigment extends from the cleithrum to the anus at this stage. The head is usually pigmented on the isthmus, at the symphysis of the lower jaw, over the brain, and internally on the floor of the cranium.

As development continues, the lateral melanophore zone extends posteriorly and the unpigmented nape and dorsum gradually become covered (Figures 2 and 3). The dorsal aspect of the head becomes solidly pigmented, whereas the cheek region remains relatively unpigmented (Figure 3). By 12-mm length, 70% of the body is covered by melanophores, and some pigment can be seen over the hypural plates. The pectoral fin has a few melanophores at the fin base and some which extend out onto the upper rays. At 15-mm length, 90% of the body is pigmented, leaving only the caudal peduncle unpigmented. By 20-mm length, the caudal peduncle is completely pigmented, and melanophores are present over the hypural region as well

as at the base of the caudal fin rays. Pigment forms in the anterior part of the dorsal and anal fins in a narrow band adjacent to the base of the rays. It gradually spreads posteriorward and also increases in width. In juveniles the pigmented area on the dorsal fin extends over much of the fin. The pigmented zone on the anal fin is narrowest and extends out on the fin for a third or less of its width. Pigment gradually spreads throughout the caudal fin, but the individual melanophores are smaller and their distribution is less dense than on the dorsal and anal fins.

DISTRIBUTION

Larvae of *P. simillimus* occur in comparatively low numbers in CalCOFI samples (Ahlstrom 1965); however, this may reflect the relatively low sampling effort in the nearshore region inhabited by this species. Horn (1970) summarized the geographic and seasonal distribution of *P. simillimus* larvae sampled by CalCOFI during 1955-59 and showed that larvae are taken at coastal stations from Point Conception, California, southward to the vicinity of Bahia Magdalena, Baja California. Larvae occurred in the samples throughout the year but were collected in greatest number during May, June, and July. Greatest larval catch was in upper central Baja California in the vicinity of Bahia Sebastian Viscaino (ca. 28°N).

The distribution and relative abundance of *P. simillimus* larvae on CalCOFI cruises during 1975 (Figure 4) was similar to 1955-59. Larvae occurred from Point Conception south to Bahia Magdalena with three major areas of concentration; i.e. the Southern California Bight, Bahia Sebastian Viscaino area, and in the bight north of Bahia Magdalena. These are regions where the shelf is relatively broad with a mud or sand substrata. The enlarged adult habitat in these regions (contrasted with intervening regions that have narrow shelves) is reflected by greater larval catch and more extensive offshore larval distribution (Figure 4). Relative abundance and extent of offshore distribution are greatest in the Bahia Viscaino area were the shelf is broadest.

In 1975 the number of *P. simillimus* larvae reached a peak during summer cruises, but larvae occurred relatively frequently on the October cruise. In fact, cruise 7510 (October 1975) accounted for 45% of the total occurrences for the year. During 1955-59 almost no *P. simillimus* larvae were taken after August, and occurrences during the October cruises of 1955-59 accounted for 2% of the total occurrences.
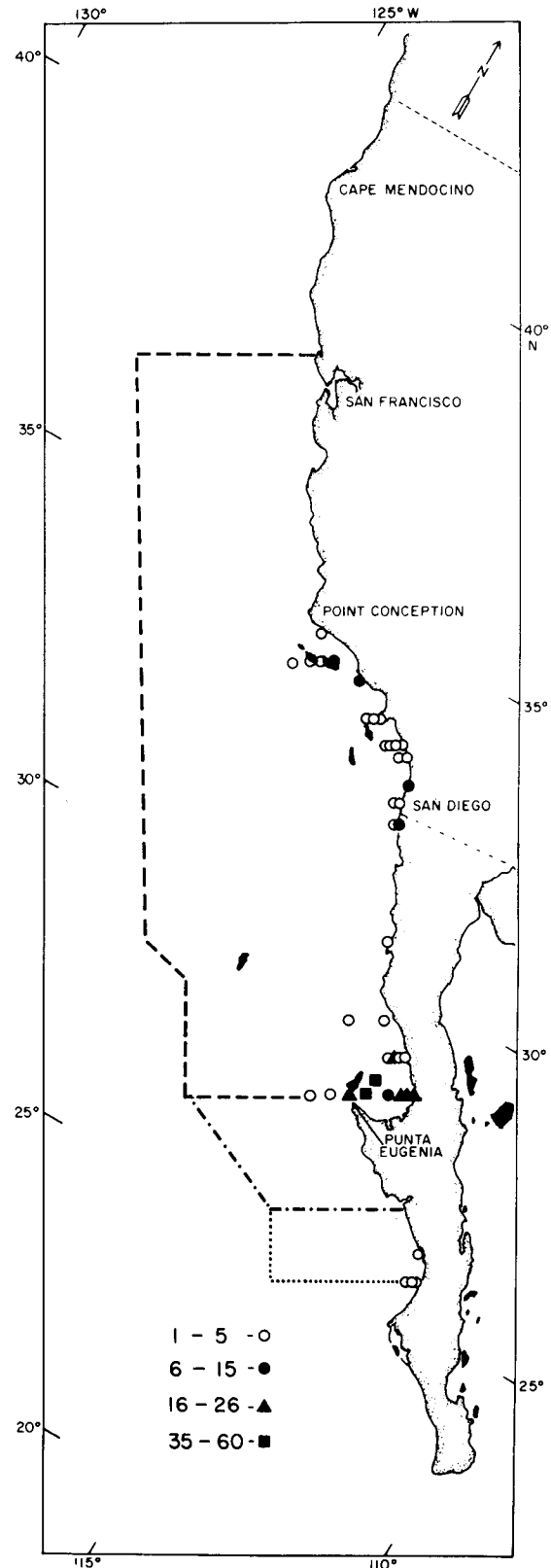
ACKNOWLEDGMENTS

Figure 4. Distribution of total catch of *Peprilus simillimus* larvae collected on five CalCOFI cruises during 1975. Legend indicates actual numbers of larvae taken on each CalCOFI station. Dashed lines indicate approximate area sampled by five cruises. More southerly areas were sampled by four (. _ .) and by three (. . .) cruises.

produced the original wash drawings of four of the larvae from which tracings were made. Henry Orr provided drafting assistance. We are grateful to Morgan Busby, John Butler, Richard Charter, Elaine Sandknop, Betsy Stevens, and Barbara Sumida-MacCall for advice and assistance during the preparation of the manuscript. Kate Coleman and Lorraine Prescott typed drafts of the manuscript.

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DISTRIBUTION, ABUNDANCE, AND RECRUITMENT OF SOFT-BOTTOM ROCKFISHES (SCORPAENIDAE: *SEBASTES*) ON THE SOUTHERN CALIFORNIA MAINLAND SHELF[1]

ALAN J. MEARNS[2], M. JAMES ALLEN[3], MICHAEL D. MOORE[4], AND MARJORIE J. SHERWOOD[4]

ABSTRACT

Data from nearly 400 small-mesh otter trawls taken throughout the southern California borderland between 1969 and 1979 were examined to reveal spatial and temporal patterns in the abundance and distribution of rockfishes. Rockfishes were common in all samples taken between 15 and 450 m. Predictably, species composition changed with depth. Catches were numerically dominated by either *Sebastes saxicola* (from 1971-75) or *S. dalli* (from 1975-79) on the mainland shelf south of Point Dume and inshore of 60 m; variability in the recruitment of the young of these species was the major source of seasonal and year-to-year fluctuations in rockfish catches. These variations in recruitment were related to changing oceanographic conditions.

RESUMEN

Se examinaron los datos de casi 400 arrastres de fondo (con tablas), de malla pequeña, tomados en la zona fronteriza del sur de California entre 1969 y 1979, para presentar patrones especiales y temporales en la abundancia y distribución de peces del género *Sebastes*. Estos peces eran comunes en todas las muestras tomadas entre 15 y 450 m. Como se esperaba, la composición en especies cambió con la profundidad. Las capturas estaban dominadas numéricamente por *Sebastes saxicola* (de 1971-75) o *S. dalli* (de 1975-79) en la plataforma continental al sur de Point Dume y dentro de los 60 m de la costa; la variabilidad en el reclutamiento de los juveniles de estas especies fue la mayor causa de las fluctuaciones estacionales y de cada año en las capturas de *Sebastes*. Estas variaciones en el reclutamiento aparecen relacionadas con las variaciones en las condiciones oceanográficas.

INTRODUCTION

This report summarizes data on variations in the abundance, recruitment, and apparent growth of prominent rockfishes caught by small-mesh otter trawls on the southern California mainland shelf. It is intended to complement an earlier report on nearshore fish (Mearns 1979b).

Rockfishes (Genus *Sebastes*, Family Scorpænidæ) are among the most important groups of fishes in California. As adults, some rockfish (notably bocaccio, *Sebastes paucispinis*) make important contributions to re-

creational and commercial fisheries. In routine trawl surveys along the southern California coast between the 20- and 200-m isobaths, young and adult rockfishes are frequently the most abundant species and, over many seasons, are the most diverse family of fishes collected (Mearns 1977, 1979a). The young are an important food source for many fishes and seabirds. And, because they occur in a variety of habitats close to shore, they can affect, and have been affected by, man's coastal activities, including waste-water discharges (Sherwood 1979; Sherwood and Mearns in press).

Our interest in rockfishes was reinforced in 1975 when investigators conducting routine trawl-monitoring surveys reported a dramatic influx of previously "rare" calico rockfish (*S. dalli*) off Orange and Los Angeles Counties between depths of 15 and 60 m (Mearns 1977; John Stephens, Occidental College, personal communication). An initial investigation of trawl data collected by the Orange County Sanitation Districts (OCSD) and the Southern California Coastal Water Research Project (SCCWRP) revealed that prior to July of 1975 catches between 15 and 150 m were dominated by stripetail rockfish (*S. saxicola*); after the summer of 1975, *S. saxicola* were rare except in the deepest (130-140 m) samples, and through 1978, *S. dalli* dominated the inshore (20-60 m) rockfish catch (Mearns 1979a, 1979b).

Neither *S. saxicola* nor *S. dalli* is commercially harvested or of sportfishing interest in this area; thus, the cause of this dramatic change must be due to factors other than fishing. The area is the site of a 60-m deep sewage outfall (680 million liters/day), which had begun discharge four years earlier (April 1971); however, it is unlikely this discharge was the cause since the *S. dalli* influx was observed at distant sites (e.g. Santa Monica Bay, 20 to 50 km away). This leaves the possibility that the event was natural and in some way related to changing oceanographic or climatic conditions or to biological interactions. In fact, evidence has already been presented that suggests that recruitment of nearshore bottomfish is related to interannual variations in sea-surface temperature and turbidity (Mearns 1979a, 1979b).

As a result of these earlier findings, we felt a more rigorous analysis of spatial and temporal variations of rockfish assemblages was in order. Specific objectives of this study were to identify the most abundant species along the shelf during the 1970's, to determine depth and geographic distributions of certain species both before and after 1975, to seek out any correlations that might
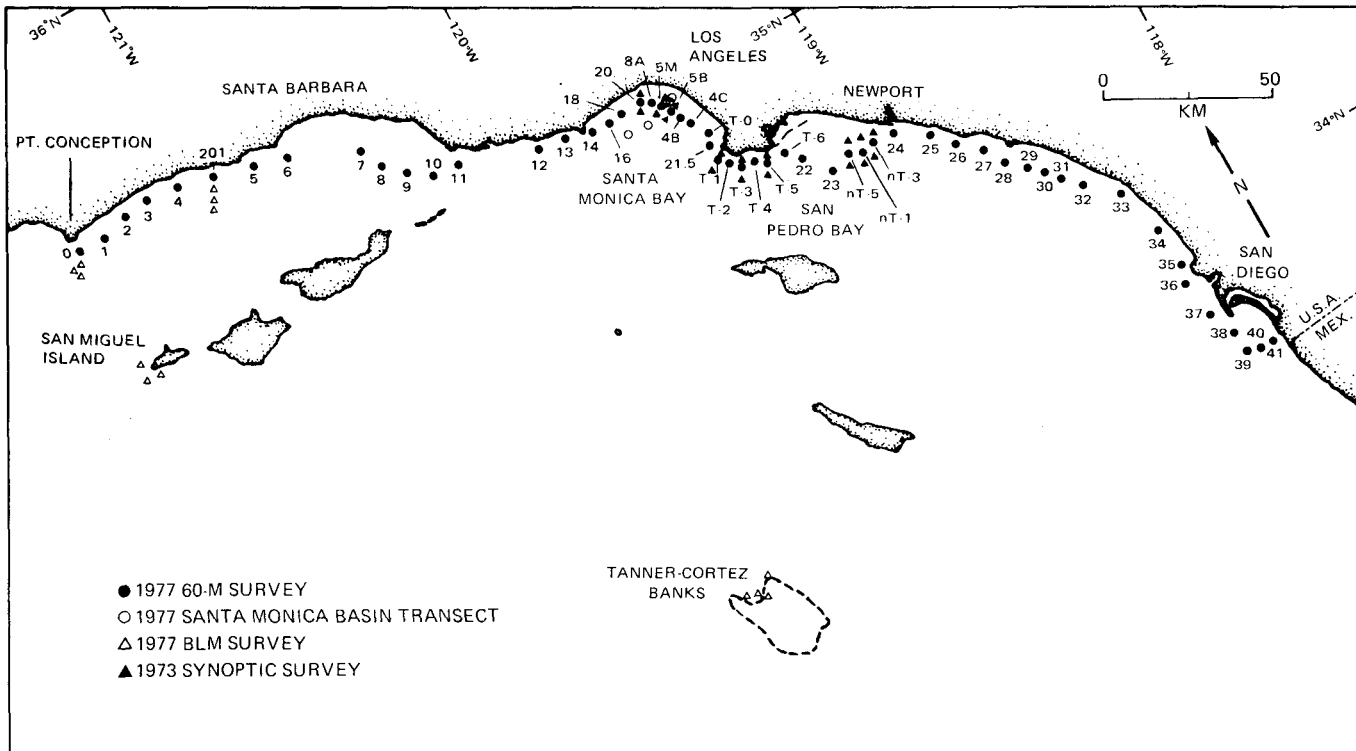
Figure 1. Trawl locations in the Southern California Bight, 1973-79.

exist between variations in rockfish catch and oceanographic changes, and to identify possible biological interactions between rockfish species.

METHODS

Rockfish catch and length-frequency data were compiled from several one-time geographical trawl surveys (one in 1973 and three in 1977, Figure 1) and from a series of quarterly trawl surveys taken between 1969 and 1979 off Orange County (Figure 2).

Trawl Gear and Towing Methods

Two kinds of otter trawls were used, one built by the Marinovich Trawl Company (Biloxi, Mississippi) and the other built by Mr. James Willis, Netmaker, Morro Bay, California. Both nets were 7.62-m (25-foot) headrope length, semi-balloon trawls, fitted with 1.27-cm (0.5-inch) stretch-mesh cod-end liners. However, the Willis nets and doors were constructed of heavier materials and had a slightly larger body mesh than the Marinovich nets (4.13 cm versus 3.81 cm, stretch).

In most cases, tows were taken along isobaths at a speed of 1.3 m/second (2.5 knots). On-bottom tow times were generally 10 minutes but ranged from 10 to 25 minutes (specified below).

This gear is not expected to catch many large, old, fast-swimming rockfish. However, in a comparative hook-and-line and trawl study in Santa Monica Bay, Allen et
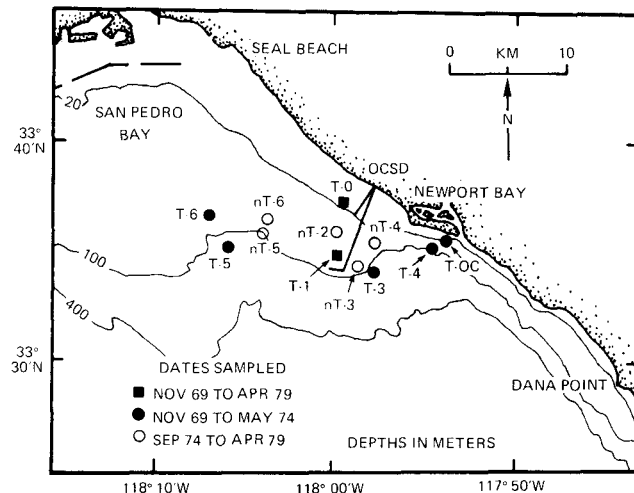
Figure 2. Sampling location for quarterly trawls off Orange County, August 1969 through October 1979.

al. (1975) did demonstrate that this small otter trawl took the same upper size limits of rockfish also captured by hook-and-line (e.g. *S. paucispinis*, trawl to 500-mm standard length [SL], hook-and-line to 450-mm SL; *S. miniatus*, trawl to 260-mm SL, hook-and-line to 300-mm SL; *S. rosenblatti*, otter trawl to 420-mm SL, hook-and-line to 410-mm SL). However, the trawl did take a lower proportion of larger rockfish than did bottom hook-and-line gear (Allen et al. 1975).

Catch Processing and Identification

All fishes from these surveys were sorted aboard ship, identified, examined for external abnormalities and parasites, and measured to the nearest 0.5-cm standard length (SL). Catches from 1973 onward were also weighed by species. Voucher specimens and specimens of uncertain identity were preserved and returned to our laboratory for archiving and confirmation.

Juvenile rockfishes from these and other SCCWRP surveys were identified using keys and data in Phillips (1957), Chen (1971), and Miller and Lea (1972). Wherever possible, we also arranged fresh specimens in size series. This effort resulted in a guide which incorporated color as well as morphological features for juvenile rockfishes (Allen 1977). Using this information, we confirmed identification of all specimens collected from August 1971 through 1979. However, we were unable to confirm identifications of specimens collected by OCSD between August 1969 and May 1971.

Geographical Surveys

During the period 24-26 September 1973, SCCWRP conducted a synoptic trawl survey of the coastal shelf between Malibu, in Los Angeles County, and Newport Beach, in Orange County (Mearns and Greene 1974). Single trawls were taken during daytime at each of three depths (23, 61, and 137 m) at each of nine transects located in Santa Monica Bay, off Palos Verdes, and on the southern San Pedro Bay coastal shelf (Figure 1). All tows were 10-minute duration (on-bottom time) and were made aboard the R/V *Van Tuna* using a Marinovich 7.62-m otter trawl.

On 6 and 7 April 1977, SCCWRP sampled a series of seven depths in a transect extending due west of Marina del Rey across Santa Monica Bay and into Santa Monica Basin. Depths sampled were 18, 61, 137, 183, 305, 458, and 610 m (Figure 1). A single 10-minute (on-bottom time) haul was taken at each station.

During spring and summer (28 April to 9 August) 1977, SCCWRP conducted a trawl, grab, and water quality survey of the entire southern California mainland shelf (Point Conception to the U.S-Mexico border) along the 60-m isobath (Figure 1; see also Word and Mearns 1979). Fifty-three of 70 stations were each trawled once during daytime for bottomfish using the same Willis bottom trawl described above. Tows were made using several vessels, but mainly the M/V *Marine Surveyor* and the *Fury II* (Orange County Department of Education). Tows were 10 minutes (on-bottom time) at 1.3 m/second.

Also during 1977, SCCWRP conducted a series of trawl surveys at Tanner Bank, on the seaward shelf off San Miguel Island, off Point Conception and off Goleta Point (near Coal Oil Point) in Santa Barbara County (Figure 1). Sampling was conducted in March and July.

Depth distributions of the samples were:

Tanner Bank	185, 185, 185, and 216 m	137, 183, and 274 m
San Miguel Island	183, 183, and 227 m	132, 183, 192, and 274 m
Point Conception	73, 135, 183, and 220 m	137 and 183 m
Coal Oil Point	73, 137, 174, and 185 m	137, 174, and 220 m

All samples were taken aboard the R/V *Velero* (University of Southern California) at 1.3 m/second (2.5 knots) but with on-bottom time ranging from 10 to 25 minutes.

Time Series 1969-79

During the period from August 1969 to the present, the County Sanitation Districts of Orange County (CSDOC) contracted and conducted a series of quarterly trawl surveys at six to eight stations on the southern San Pedro Bay coastal shelf off Huntington Beach and Newport Beach (Figure 2, Pamson et al. 1978; Mearns 1979a). At least one of us was on board to confirm identifications on all but one occasion between August 1971 and October 1979.

A single daytime tow with a Marinovich 7.62-m trawl was taken at each station during each survey. All tows were 10-minute (on-bottom time) and were made aboard the M/V *Fury II* (August 1969 to May 1970) and the R/V *Van Tuna* (August 1970 to October 1979).

Between November 1969 and May 1974, the survey grid included eight stations ranging in depth from 18 to about 150 m; in August 1974 the two deepest stations (133 and 148 m) were deleted, and several stations were rearranged; the result was a grid of seven stations ranging in depth from 18 to 64 m. However, a deep (150 m) site was resampled in January 1977 and October 1979.

Data Analysis and Interpretation

Abundance and length-frequency data on all rockfish was extracted from computerized site-species and species length-frequency matrices and recompiled to determine total species and numbers caught, depth distribution, and length-frequency distribution of selected species, both along shore (60-m survey of 1977) and over time (1971-79 time series).

This analysis is restricted to the genus *Sebastes*; data on other scorpaenids (*Scorpaena guttata* and *Sebastolobus* spp.) were collected and will be reported later.

RESULTS

Species Encountered and General Abundance

Over 38,000 specimens of at least 27 species of rockfish were taken in the trawls examined for this report. Species taken, and their common names, are listed in Table 1.

Considering only the major coastal shelf surveys (22 to 137 m), rockfish catches were dominated by *S. saxicola* (19,521 specimens, 53.7% of the rockfish catch); *S. dalli* (25%); halfbanded rockfish, *S. semicinctus* (11.5%);

TABLE 1

Scientific and Common Names of Rockfishes Taken in Otter Trawls by the Southern California Coastal Water Research Project, 1973 to 1979, 78 to 458 m.

Scientific name	Common name
Sebastes aurora	Aurora rockfish
S. babcocki	Redbanded rockfish
S. caurinus[1]	Copper rockfish[1]
S. chlorostictus	Greenspotted rockfish
S. crameri	Darkblotched rockfish
S. dalli	Calico rockfish
S. diploproa	Splitnose rockfish
S. elongatus	Greenstriped rockfish
S. ensifer	Swordspine rockfish
S. eos	Pink rockfish
S. flavidus	Yellowtail rockfish
S. goodei	Chilipepper
S. hopkinsi	Squarespot rockfish
S. jordani	Shortbelly rockfish
S. levis	Cow rockfish
S. macdonaldi	Mexican rockfish
S. melanostomus	Blackgill rockfish
S. miniatus	Vermilion rockfish
S. mystinus	Blue rockfish
S. paucispinis	Bocaccio
S. rosaceus	Rosy rockfish
S. rosenblatti	Greenblotched rockfish
S. rubrivinctus	Flag rockfish
S. saxicola	Stripetail rockfish
S. semicinctus	Halfbanded rockfish
S. serranoides	Olive rockfish
S. umbrosus	Honeycomb rockfish

[1]We include here specimens of *S. vexillaris*, which Miller and Lea (1972) consider indistinguishable.

TABLE 2

The Abundance of *Sebastes* Species and Their Percentage of Total *Sebastes* Catch in Samples from Three Southern California Trawl Surveys, 1969-78.

(Number of samples) Scientific name	Orange County (n=286) Number	%	1973 Synoptic (n=27) Number	%	1977 60-m (n=53) Number	%	Total (n=365) Number/%	
Sebastes saxicola	6889	(34.9)	4558	(83.4)	8074	(72.6)	19521	(53.7)
S. dalli	6252	(31.7)	13	(0.2)	2812	(25.3)	9077	(25.0)
S. semicinctus	4022	(20.4)	51	(0.9)	94	(0.8)	4167	(11.5)
S. diploproa	1491	(7.6)	494	(9.0)	5	(<0.1)	1990	(5.48)
S. miniatus	287	(1.5)	47	(0.8)	21	(0.2)	355	(1.8)
S. jordani	128	(0.7)	189	(3.4)	8	(0.1)	325	(1.7)
S. goodei	177	(0.9)	33	(0.6)	8	(0.1)	218	(1.1)
S. levis	93	(0.5)	26	(0.5)	49	(0.4)	168	(0.9)
S. crameri	95	(0.5)	27	(0.5)	1	(<0.1)	123	(0.6)
S paucispinis	49	(0.3)	20	(0.4)	5	(<0.1)	74	(0.3)
S. rosenblatti	32	(0.2)	16	(0.3)	7	(<0.1)	55	(0.3)
S. rubrivinctus	60	(0.3)	1	(<0.1)	1	(<0.1)	62	(0.3)
S. mystinus	37	(0.2)	0	(–)	2	(<0.1)	39	(0.2)
S. rosaceus	37	(0.2)	0	(–)	0	(–)	37	(0.2)
S. elongatus	10	(<0.1)	18	(0.3)	1	(<0.1)	29	(0.1)
S. chlorostictus	20	(0.1)	0	(–)	2	(<0.1)	22	(0.1)
S. caurinus	3	(<0.1)	1	(<0.1)	11	(0.1)	15	(<0.1)
S. serranoides	7	(<0.1)	0	(–)	3	(<0.1)	10	(<0.1)
Sebastes unidentified	16	(<0.1)	9	(–)	0	(–)	16	(<0.1)
S. flavidus	6	(<0.1)	0	(–)	0	(–)	6	(<0.1)
S. umbrosus	5	(<0.1)	0	(–)	0	(–)	5	(<0.1)
S. eos	3	(<0.1)	1	(<0.1)	0	(–)	4	(<0.1)
Sebastes (*Sebastomus*), unidentified	0	(–)	0	(–)	4	(<0.1)	4	(<0.1)
S. hopkinsi	1	(<0.1)	1	(<0.1)	1	(<0.1)	3	(<0.1)
S. macdonaldi	0	(–)	2	(<0.1)	0	(–)	2	(<0.1)
Total Species (Taxa)	22		16		19		25	
Specimens	19720		5498		11109		36327	

splitnose rockfish, *S. diploproa* (5.5%); vermilion rockfish, *S. miniatus* (1.8%); and shortbelly rockfish, *S. jordani* (1.7%; Table 2). The Orange County time series from 1968 through 1978 took 22 species with overall catches equally dominated by *S. saxicola* and *S. dalli*. The data indicate that *S. semicinctus* were abundant only during the period August 1969-May 1971. As noted above, this was prior to SCCWRP participation. Because of the similarity of juvenile *S. semicinctus* and *S. saxicola* and because of the *S. saxicola* dominance following our participation, we believe that the data for *S. semicinctus* could include many *S. saxicola*.

Data from our own independent 1973 synoptic survey (Table 2) indicate that catches between 18 and 137 m were dominated by *S. saxicola, S. semicinctus,* and *S. diploproa; S. dalli* were rare (0.2% of the catch; Table 2), confirming that they were generally absent from the Los Angeles-Orange Counties coastal shelf prior to the 1975 influx indicated above. However, when we conducted the 60-m survey of the entire coastal shelf in 1977, *S. dalli* made up 25.3% of the rockfish catch (third column, Table 2).

General Depth and Geographic Distributions

Data from surveys taken from March to July 1977 at Tanner Bank, San Miguel Island, Point Conception, Coal Oil Point, and in Santa Monica Bay and Basin were composited to gain insight into the general depth distribution patterns of prominent rockfish captured by our small otter trawls. Trawls in this set varied between 10- and 25-minute duration. Although not exhaustive and biased toward the northern half of the southern California borderland, these data suggest several important trends (Table 3). First, our trawls captured rockfish throughout the depth range 18 to 458 m, but none were caught in a single 610-m haul in Santa Monica Basin. Next, the number of rockfish species per individual haul was relatively constant with depth, ranging from 1.7 to 3.2 with slightly more species per haul inshore of 185 m. Abundance (mean number of specimens/haul) was highest inshore (80 fish/haul at 18-73 m), moderate between 132 and 305 m, and low beyond 458 m. The high catches between 18 and 185 m are due almost exclusively to large numbers of small fish.

These data (Table 3) suggest three major breaks in

TABLE 3

Composite Depth Distributions of Rockfish Taken in 37 7.6-m (Headrope-Length) Otter Trawl Hauls in Santa Monica Bay and Basin, and at Tanner Bank, San Miguel Island, and Point Conception, March-July 1977.[1]

Depth Interval (m)	18-73	132-137	174-185	192-227	275-305	458
Number of Trawls	7	7	13	5	3	1
Number Species ($\bar{x}$)	2.7	2.6	3.2	2.0	1.7	2.0
Number Specimens ($\bar{x}$)	80.1	60.6	60.9	15.0	38.0	12.0
Sebastes mystinus	0.14	____	____	____	____	____
S. semicinctus	0.14	____	____	____	____	____
S. miniatus	0.14	____	____	____	____	____
S. caurinus	0.57	____	____	____	____	____
S. dalli	2.43	____	____	____	____	____
S. levis	0.14	____	0.08	____	____	____
S. saxicola	75.9	18.6	24.3	4.0	____	____
S. jordani	0.14	15.4	11.5	0.60	____	____
S. ensifer	0.43	1.0	0.39	____	____	____
S. paucispinis	____	1.30	0.08	____	____	____
S. rosenblatti	0.14	0.29	0.39	0.20	0.30	____
S. elongatus	____	1.43	5.08	1.00	4.30	____
S. diploproa	____	22.3	17.6	4.00	30.3	11.0
S. crameri	____	0.29	0.77	____	____	____
S. babcocki	____	____	0.15	____	____	____
S. eos	____	____	0.15	____	____	____
S. macdonaldi	____	____	0.08	____	____	____
S. serranoides	____	____	0.08	____	____	____
S. goodei	____	____	0.23	5.4	____	____
S. melanostomus	____	____	____	____	0.30	____
S. aurora	____	____	____	____	____	1.0

[1]Data for species are average number fish per 10- to 25-minute haul (see text).

TABLE 4

Rockfish (Sebastes) Catch per 10-Minute Tow with a 7.6-m Headrope-Length Otter Trawl at Three Depth Intervals Sampled in September 1973 off Los Angeles and Orange Counties.

Depth (m)	23	61	137	Total
Number of Samples	9	9	9	27
Number of Specimens ($\bar{x}$)	4.44	288	318	204
Number of Species ($\bar{x}$)	0.89	5.00	5.11	3.6
Sebastes hopkinsi	____	0.11	____	0.04
S. rubrivinctus	____	0.11	____	0.04
S. caurinus	____	0.11	____	0.04
S. dalli	____	1.44	____	0.48
S. goodei	____	3.67	____	1.22
S. semicinctus	____	5.67	____	1.89
S. miniatus	1.30	3.89	____	1.74
S. paucispinis	0.89	0.56	0.77	0.74
S. saxicola	2.22	266	238	169
S. jordani	____	5.11	15.9	7.0
S. levis	____	0.89	2.00	0.96
S. crameri	____	0.22	2.78	1.00
S. elongatus	____	0.11	1.89	0.67
S. diploproa	____	____	54.9	18.3
S. rosenblatti	____	____	1.78	0.59
S. macdonaldi	____	____	0.22	0.07
S. eos	____	____	0.11	0.04

depth distribution of rockfish: the inshore group dominated by S. saxicola but characterized by other fish such as S. dalli, S. caurinus, S. miniatus, and S. semicinctus; an outer shelf assemblage (132-185 m) dominated by S. saxicola and S. diploproa but also characterized by S. jordani and, in part, S. elongatus; and a slope assemblage (192-305 m) dominated, in our catches, by S. diploproa, S. goodei, and S. elongatus but also characterized by a reduced abundance of S. saxicola.

The 1973 synoptic surveys off Los Angeles and Orange Counties provided some insight into rockfish depth distributions on the shelf prior to the 1975 influx of S. dalli (Table 4). During this survey, rockfish catches were low inshore (4.4 fish/tow at 23 m) but were very high at the 61- and 137-m depth intervals (288 and 318 fish/haul, respectively). Number of species was low inshore (0.89 species/tow) but increased dramatically at 61- and 137-m depth intervals (5.0 and 5.1, respectively). S. saxicola dominated catches at all depths (Table 4) and were, of course, the most abundant rockfish overall (84%; Table 2). In contrast, S. dalli occurred only at 61 m (Table 4) and were in very low abundance (0.2% of the catch; Table 2). Overall, the coastal zone between Point Dume and Newport (about 80 km) contained a S. saxicola-dominated rockfish assemblage inshore of the 61-m isobath.

The 1977 survey at 53 60-m deep stations indicated that S. saxicola was also the dominant rockfish at this

depth between Point Conception and the U.S.-Mexico border (8,074 specimens, 74% of the catch; Table 2). However, as indicated above, S. dalli were no longer rare and, in fact, accounted for over 25% (2,812 specimens) of the combined rockfish catch. The next most abundant species were S. semicinctus (94 specimens, 0.8%), S. levis (49 specimens, 0.4%) and S. miniatus (21 specimens, 0.2%).

A north-to-south plot of the catch per unit effort of these major rockfish species revealed some fascinating trends (Figure 3). First, large numbers of rockfish were concentrated in three or four major regions of the mainland shelf; two areas on the Santa Barbara Shelf, one off southern Orange County, and another off San Diego County.

Sebastes saxicola dominated northern catches while S. dalli dominated catches south of Los Angeles (Figure 3). Sebastes semicinctus appeared to be generally distributed throughout the area (Figure 3). Other species such as cow rockfish, S. levis, and copper rockfish, S. caurinus, were mainly northern while still others such as vermilion rockfish, S. miniatus, were mainly southern (Figure 3). In general, more species were encountered in the north and central areas than in the south (Figure 3). Length-frequency plots of the two prominent species were examined. As shown in Figure 4, our survey apparently encountered a 1977 recruitment of S. saxicola into much of the coast. In fact, the coastal zone from Point Conception south to northern Santa Monica Bay (170-190 km) was nearly continuously occupied by small (25- to 55-mm SL) S. saxicola (Stations 0 to 20). Larger S.

saxicola (70- to 130-mm SL) were prevalent at this depth mainly in the coastal area between Coal Oil Point (Station 201) and Rincon Point (Station 7).

Sebastes dalli were rare north of Point Mugu (Station 11). However, from about Point Mugu south to the center of Santa Monica Bay (Station 20), medium-sized *S. dalli* (90- to 120-mm SL) became prominent. Farther south, in the San Pedro Bay and Orange County area, medium-sized *S. dalli* dominated the catches (Stations 22 to 25), with young of the year (35- to 65-mm SL) occurring at the two San Pedro Bay stations sampled in late July (Stations 22 and 23). South of Dana Point (Station 25), *S. dalli* were again rare, with *S. saxicola* once again dominating the catches. However, from La Jolla to the border, medium-sized *S. dalli* once again dominated catches, occasionally occurring together with young *S. saxicola*.

Overall, there was very little overlap in the length-frequency distribution of small *S. dalli* and *S. saxicola* at any station. Exceptions were at Stations 22 (San Pedro Bay) and 24 (off Newport Beach). The strongest overlap was for larger fish (e.g. 80- to 110-mm SL) at Station 39 off San Diego.

Figure 4. Length-frequency distributions of stripetail rockfish (*Sebastes saxicola*) and calico rockfish (*S. dalli*) at 55 trawl stations sampled in spring and early summer of 1977 between Point Conception (Station 0) and the U.S.-Mexico border (Stations 40-42). Data indicate a decrease in occurrence of small *S. saxicola* and an increase in the size distribution of *S. dalli* south of Santa Monica Bay (Stations 13 to 4c).

Figure 3. Coastal distribution of rockfish species during 60-m trawl survey in 1977 by the Southern California Coastal Water Research Project.

Fluctuations off Orange County

Mearns (1977, 1979b) summarized catch data from the first eight years of quarterly trawls off Orange County. An additional year of trawling (through October 1978) produced a total of 131,835 fish representing at least 112 species of sharks, rays, and bony fishes. This cumulative catch included over 19,000 specimens and 23 species of rockfishes (Table 2). Thus, rockfish accounted for 15% of the specimens and 21% of species taken in this area.

Over the full nine-year period, a total of 286 hauls were made during 38 quarterly surveys. Average catch per 10-minute haul was 459±24 SE fish[1]; the catch per unit effort for rockfish was 68.6±10.1 SE[1] (or about 15% of the total catch).

As shown in Table 2, the rockfish catch was dominated by *S. saxicola* (6,889 specimens, 24.9% of the rockfish

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[1]Mean and standard error of 38 survey means.

catch) and *S. dalli* (6,252 specimens, 31.7% of the rockfish catch). Next in abundance was *S. semicinctus* (4,022 specimens, 20.4% of the catch), and *S. miniatus* (287 specimens, 1.5% of the catch). Species each contributing 0.5 to 1.0% of the catch were chilipepper, *S. goodei*; shortbelly rockfish, *S. jordani*; dark blotched rockfish, *S. crameri*; and cow rockfish, *S. levis*.

Fluctuations in catch over time were examined for total rockfish catch and for the three most abundant species. As shown in Figure 5a, there were major seasonal and year-to-year differences in rockfish catch per unit effort over the nine-year period. Highest catches generally occurred mid-year (late spring-early fall) and lowest catches in the winter. With the exception of 1969, odd-numbered years produced considerably higher catches than even-numbered years, with highest catches occurring in 1975, 1971, 1973 and 1977. In addition, a long-term trend of decreasing "baseline" catch is apparent during the period 1971 through 1978.

Data on the fluctuations in catch of the three most abundant species of rockfish show specific sources of the variations in total catch (Figure 5). During the four-year period from mid-1971 to mid-1975, *S. saxicola* dominated catches and also appeared to make the major contribution of the 1971, 1973, and 1975 odd-year peaks in total rockfish catch. Then, from mid-1975 through 1978, *S. dalli*, which formerly were rare, dominated catches and

were major contributors to peaks in total rockfish catch in 1975 and 1977.

There is some concern that the change in stations and loss of deep-water stations (133-148 m) might affect the interpretation of these changes (i.e. perhaps *S. saxicola* abundance shifted to deeper water after 1974 and were undersampled). As shown in Figure 6, *S. saxicola* were indeed more abundant and occurred over a wider depth range than *S. dalli* prior to August 1974. However, during this period, peak abundance of *S. saxicola* did occur at the depth interval 51-64 m. Also the two influxes of *S. saxicola* (May 1973 and May 1974) were more prominent in the depth range of 34-64 m than at 133-148 m or in shallow water. Peak abundance of *S. dalli* during this period was also at the 51-64-m depth interval, but they occurred infrequently.

In September 1974 the deeper (137-146-m) stations were deleted from the survey grid. Nevertheless, the survey did sample a large influx of *S. saxicola* at both the 31-37-m and 51-64-m depth intervals in May 1975. But in July, there were few *S. saxicola* in any of the trawls; instead, the survey sampled a large influx of *S. dalli* at all depths between 15 and 64 m with the population persisting in abundance through 1978 and 1979 at the 51-64-m depth interval.

Although routine deeper sampling was officially discontinued, two single deep trawls (137-150 m) were taken recently; *S. saxicola* were abundant (105 in January 1977 and 25 in October 1979) and there were no *S. dalli*. These two catches average 65±49 (95% confidence limit) *S. saxicola* per haul. Previous (1971-74)
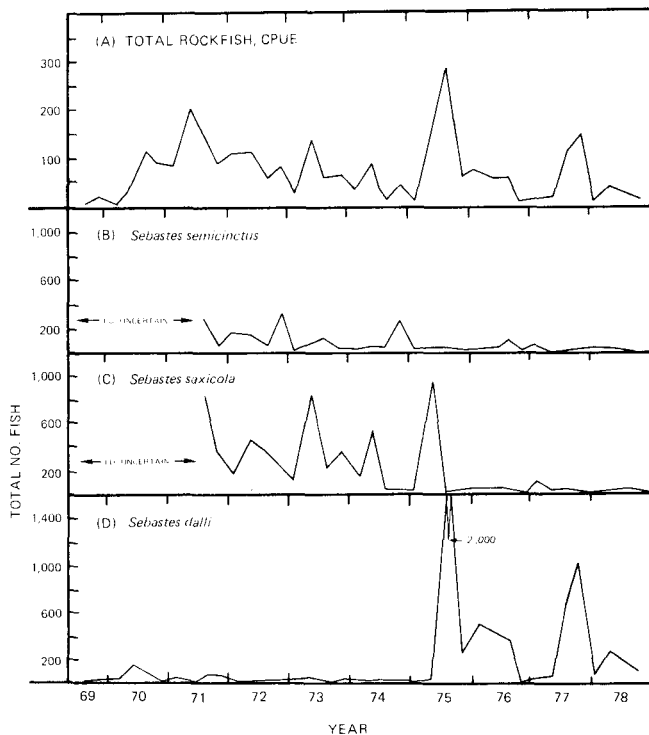

Figure 5. Long-term variations in catch per unit effort (CPUE; number per 10-minute haul) of total rockfish and of *Sebastes semicinctus, S. saxicola,* and *S. dalli* in quarterly trawls off southern San Pedro Bay by the County Sanitation Districts of Orange County.
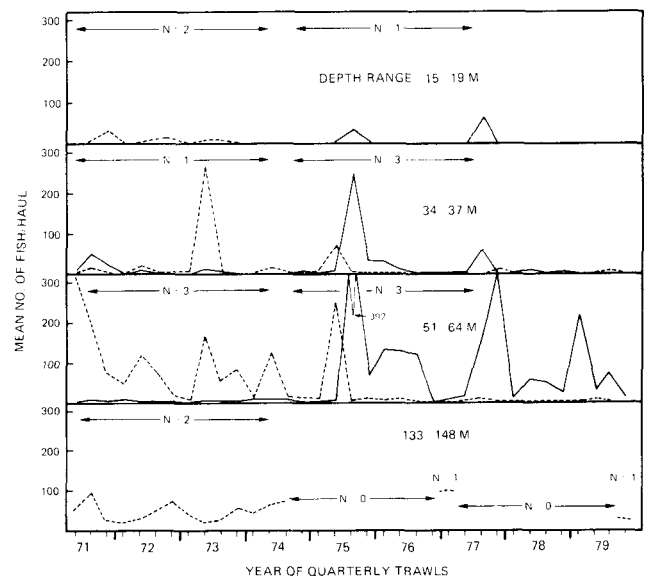

Figure 6. Long-term variation in abundance of *Sebastes saxicola* (dashed line) and *S. dalli* (solid line) at each of four depth ranges in quarterly trawls off Orange County, 1971-79.
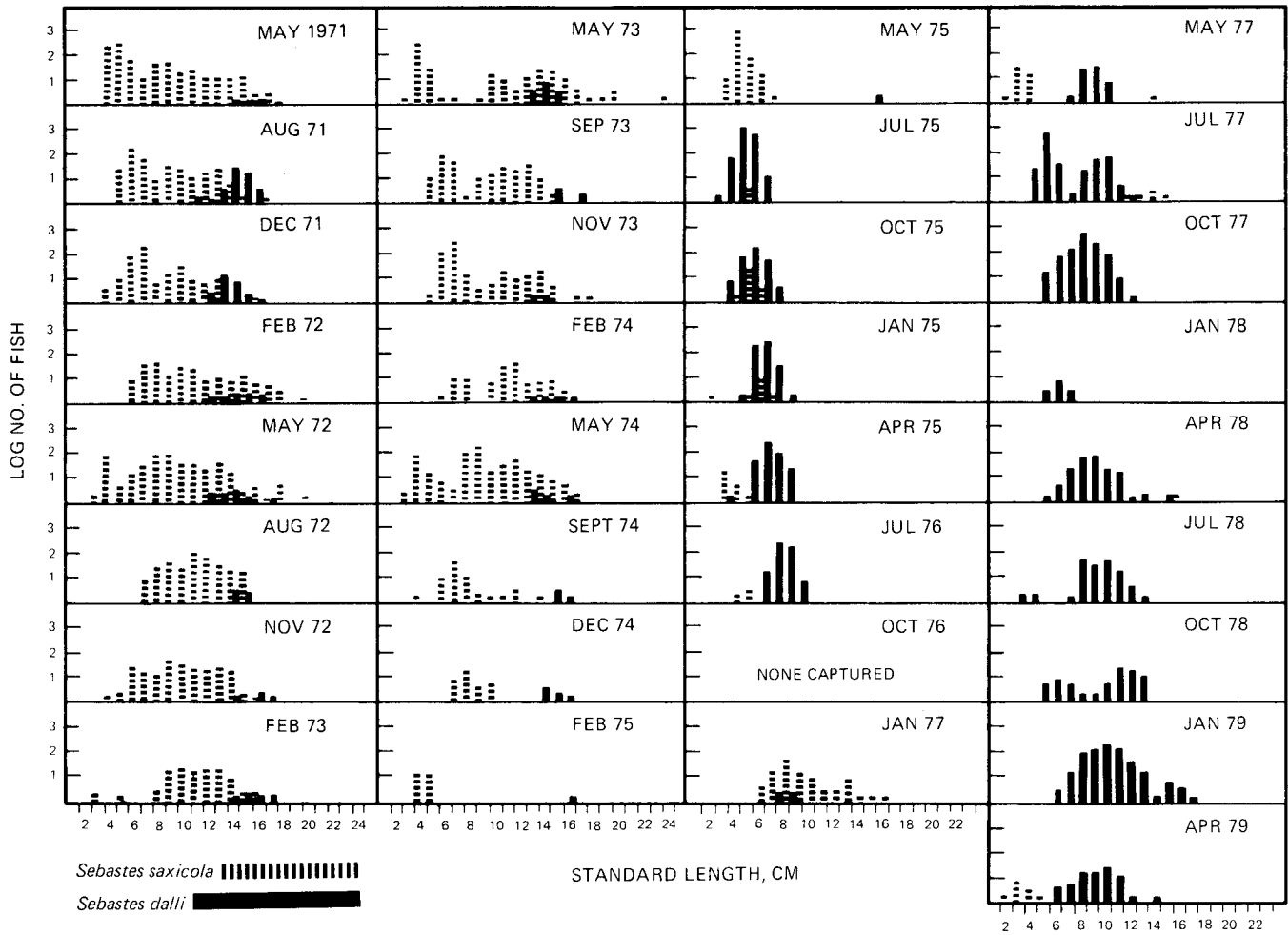
Figure 7. Length-frequency distribution of *Sebastes saxicola* and *S. dalli* in quarterly trawl surveys off Orange County, May 1971 through January 1979.

fall-winter catches at these depths captured 43±27 (95% CL) *S. saxicola* per haul ($N = 12$). Thus, there were slightly but not significantly more *S. saxicola* in deeper water after 1975 than before (1.5-fold increase), and there is only a remote possibility that the entire *S. saxicola* population moved to deeper water following the *S. dalli* influx.

The large increases in abundance of *S. saxicola* in 1971, 1973, and 1975, and of *S. dalli* in 1975 and 1977 were due to recruitment of very young fish into the survey area. As shown in Figure 7, *S. saxicola*, ranging in size from 25 to 45 mm (SL), were encountered during May trawls each year through 1977 with the largest recruitment episodes occurring in odd-numbered years. No young of the year *S. dalli* occurred any time during this period although there were always a few larger fish (120- to 160-mm SL). In contrast, the period from summer 1975 through 1979 was marked by two major odd-year (1975 and 1977) influxes of 25- to 45-mm young of the year *S. dalli* but few *S. saxicola*. The January 1978 deep

trawl (137 m) contributed the only rockfish to that survey, and all were earlier year class *S. saxicola*.

Relation of Catch Variations to Oceanographic Conditions

The odd-year episodes in rockfish abundance and recruitment and the apparent shifts in dominant species stimulated a comparison between catch variations and variations in oceanographic conditions. Time series oceanographic data from this survey are limited. However, as indicated in the methods section (above) and in Mearns (1977, 1979b), a considerable detailed time series of weekly and monthly sea-surface temperatures and Secchi disk readings was available for Santa Monica Bay, some 30 to 50 km north of this survey area.

Comparison of catch variations with changes in physical data produced some interesting relationships (Figure 8). In terms of seasonality, highest catches occurred during or just following the month of lowest sea-surface temperatures (generally spring, Figure 8 middle). In
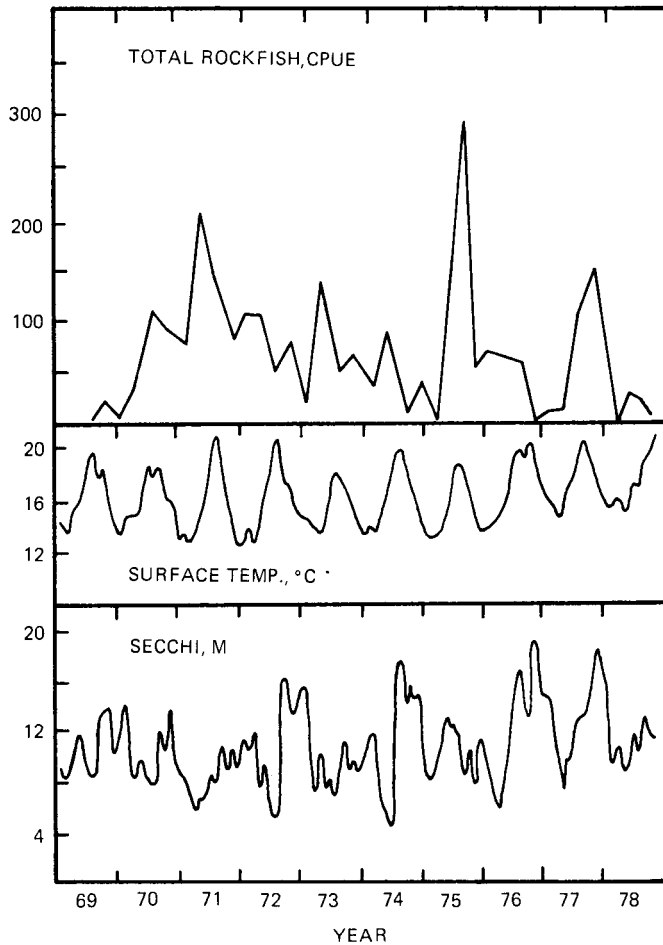
Figure 8. Comparison of (top) long-term fluctuation in abundance of rockfish catch off Orange County with (middle) average monthly sea-surface temperature and with (bottom) Secchi depth visibility in Santa Monica Bay, 1969-78.

addition, peak catches generally occurred during conditions of decreased visibility (increased turbidity), whereas poor catches occurred mainly during periods of increased visibility (low turbidity) as measured by Secchi disk depths (Figure 8 bottom).

As explained above, peak catches were due mainly to recruitment of the young *S. saxicola* and *S. dalli*. Thus, there are either more young recruiting into the area and the year during conditions of cool water and increased turbidity, or the young fish are avoiding gear during periods of warm water and low turbidity.

Some of the year-to-year differences may be related to longer term physical conditions. For example, the peak catch years of 1971, 1973, 1975, and 1977 followed fall and early winter periods of exceptionally low turbidity, which also occurred at two-year intervals (e.g. the fall-winter of 1972-73, 1974-75 and 1976-77, where Secchi depths averaged 15 to 18 m for periods of 3 to 5 months; ⌐igure 8 bottom).

᠈ long-term trend of decreasing "baseline" catch of

rockfish also appears to relate to long-term changes in physical conditions. As shown in Figure 8 (middle), winter minimum temperatures were becoming increasingly cooler from 1969 to 1971-72 but increasingly warmer from 1972-73 to 1978. In fact, annual average rockfish catches were inversely related to annual sea-surface temperature over the range 15.3 to 17.4°C (Figure 9). Similarly, turbidity has undergone a general increase from 1971 through 1978. Thus, both the trend of increasing winter sea-surface temperature and increasing turbidity appear to be associated with generally decreasing catches of rockfish.

In addition, there appear to be temperature-related species groups; for example, catches, dominated by *S. dalli* ("c" in Figure 9), occurred during consecutive warm-water years of 1976, 1977, and 1978, which averaged 17°C or higher. In contrast, *S. saxicola* ("s"; Figure 9) dominated catches during years that averaged 16.2°C or lower; highest *S. saxicola* catches occurred during the two coldest years of 1971 and 1975 (15.8 and 15.3°C). Since large catches are mainly due to small recruiting fish, it appears that cooler years favor recruitment of *S. saxicola* into the area whereas warmer years favor recruitment of *S. dalli*.

DISCUSSION AND IMPLICATIONS

A diverse assemblage of rockfish inhabit waters of the softbottom coastal shelf of southern California. During the 1970's, this assemblage has included large numbers of relatively small species, mainly *S. saxicola* and *S.*
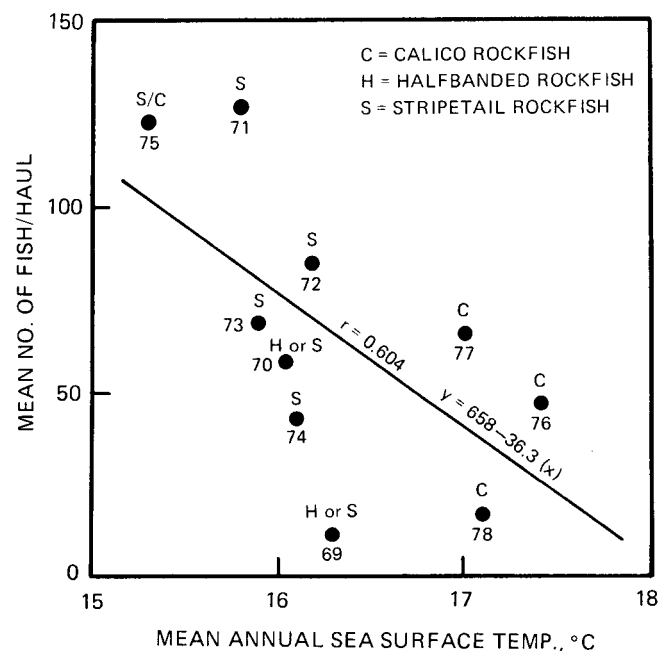

Figure 9. Average annual rockfish catch versus average annual sea-surface temperature. Year and species characterizing each point are indicated.

dalli, depending on the year, location, and depth. *S. semicinctus, S. diploproa, S. miniatus,* and *S. jordani* are also important, but secondary, near-bottom species, with importance dependent on depth and the number of recently settled young rockfish.

The relative abundance of trawl-caught rockfish species caught by small research otter trawls is markedly different than relative abundances landed in commercial and sport fisheries. For example, *S. levis, S. serranoides, S. caurinus, S. miniatus,* and *S. paucispinis* have dominated past party-boat landings in southern California, whereas *S. paucispinis, S. goodei* and *S. miniatus* dominated commercial trawl and set-line catches (Young 1969). Only *S. miniatus* is abundant in all three "fisheries." This fact, coupled with the lack of significant *S. saxicola* and *S. dalli* landings suggests that rockfish assemblages are more complex and diverse than reflected by any single sampling method and, further, that data taken by all these methods should be used to assess the ecology of local rockfish populations.

Obviously, *S. saxicola* and *S. dalli* are among the most important rockfish in southern California. According to Miller and Lea (1972), both *S. saxicola* and *S. dalli* are considered common in southern California. Both range from Sebastian Viscaino Bay, Baja California, north to San Francisco, but *S. saxicola* continues its range into southeastern Alaska; also, *S. saxicola* has a reported depth range that is greater than that of *S. dalli* (58 to 400 m and 18 to 255 m, respectively). These observations suggest that *S. saxicola* is a more northerly, cooler-water species than *S. dalli*.

The disappearance of *S. saxicola* and influx of *S. dalli* on the inner coastal shelf of central southern California in 1975 is an interesting ecological event that deserves further investigation. Neither species is subject to direct fishing pressure. Yet data presented here suggest that the event was, in fact, large-scale (in that it covered at least 100 km of coastline) yet limited to the coastal area south of Point Dume and inshore of the 60- to 130-m isobaths. In this region, at 130-150 m, *S. saxicola* populations were apparently not measurably impacted by the lack of inshore recruitment from 1975 to 1979.

The 1975 inshore switch in dominance from *S. saxicola* to *S. dalli* raises the question: Which condition, if either, is normal for this area? One is tempted to believe that conditions first observed are the "norm" and any change that follows is "abnormal." However, data from an earlier quarterly trawl survey in Santa Monica Bay (Carlisle 1969) indicate that *S. dalli* was more abundant than *S. saxicola* following the warm-water years of 1957-63. It is therefore possible that *S. dalli* dominance is more the norm than *S. saxicola* dominance.

However, *S. saxicola* appear to be more successful in cool-water years and *S. dalli* in warm-water years. There is a long history of warm- and cool-water episodes in southern California; these episodes are accompanied by occurrences and invasions and mass strandings of unusual species of fishes and invertebrates (Radovich 1961). It is unreasonable to assume that such physically triggered events are limited only to the pelagic species that have characterized them in the past (pelagic red crabs, jumbo squid, etc.). Profound ecological changes should be expected in the benthic fauna as well, and it is possible that southern California rockfish populations are continuously affected by such aperiodic but frequent oceanographic changes. Indeed, 1973 in southern California coastal waters was marked by invasions and mass strandings of pelagic red crabs (*Pleuroncodes planipes*; Mearns 1979) and, in deep water offshore, by an unusually heavy recruitment of a large benthic echiuroid, *Listriolobus peloides*, which persisted in larger numbers through 1977 and effectively bulldozed shelf sediments and increased benthic infaunal diversity at several locations (Word 1979). The following year, 1974, was marked not only by the change in rockfish species dominance but also by a major late spring red tide and an invasion of large jellyfish (*Pelagia* sp.; Mearns 1979a). The two years (1975 and 1976) were characterized by brief, but intense, mass strandings of subtropical jumbo squid (*Dosidiscus gigas*) and, later, by a strong catch of swordfish. With concurrent bottomfish and physical data now available, it would be worthwhile determining to what extent fluctuation in coastal zone fish populations is related to the larger scale oceanographic events that triggered these invasions.

Whichever rockfish species is dominant, successful recruitment has occurred only during odd-numbered years. This two-year "periodicity" is somewhat related to two-year episodes of turbidity, suggesting that the cause may be related to oceanographic conditions (such as plankton blooms) that have changed at two-year intervals. However, the cause may also be biological in origin, i.e. an inherent spawning cycle not unlike the two-year cycles experienced by Alaskan populations of pink salmon.

The 1974 switch in dominance from *S. saxicola* to *S. dalli* was an event clearly affecting the distribution and abundance of post-larval juveniles, not adults. This suggests the importance of carefully surveying juvenile rockfish populations in the future. The event also suggests that at least inshore, these two species are competing for food resources. Work is now in progress at the Coastal Water Research Project to determine feeding habits of the young of both species and to examine additional sources of data including an equally long time series off Palos Verdes and other southern California coastal sites.

ACKNOWLEDGMENTS

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NUTRIENTS AND PHYTOPLANKTON COMMUNITY COMPOSITION IN SOUTHERN CALIFORNIA COASTAL WATERS.[1]

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ABSTRACT

Analysis of portions of a phytoplankton data set collected in Santa Monica Bay from 1957 to 1972 suggested seasonal and distributional relationships between diatoms and dinoflagellates. Blooms of both groups overlapped and tended to be concentrated into a period from spring through summer. However, while diatom biomass was advected into the Bay from offshore, dinoflagellate blooms seemed to arise inshore near sources of anthropogenically derived nutrients.

Differences in abundance and community composition were explained on the basis of groups of environmental factors (parameter sets) favoring each group. Supplement of limiting factors (such as nitrogen) enhances total biomass, but differences in parameter sets may result in inshore-offshore distributional patterns. It was suggested that the relative abundance of ammonia-N may be a tag for the dinoflagellate parameter set.

RESUMEN

El análisis de porciones de la serie de datos de fitoplancton colectadas en la Bahía de Santa Mónica de 1957 a 1972 sugirió que existen relaciones estacionales y distribucionales entre diatomeas y dinoflagelados. Los florecimientos de los dos grupos son concurrentes y tendieron a concentrarse en el período de primavera a verano. Sin embargo, mientras la biomasa de diatomeas se desplazaba desde mar afuera hacia la Bahía, florecimientos de dinoflagelados parecían originarse en la zona costera cerca de concentraciones de nutrientes derivados antropogénicamente.

Las diferencias en la abundancia y en la composición de la comunidad se explicaron basándose en grupos de factores ambientales (series de parámetros) que favorecen a cada grupo. El suplemento de factores limitativos (como el nitrógeno) aumenta la biomasa total, pero diferencias en las series de parámetros pueden dar lugar a patrones distribucionales cerca de la costa y mar adentro. Se sugirió que la abundancia relativa de amoníaco-N puede ser un indicador para la serie de parámetros de dinoflagelados.

NUTRIENTS AND PHYTOPLANKTON COMMUNITY COMPOSITION IN SOUTHERN CALIFORNIA COASTAL WATERS

The abundance, distribution, and succession of phytoplankton in southern California coastal waters is regulated by interactive processes occurring both offshore—at and beyond the coastal shelf edge—and inshore, along the shelf (cf. Eppley et al. 1978, 1979 a, b). Whereas oceanic processes tend to influence large segments of the coastal system, and the effects of inshore processes are often more localized, both significantly influence the coastal phytoplankton (cf. Thomas 1972; SCCWRP 1973; MacIsaac et al. 1979). For example, a municipal wastewater outfall may, during periods of strong upwelling, be insignificant as a source of nutrients to surface waters. However, when upwelled nutrients are unavailable, the outfall can be a determinant of both numbers and types of phytoplankton present in a certain area. Locally fertilized areas, in turn, tend to concentrate planktonic and pelagic grazers and carnivores (Brewer et al. 1979).

In this paper I will examine some of the interactions between offshore- and inshore-derived nutrients as they relate to the regulation of phytoplankton numbers and community composition in coastal waters.

There is an imbalance between the amount of effort spent in relating macro- and mesoscale phenomena to changes in total phytoplankton biomass (as chlorophyll, or particulate C or N) and that spent in discerning the importance of small-scale events and the interactions between large- and small-scale events as they affect the abundance and types of phytoplankton in the coastal zone (Ryther and Officer 1979). Unfortunately, the costs and difficulties of studying the fine details of coastal phytoplankton dynamics often prohibit their consideration.

However, since the development of marine food webs is largely dependent upon these details (cf. Tont 1976; Lasker 1975), the value of the phytoplankton as a source of information about coastal ecosystems is seriously reduced if we fail to consider them. Thus, Ryther (1954) observed that changes in nutrient composition due to waste-water loading to Long Island bay waters altered phytoplankton community structure to the extent that diatoms, the principal food of the hardshell clam, were significantly reduced. The result of this alteration was expressed by the demise of the clam fishery in that area.

Thus, in terms of the food web, changes in total phytoplankton biomass explain little unless accompanied by information about the taxa that compose that biomass. Simply put, many food webs in coastal waters develop around localized phytoplankton communities, and these communities represent a response to interactions between numerous environmental conditions or parameter sets that favor the growth of certain taxa over others. For the time being these parameter sets must remain undefined. However, nitrogen, in various forms, appears to be a com-

ponent of some these hypothetical sets. Thus, the form of nitrogen may serve as a "tag" for different parameter sets, thereby providing a means for understanding and predicting phytoplankton composition on the basis of a few measurements.

Figure 1 shows the locations of 18 stations in Santa Monica Bay sampled weekly from 1957-72 by Hyperion Treatment Plant personnel using vertical net (#20 silk 10.6-cm aperture diameter) tows from about 15 m. Further details of sampling are given in SCCWRP (1973). The stations along lines 7, 3, and 2 are considered in this discussion and have been connected by dashes.

Figure 2 is a plot of weekly abundances (as sample volume, in ml) of diatoms at an offshore station (7C) and dinoflagellates at an inshore station (3C) during 1965, a year representative of average conditions in the Bay. Rapid increases in the biomass (which I will refer to as blooms) occurred in mid- to late winter, early spring, and during mid-summer. Bloom intensities increased to a maximum of 10 ml for diatoms and 8.5 ml for dinoflagellates, then decreased to late fall-early winter minima. Diatom blooms both offshore and inshore were characterized by dramatic but short-lived changes in biomass; dinoflagellate populations were more stable, sample volumes rarely falling below 0.1 ml from winter through late summer.

Figure 3a shows how mean monthly diatom abundances changed from offshore to inshore; Figure 3b provides the same analysis for dinoflagellates. The plots are for data collected at eight stations along lines 7, 3, and 2 (Figure 1). Diatom densities generally decreased inshore indicating that biomass is advected into the Bay from at or beyond the coastal shelf edge (Figure 4).

Figure 3b shows that dinoflagellate densities tended to increase inshore. There were three centers of maximum biomass: 1) at the mouth of Ballona Creek; 2) near the Chevron Oil Company refinery at El Segundo; and 3) in the vicinity of the 1-mile Hyperion outfall, which was

operative twice weekly (discharging at 10 million gallons/day) throughout the 1960's (J. Nagano personal communication). It would appear that growth of dinoflagellates was initiated within the Bay, possibly from "seed beds," at these locations.

The Mann-Whitney U test (Downie and Heath 1971) was used to discern whether the apparent offshore-inshore distributional patterns in Santa Monica Bay phytoplankton communities were significant. The results, shown in Table 1, suggest that during 1963, a red tide year, dinoflagellates were more abundant inshore than offshore ($P<0.05$). In 1965, when data from months with highest and lowest biomass values were disregarded, U was again significant ($P<0.05$) for both dinoflagellates and diatoms. U, being a rank order statistic, was destabilized by data points representing extreme events such as blooms (July) and biomass minima (November, December). On the average, however, there are distributional differences between inshore and offshore communities.

It seems that two types of parameters regulate phytoplankton dynamics in Santa Monica Bay: 1) those that influence total abundance, and 2) those that influence community structure.

Since nitrogen is believed to be one of the substances that most limit the growth of phytoplankton in coastal waters (Ryther and Dunstan 1971; SCCWRP 1973; Thomas 1972), it is reasonable that changes in nitrogen concentration, particularly inorganic-N, will result in changes in total biomass or numbers (Eppley et al. 1979 a, b). Some examples of nitrogen sources to coastal waters, presented in Table 2, show that upwelled nitrate provides most of the nitrogen along the coast (SCCWRP 1973). However, significant upwelled nitrate inputs occur only during a few months of the year in most places. Municipal effluents, discharged at 60 m, represent a potentially continuous nutrient source (Schafer 1978), but it is not known how often 60-m outfall discharges reach the surface (Eppley et al. 1977; Hendricks 1975), especially considering that initial dilution reduces the nitrogen in the waste field by about 200 times within 100 seconds of
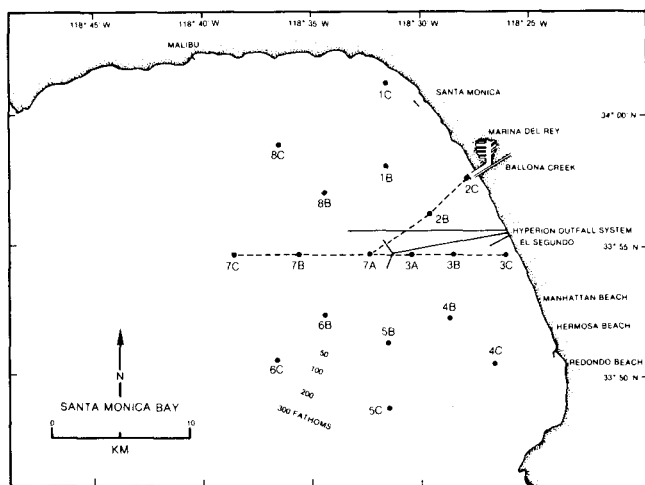

Figure 1. Stations sampled each week in Santa Monica Bay from 1957-72. Locations of 5- and 7-mile Hyperion outfalls are shown. Dashed lines connect stations considered in this discussion.
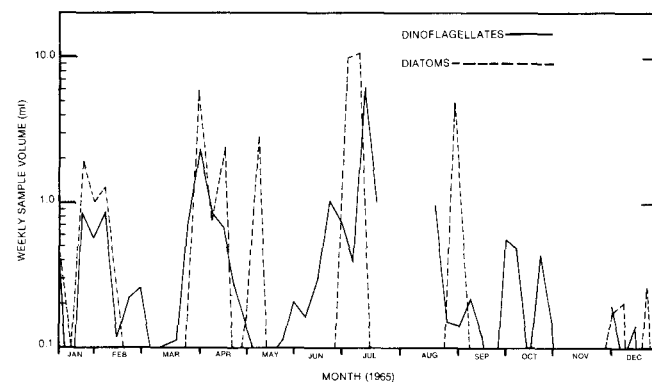

Figure 2. Weekly sample volumes of dinoflagellates (solid line) from an offshore station (7C) and diatoms (dashed line) from an inshore station (3C) in Santa Monica Bay during 1965.
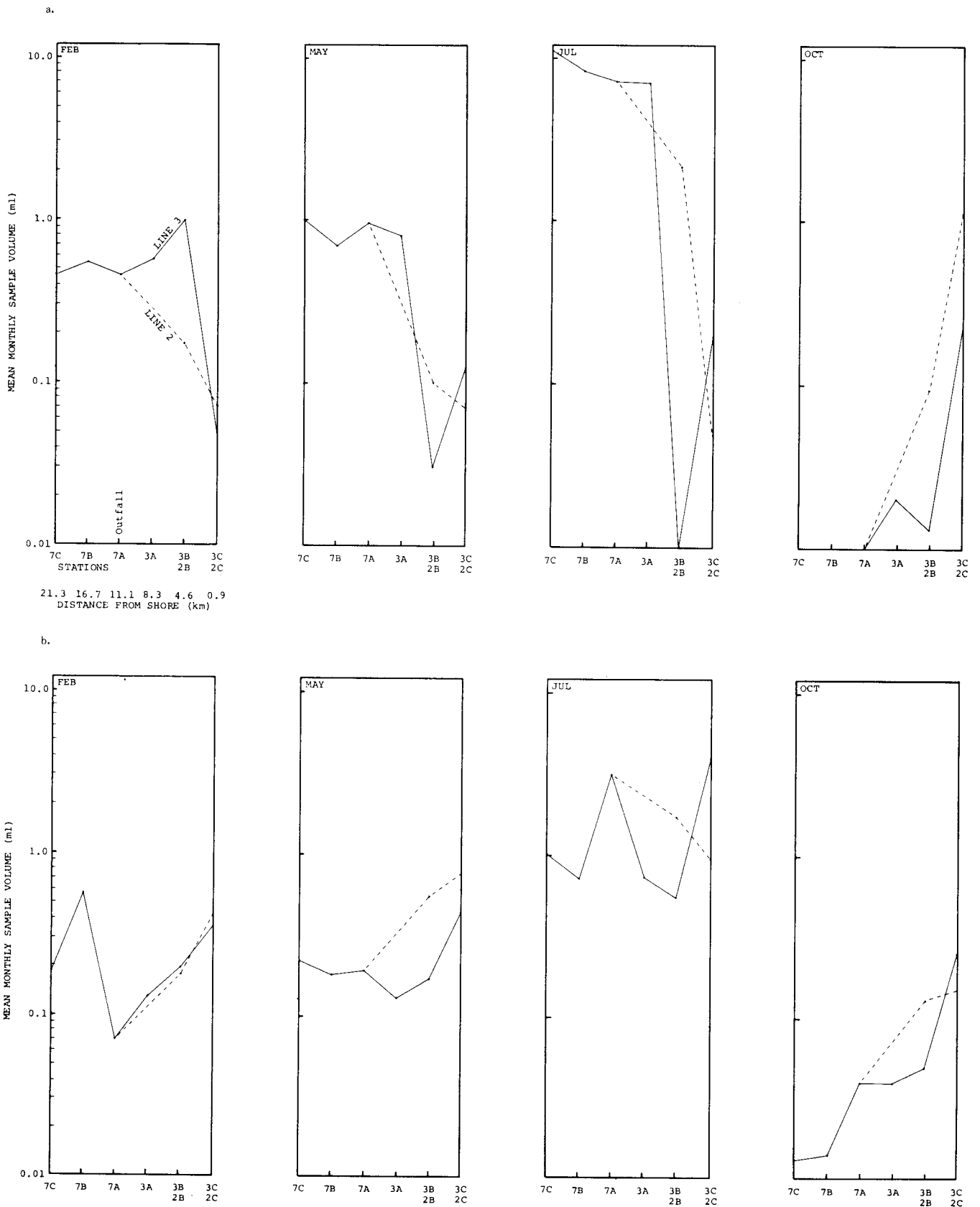
Figure 3. a) Mean monthly diatom abundance (as ml of diatoms per sample) at stations along lines 7, 3, and 2 in Santa Monica Bay in certain months, 1965. b) Same as in a) but for dinoflagellates. Station locations, outfall location (5-mile), and distance from shore are shown. The figures give representative seasonal patterns.
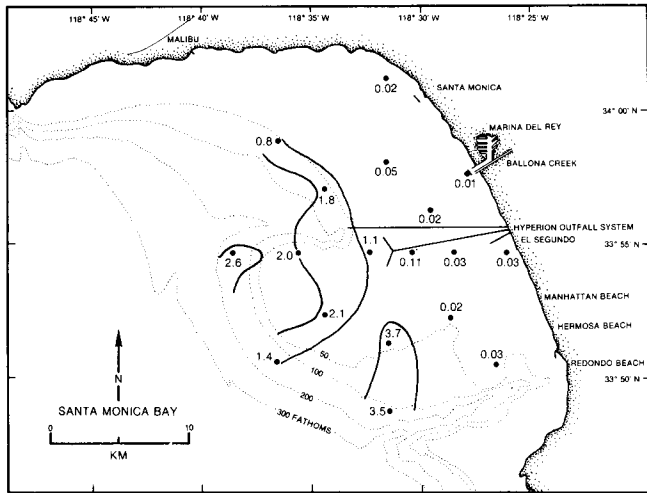
Figure 4. The distribution of diatoms (as mean sample volume in ml) in Santa Monica Bay, May 1965.

discharge (Table 3) and the presence of well developed thermal stratification may confine the remaining N below the surface for several days (Hendricks 1975). The effects of these discharges upon near-surface phytoplankton are uncertain at best (SCCWRP 1973; MacIsaac et al. 1979), but Figure 3 suggests that the 60-m effluents represent only a periodic nutrient source for the phytoplankton.

Inshore, nitrogen is supplied through tidal exchange with harbors, rainfall runoff from shore, and shallow-water discharges at industrial outfalls. Table 2 shows that most inshore nitrogen sources provide ammonia-N, a form more easily utilized by phytoplankton than nitrate (Soeder and Stengel 1974; Samuels 1979). Though inputs from runoff vary seasonally, sources such as shallow outfalls add nutrients on a fairly continuous basis. Unlike upwelling and the 60-m municipal effluents, inshore sources deliver most of their nutrients directly to the euphotic zone. This difference between inshore and offshore nutrient sources is very likely important to coastal phytoplankton as nutrient uptake kinetics, and hence community structure may be altered due to the change in the availability, the consistency of delivery, and the form of nitrogen present in inshore waters. For instance, following initial dilution, only 6.1 of the 1228.6 μg-atoms/liter ammonia-N discharged from the Hyperion 5-mile outfall remains in the waste-water plume (Table 3). This ammonia-N may not be available to the phytoplankton for several days during which time it is further diluted prior to surfacing. The Chevron Oil Co. outfall at El Segundo, on the other hand, continuously discharges on the average of 2050μg atoms/liter of ammonia-N into the euphotic zone. The data presented in Figure 3b, as well as those of others (Eppley et al. 1979 b; R. Eppley personal communication) suggest that the Chevron Oil Co. discharge supports a relatively constant enhancement of dinoflagellate biomass.

TABLE 1

Mann-Whitney U Values for Differences between Inshore (Station 3C) and Offshore (Station 7C) Populations of Diatoms and Dinoflagellates.[1]

	1963	1965
Diatoms		
Annual	†49.5	*41
[2]Extremes removed	*16.5	**17
Dinoflagellates		
Annual	**38.5	†47
[3]Extremes removed	____	*21

[1]The U test gives 2 values; the values reported here are the lower of the 2 values from which significance was then determined (cf. Downie and Heath 1971).
[2]Extreme months for 1963 diatoms were offshore biomass minima during January and February; extreme months for 1965 were offshore biomass minima in September and October.
[3]Extreme months for 1965 dinoflagellates were inshore July biomass maximum and offshore minima in November and December.
†U not significant ($P>$ 0.05); *$P<$ 0.05; **$P<$ 0.01.

TABLE 2

Some Nitrogen Sources along the Southern California Coastal Shelf.

Source	Predominant form	Average concentration μg-atoms/liter	Annual mass emission (metric tons/year)	Constancy
[1]Upwelling (7,500 km)	NO_3-N	14.3	180,000	3 months/year (April-June)
[2]Municipal outfalls	NH_3-N	28,200	41,200	?
[3]Surface runoff	Total N	____	2,500	rainy season
[3]Chevron Oil. Co.	NH_3-N	2,050	235	continuous
[4]Long Beach Harbor	NH_3-N	7.48	____	4-month period (December-March)

Sources: 1. Southern California Coastal Water Research Project 1973.
2. Schafer 1978.
3. State Regional Water Quality Control Board, Los Angeles.
4. Environmental Quality Analysts and Marine Biological Consultants 1977.

TABLE 3

Examples of the Effects of Initial Dilution (200 Times) on Effluents from Major Outfalls.[1]

Location of Discharge	Ammonia-N μg-atoms/liter	Diluted NH_3-N μg-atoms/liter	Mass emission[2] (metric tons/year)	Diluted emission (metric tons/year)
Hyperion:				
5-mile	1,228.6	6.1	7,590	38.0
7-mile	18,500.0	92.5	1,650	8.3
JWPCP	2,785.7	13.9	18,000	90.0
Orange County	2,571.4	12.9	9,830	49.2
Point Loma	1,700.0	8.5	3,810	19.1
Oxnard	1,464.3	7.3	317	1.6

[1]About 0.5% of emission remains in the waste field. Diluted NH_3-N is probably dispersed to the extent that under most conditions noticeable phytoplankton biomass enhancements do not occur directly above outfalls.
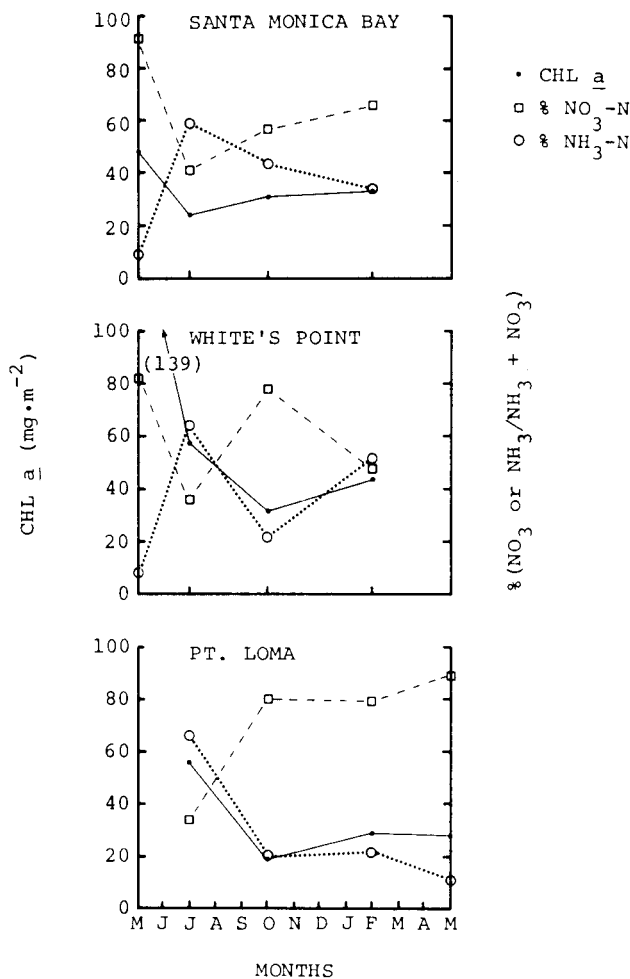[2]Source: Schafer 1978.

Figure 5. Euphotic-depth integrated chlorophyll concentration, % NH₃—N and % NO₃ during cruises from May 1971-May 1972 to stations adjacent to municpal outfalls at (top) Santa Monica Bay (Hyperion 5-mile outfall), (middle) White's Point (JWPCP outfall), and (bottom) Point Loma (San Diego County outfall). Values represent medians for all stations around each outfall.

Figure 5 was plotted from data reported by SCCWRP (1973). Water samples were collected from within the euphotic zone and analyzed for nutrient and chlorophyll content at stations above and adjacent to municipal waste-water outfalls in Santa Monica Bay (Hyperion 5-mile outfall), White's Point (JWPCP-Los Angeles County outfall), and off Point Loma (San Diego County outfall). The stations at each location were visited four times between May 1971 and May 1972. The data from each station were depth integrated, and the median value for each parameter was reported for each location. In Figure 5, phytoplankton biomass as chlorophyll a is plotted against time. The assumptions inherent in using chlorophyll a as an indication of biomass are discussed elsewhere (Eppley 1972; Kleppel 1979). If N is limiting, fluctuations in biomass should follow changes in nitrogen availability. In an attempt to determine whether the phytoplankton responded more to one form of N than another, median NH₃-N and NO₃-N values were plotted as the

ratio of each form to their sum (NH₃-N/NH₃-N + NO₃-N and NO₃/NH₃—N+NO₃—N). In Santa Monica Bay (Figure 5a), the phytoplankton responded consistently to relative abundance of nitrate. Using the relative preference index (McCarthy et al. 1977), Eppley et al. (1979b) observed an increase in NO₃-N preference by diatoms during upwelling relative to inshore populations not exposed to upwelling. Since Santa Monica Bay in the vicinity of the outfall is both dominated by diatoms and adjacent to the Santa Monica Canyon, it would appear that local phytoplankton responded to upwelled nitrate more so than to ammonia-N.

At White's Point (Figure 5b), the biomass responded to nitrate when it was very abundant but switched to ammonia when nitrate was less abundant. Since sewage effluent is a principal source of ammonia, the JWPCP effluent may represent the nutrient source for phytoplankton in this area. However, the amount of ammonia reaching the surface did not appear to increase the biomass greatly relative to other areas. That is, while ammonia may be the more important form of nitrogen in these waters, it did not seem to be present at the surface in high enough concentrations to enhance production beyond background levels. The implications to community structure – whether diatom or dinoflagellate dominated – are presently unknown. Point Loma (Figure 5c) chlorophyll a followed the relative abundance of ammonia-N, again suggesting an anthropogenic or inshore influence upon the phytoplankton.

Although nitrogen loading is associated with changes in total phytoplankton biomass, it is apparent that the form and availability of the nitrogen (in relation to other parameters) may determine the structure of the planktonic community. This latter aspect of coastal phytoplankton dynamics is most important, as food web development hinges upon the composition of the planktonic community. For instance, the survival of first-feeding northern anchovies is partially dependent upon the juxtaposition of the larvae and a well-structured chlorophyll maximum composed largely of *Gymnodinium splendens* and other dinoflagelllates, which are the principal foods of the larvae (Lasker and Zweifel 1978).

In Santa Monica Bay, dinoflagellates appear to respond to a set of parameters characterized by inshore conditions (Figure 3b). The preponderance of ammonia sources in these waters suggests that ammonia may be a "tag" for the dinoflagellate parameter set. Conversely, diatoms respond to parameters characteristic of offshore waters, identifiable by changes in the relative abundance of nitrate. Similarly, Estrada and Blasco (1979) reported that dinoflagellates in the Baja upwelling system become dominant in the presence of low salinity, nutrient-rich water, supplied during periods of reduced upwelling, whereas diatoms are enhanced in the presence of high

salinity, upwelled waters. The implications are that dino-flagellates are enhanced in the presence of waters de-rived inshore, and in this case, salinity is a "tag" for identifying associations of phytoplankton with various parcels of water.

Further work is needed to better define the dinoflagel-late and diatom parameter sets in coastal waters. Recent studies in estuaries and coastal systems have revealed the importance of the often ignored interactions between phytoplankton community structure and the availability of silica, a macronutrient for diatoms, which is relatively unimportant for most dinoflagellates (Samuels 1979; Ryther and Officer 1979; L. Haury personal communi-cation). In addition, the problems of heterotrophy are not well understood. Organic forms of carbon and nitrogen are more abundant inshore than offshore and are sus-pected of being utilized facultatively by several taxa of phytoplankton (Wheeler et al. 1977; B. Abbott personal communication).

The implications of identifying the factors regulating phytoplankton community structure are exciting with re-spect to understanding, and perhaps even manipulating, coastal food webs.

ACKNOWLEDGMENTS

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TROPHIC STRUCTURE AND POLLUTANT CONCENTRATIONS IN MARINE ECOSYSTEMS OF SOUTHERN CALIFORNIA [1]

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ABSTRACT

The relationship between trace chemical concentrations and trophic level of fishes and several invertebrates was investigated in four southern California marine ecosystems: the Salton Sea, a saline lake; Newport Bay, a back-bay area; the Palos Verdes shelf, a waste-water contaminated coastal zone; and the San Pedro Channel, which contains a coastal pelagic food web. Feeding habits were investigated and used to assign assumed trophic levels to each species. These assignments were directly related to the cesium/potassium ratio (Cs/K), a possible chemical trophic step indicator. Trophic structure amenable to food web increases of pollutant concentrations was relatively strong in the Salton Sea and coastal pelagic ecosystems and was weaker in the nearshore ecosystems. As expected, organic mercury and the chlorinated hydrocarbons generally increased with increased trophic level; however, other trace metals did not.

RESUMEN

La relación entre sustancias químicas a bajas concentraciones y el nivel trófico de peces y varios invertebrados fueron investigados y usados para asignar presuntos niveles tróficos ·a cada especie. Estas asignaciones fueron port, una bahía apartada; la plataforma submarina de Palos Verdes, una zona costera contaminada con aguas residuales; y el canal de San Pedro, que contiene una red alimenticia pelágica costera. Los hábitos de alimentación fueron investigados y usados para asignar presuntos niveles tróficos a cada especie. Estas asignaciones fueron directamente relacionadas con la proporción de cesio/potasio (Cs/K), que es posiblemente un indicador químico del grado trófico. La estructura trófica sujeta a incrementos de concentraciones de contaminantes en la red alimenticia fue relativamente fuerte en el Salton Sea y en ecosistemas pelágicos costeros, y más débil en los ecosistemas de cerca de la costa. Como se esperaba, el mercurio orgánico y los hidrocarburos clorinados generalmente aumentaron con el aumento en el nivel trófico; sin embargo, no aumentaron otros metales de bajas concentraciones.

INTRODUCTION

The objective of the research described here was to determine the degree to which southern California marine

food webs are "structured," i.e. composed of species with distinct feeding relationships that can cause successively increased concentrations of some pollutants (Isaacs 1973). Public apprehension regarding the accumulation of pollutants in seafood is based largely in the assumption that such food chain or food web increases of organic and inorganic contaminants (Odum 1971), which has been demonstrated in certain terrestrial and freshwater systems, also occurs widely in marine ecosystems. However, in recent years, there have been an increasing number of reports that contradict this assumption, at least in part. The evidence obtained to date indicates that there is measurable structure to the coastal marine ecosystems of the Southern California Bight. Despite this structure, concentrations of most trace metals of present concern decrease with increase in presumed trophic levels. An important exception is organic mercury; this trace constituent, and the higher molecular weight chlorinated hydrocarbons—total DDT and PCB 1254—appear to increase in concentration with increase in trophic level.

BACKGROUND

An unstructured food web is composed primarily of opportunistic, multidirectional feeders; under this condition, differences in pollutant concentrations in member organisms are not necessarily related to feeding relationships. Evidence supporting the unstructured food web hypothesis was obtained by Young (1970) in a comparative study of the distribution of two alkali metals, cesium (Cs) and potassium (K), in marine organisms from the Salton Sea in southern California and the Gulf of California. Potassium, an essential electrolyte, must be maintained at fairly constant levels in tissues; this is not the case for cesium, which is usually found in trace quantities. Increases in the ratio of cesium to potassium over known food chain links or trophic level steps (Odum 1971) can be expected because cesium has been found to have a biological half-life that is generally two to three times that of potassium. Thus, the relative values of the Cs/K ratio in organisms in a given ecosystem should give indication of the degree of trophic structure in that ecosystem, and thus indicate the potential for food chain increases of pollutant concentrations within the system.

The Salton Sea is a large saline lake with a very specialized and simplified food web (Walker 1961) that resembles the classical food chain situation. This structured ecosystem provided Young (1970) and Isaacs (1972, 1973) with an opportunity to measure cesium and potassium concentrations in the muscle tissues of widely

differing marine fishes and to compare the Cs/K ratios for the fishes with those for their food. The results indicated median predator/prey increase factors of 2.2 for cesium and 2.5 for Cs/K ratio (Table 1). These values are in good agreement with those reported previously for various terrestrial and freshwater organisms (Anderson et al. 1957; McNeill and Trojan 1960; Green and Finn 1964; Pendleton 1964; Hanson et al. 1964; Pendleton et al. 1965; Hanson 1967; and Gustafson 1967). In addition, cesium concentrations and Cs/K ratios in muscle tissue of a given fish species were found to increase reguarly with the number of trophic level steps in the food chain leading to that particular species (Table 2). The values, on the average, doubled with each step between the bottom (Level II) and the top (Level IV-V) of the trophic structure; these factor-of-two increases are consistent with the median predator/prey increase factor.

Subsequently, Young (1970) and Isaacs (1972) compared the Cs/K ratios for Salton Sea fishes with those for the same species in the Gulf of California and found that the latter did not show any major differences with increase in presumed trophic level (Table 3). This suggested that, in contrast to the Salton Sea community, the part of the food web sampled in the nearby Gulf of California was "homogeneous" in nature and unstructured, rather than characterized by structural feeding or trophic levels.[1]

On the basis of these and other findings, Isaacs (1972, 1973, 1976) has proposed that marine food webs are generally unstructured and has developed mathematical models applicable to such situations. However, since the limited investigation in the Gulf of California, no further field work has been done to test these models or the assumptions behind them. In view of the concern over increases of pollutant concentrations in marine food webs, particularly in those leading to man, it is important that such uncertainties be resolved.

ANALYTICAL PROCEDURES

The major problem facing us in the initial stages of this program was the development of a procedure for measuring, with sufficient precision, the very low concentrations of cesium that occur in marine organisms. Typical levels of this trace alkali metal in wet fish muscle are 10-50 $\mu g/kg$, or parts per billion (ppb); this is near or below our detection limits for other metals of interest (e.g. chromium and nickel), using atomic absorption spectrometry (AAS) without chemical concentrations follwing sample digestion. Thus, it was necessary to develop a procedure by which cesium could be separated from the host of interfering compounds found in tissues and concentrated

[1] It should be noted that the *absolute* values for cesium and Cs/K ratios in the specimens from the Salton Sea and Gulf of California (or other truly marine ecosystems) are not comparable because of the different levels of cesium and potassium in the waters of these two saline environments. Rather, it is the *relative* values for specimens within a given ecosystem that should be examined in evaluating the degree of structure in the food web.

TABLE 1
Predator-to-prey Increases of Cesium Concentrations in Organisms from the Salton Sea in 1967.[1]

| Organism | Major food | Ratio, Concentration in Organisms to Concentration in Major Food | | Cs/K ratio $\times 10^{-6}$ |
		Cesium	Potassium	
Corvina	Croaker	2.2	1.06	2.0
Croaker/sargo	Pile worm	5.6	1.00	5.6
Shad	Zooplankton	2.0	0.7	2.7
Mullet	Algal mat	2.3	1.02	2.3
Median		2.2	1.01	2.5
Mean		3.0	0.94	3.2

[1] After Young 1970.

TABLE 2
Variations in Muscle Tissue Concentration (Mean ±1 Standard Error) of Cesium and Potassium and Cs/K Ratios with Differences in the Trophic Positions of Organisms from the Salton Sea in 1967.[1]

Organism	Assumed trophic level	Food chain to organism	Cesium (μg/wet kg)	Potassium (g/wet kg)	Cs/K ratio $\times 10^{-6}$
Corvina	IV-V	Croaker: pile worm: detritus[2]	202±22	3.52±0.26	57.4
Croaker	III-IV	Pile worm: detritus[2]	98± 8	3.43±0.20	31.4
Sargo	III-IV	Pile worm: detritus[2]	84± 5	3.58±0.29	23.4
Shad	III	Zooplankton: phytoplankton	46± 3	3.07±0.21	15.0
Mullet	II	Algal mat	30± 3	3.38±0.25	8.9

[1] After Young 1970.
[2] Composed primarily of phytoplankton and zooplankton (Trophic levels I and II, respectively).

TABLE 3
Variations in Muscle Tissue Concentrations (Mean ±1 Standard Error) of Cesium and Potassium and Cs/K Ratios with Differences in the Trophic Position of Organisms from the Upper (Nearshore) Gulf of California.[1]

Organism	Assumed trophic position	Cesium (μg/wet kg)	Potassium (g/wet kg)	Cs/K ratio $\times 10^{-6}$
Corvina	High	39±2.6	4.70±0.10	8.3
Croaker	Intermediate	54±2.5	4.20±0.20	10.3
Sargo	Intermediate	36±2.2	4.10±0.06	8.8
Mullet	Low	51±5.2	4.03±0.09	12.6

[1] After Young 1970; Young and Folsom 1979.

sufficiently to permit AAS analyses that could clearly resolve two-fold differences in values at the 10-ppb level. This was accomplished by modifying a procedure that had been developed by Folsom and Sreekumaran (1970) and used by Young in the Salton Sea program described in the preceding section.

Basically, the technique involves digestion of wet tissue (6 to 10 grams) in nitric acid for about five hours. The digested material is then split into two equal portions, and enough cesium standard is added to one of the two replicate solutions to approximately double its estimated concentration. This technique, known as the method of standard additions, corrects for incomplete recovery of the target element and for "'matrix" effects (biases introduced by the presence of other elements in the sample).

Next, the solubilized cesium atoms are concentrated on microcrystalline ammonium-12-molybdophosphate (AMP). This step separates the cesium from most of the other elements in the tissue, including much of the sodium and potassium, which greatly interfere with analysis. The AMP is then dissolved in ammonium hydroxide, and 2.5 to 5 microliters of this solution are injected into the carbon rod (Model 63) of a Varian Tectron AAS (Model AA6) equipped with a background corrector (Model BC-6). We have found it necessary first to condition the rod by firing and then injecting a procedural blank solution. To overcome problems of matrix effects and nonlinearity, an alternating series of aqueous cesium standard, sample, and cesium-spiked sample is then injected, and subsequently re-injected in reverse order. Replicate procedural blanks (including internal standards) are analyzed with each set of samples.

Potassium is analyzed by aspirating into an air-propane flame both unspiked and potassium-spiked aliquots of the tissue digestion solution, which has been diluted by a factor of 250 in deionized distilled water. Additional details of these analytical procedures will be reported elsewhere.

To test the accuracy of our procedures for cesium and potassium analysis, we have analyzed the Standard Reference Material No. 1571 (orchard leaves) of the National Bureau of Standards (NBS) for these metals. The uncertified cesium value listed by NBS is 0.04 mg/dry kg; in our triplicate analyses, we obtained mean and standard deviation values of 0.048 ± 0.0067 mg/dry kg, suggesting agreement within about 20%. Our corresponding values for potassium were 14.4 ± 0.15 mg/dry kg, which agree within 2% with the NBS certified potassium values of 14.7 ± 0.03 mg/dry kg.

The precision of our cesium and potassium measurements was evaluated by making five blank determinations and analyzing six replicates of composite sample muscle tissue from 10 albacore caught off San Diego in summer 1978. The results, summarized in Table 4, indicated coefficient-of-variation values for cesium and potassium in fish muscle of about 14 and 3%, respectively. The uncertainty associated with the cesium blank correction is ±2 ppb, which corresponds to an uncertainty of approximately 5 to 20% in the net values presented in this paper.

We have previously reported other analytical procedures used in the work described here. Methods for analysis of nonvolatile trace metals are given in Young and Jan (1979), Eganhouse (1975), and Eganhouse and Young (1978); and procedures for analyses for chlorinated hydrocarbons are given in Young et al. (1976). Lipid content determinations were made using the procedures of Bligh and Dyer (1959).

TABLE 4
Precision of Cesium and Potassium Measurements as Indicated by Five Blank Determinations and Analyses of Six Aliquots of Homogenized Fish Muscle.

	Cesium (ug/wet kg)	Potassium (g/wet kg)
Fish muscle tissue:		
Median	48.0	3.67
Mean	48.4	3.65
Standarad deviation	6.7	0.094
Coefficient of variation	14%	2.6%
Procedural blanks:		
Median	11.0	0.03
Mean	10.8	0.03
Standard deviation	1.9	–
Coefficient of variation	18%	–

ECOSYSTEMS INVESTIGATED

To date, four different marine ecosystems have been investigated using the Cs/K ratio as a trophic step indicator. In March 1978, we participated with Mr. Glenn Black, California Department of Fish and Game, in a sampling of the North Shore region of the Salton Sea. Specimens of most of the same fish species collected there by Young in 1967 were obtained by gill net and beach seine. These included orange-mouth corvina (*Cynoscion xanthulus*), Gulf croaker (*Bairdiella icistia*), sargo (*Anisotremus davidsoni*), and threadfin shad (*Dorosoma petenense*). However, striped mullet (*Mugil cephalus*) were not obtained; therefore, we collected specimens of sailfin molly (*Poecilia latipinna*), which—like the mullet—feed near the bottom of the food web. All specimens were wrapped in plastic bags and frozen under dry ice in the field.

In July 1978, we collaborated with Dr. Michael Horn, California State University Fullerton, in collecting fishes with gill net, beach seine, and bottom trawl from Newport Bay. This is a major back bay of southern California that harbors a fauna not unlike that of the Salton Sea and also provides an important breeding area for coastal marine organisms. The inclusion of this second study area provided an opportunity to examine fundamental aspects of food web structure and corresponding increases in pollutant concentrations. The species taken from the back bay were striped bass (*Morone saxatilis*), spotted sand bass (*Paralabrax maculatofasciatus*), yellowfin croaker (*Umbrina roncador*), topsmelt (*Atherinops affinis*), and large and small striped mullet.

The third ecosystem investigated was that exposed to the submarine discharge of primary-treated municipal effluent off Palos Verdes Peninsula by Los Angeles County Sanitation Districts. Over the last two to three decades, this discharge zone has received large quantities of trace metals, chlorinated hydrocarbons, and other

waste-water constituents, which have caused extensive contamination of the bottom sediments (Young et al. 1975). Thus, inclusion of this region as a study area provided opportunity to investigate the degree to which toxic trace metals and high-molecular-weight chlorinated hydrocarbons from a major waste-water source are distributed through a coastal marine food web whose structure we have evaluated. The species selected were important seafood organisms that had been collected from the discharge zone during 1975-77 and maintained under frozen storage; these included bocaccio (*Sebastes paucispinis*), California scorpionfish (*Scorpaena guttata*), Pacific sanddab (*Citharichthys sordidus*), ridgeback prawn (*Sicyonia ingentis*), yellow crab (*Cancer anthonyi*), black abalone (*Haliotis cracherodii*), and purple-hinged scallop *(Hinnites multirugosus).*

Finally, we obtained samples of pelagic fishes taken by commercial fishermen from a relatively uncontaminated section of the Southern California Bight, the San Pedro Channel. The fishes thus obtained included several top carnivores such as albacore (*Thunnus alalunga*), and blue shark (*Prionace glauca*). Also sampled were several primary carnivores, including market squid (*Loligo opalescens*), Pacific mackerel (*Scomber japonicus*), and Pacific bonito (*Sarda chiliensis*), as well as a plankton feeder—northern anchovy (*Engraulis mordax*). The size of the animals selected varied by over three orders of magnitude, ranging fom 5-gram northern anchovy to 20-kg blue sharks. Small specimens were frozen whole and returned to the laboratory for dissection. Larger fishes were weighed; a 1-kg sample of white muscle tissue was then taken and frozen in a clean plastic bag for subsequent analysis.

Dissections were carefully performed according to an established protocol for trace contaminant analyses (Jan et al. 1977). White muscle tissue was excised and examined for cesium, potassium, chlorinated hydrocarbons (total DDT and several PCB's), and all or part of a suite of trace metals (silver, cadmium, chromium, copper, iron, total and organic mercury, manganese, nickel, lead, and zinc). If the individuals of a given species were large, we analyzed one sample from at least three specimens of similar size; for smaller organisms, three composites from a large number of individuals of the species were used. In a number of cases, additional analyses for total and organic mercury were conducted.

The relatively large number of constituents selected for investigation in this initial survey of four different ecosystems severely limited the number of replicates that could be analyzed. Therefore, to reduce the effect of outlying values that are commonly seen in trace analysis, we used the median rather than the mean as a measure of central tendency in summarizing and comparing our tissue concentration data.

There are a number of reports on the feeding habits of many of the organisms used in this study. To begin the work of assigning trophic positions, we examined this literature as well as our records of the gut contents of individuals of each species; we then attempted to assign each organism to one of five levels of trophic categories:

I, plants, including phytoplankton;

II, herbivores, zooplankton;

III, primary carnivores, including some infaunal feeders;

IV, secondary carnivores (many fish);

V, tertiary carnivores (e.g. large predatory fishes and sharks).

Most organisms and samples did not fit this scheme well and were then assigned intermediate positions. For example, Salton Sea detritus, which is food for several fish species considered, was composed of dead phytoplankton (Level I) and zooplankton (Level II) and therefore was assigned Trophic Level I-II; fish feeding primarily on the detritus were assigned to Level II-III (Young 1970). Similarly, we found algae (I), suspension-feeding bryozoans (II-III), and amphipods and small crabs (perhaps Level III) in the stomachs of yellowfin croaker (SCCWRP unpublished); as there is no evidence that this species is able to digest the algae, we assigned the fish to Trophic Level III-IV.

The resulting trophic level assignments are not meant to imply that specific organisms at a certain trophic level are necessarily prey for those placed at the next higher level. The assignments are mainly used as indicators of broad differences in food preference.

Collections of individuals of each species have been archived for detailed gut analyses.

GENERAL SUMMARY OF FEEDING HABITS

Available data indicate that we sampled animals representing low, medium, and relatively high trophic levels in each ecosystem (Table 5). In the Salton Sea and the coastal pelagic food webs, we collected organisms known to form strong predator/prey pairs (e.g. corvina← shad and small croaker; bonito and mackerel←anchovy). In Newport Bay and at Palos Verdes, we sampled animals that did not necessarily feed on one another but were otherwise readily separated into lower and higher tropic levels, which are estimated in the second column of Table 5.

SALTON SEA STUDY

The chemical data from our 1978 Salton Sea survey are presented in Table 6. Also listed are the median values obtained for percent dry weight and percent lipid weight of the wet muscle samples analyzed. The data show a distinct relationship between the estimated trophic position of the fishes surveyed and their muscle tissue concentrations of cesium and potassium. For ex-

TABLE 5
General Feeding Habits and Preliminary Trophic Level Assignments of Organisms from Four Marine Ecosystems.

Predator	Trophic assignment	Primary Prey[1]	Secondary Prey[1]	Data source
Salton Sea				
Corvina	IV-V	Fish (croaker, goby, shad)	Polychæte	Walker 1961; Young 1970; SCCWRP [2]
Croaker	III-IV	Bottom-dwelling polychætes	Barnacles, copepods	Walker 1961; Young 1970
Sargo	III-IV	Polychætes, barnacles		Walker 1961; Young 1970
Shad	III	Plankton (barnacle cypris)	Phytoplankton	Walker 1961; SCCWRP[2]
Molly	II-III	Algae and detritus		Moyle 1976
Newport Bay				
Sandbass	IV-V	Crabs, ghost shrimp, small fish		Feder et al. 1974
Striped bass	IV-V	Crustaceans, fish		Moyle 1976
Croaker	III-IV	Epibenthic invertebrates	Small fish, algæ	Joseph 1962; Skogsberg 1939; SCCWRP[2]
Topsmelt	III-IV	Small benthic crustaceans	Polychætes, gastropods	Lane 1975; Mitchell 1953
Mullet	II	Benthic diatoms, algae, detritus	Microinvertebrates	Walker 1961; Young 1970; Moyle 1976
Palos Verdes				
Bocaccio	IV-V	Small fish (rockfish, anchovy), pelagic red crab, squid		Fitch and Lavenberg 1971
Scorpionfish	IV-V	Fish, crab, shrimp, squid, octopus		Feder et al. 1974; SCCWRP[2]
Sanddab	III-IV	Epibenthic crustaceans, polychætes	Small fish	SCCWRP[2]
Crab	III-IV *	Omnivore: molluscs, detritus		Frey 1971
Prawn	III-IV	Crustaceans; possibly polychætes, clams		Frey 1971; J.Q. Word[3]
Scallop	II-III	Phytoplankton		Assumption (rocky bottom filter feeder)
Abalone	II	Microalgæ, macroalgæ		Cox 1962
San Pedro Channel				
Blue shark	IV-V	Fish (anchovy, mackerel), squid	Small fish, euphausiids	Morejohn et al. 1978; Sciarrotta and Nelson 1977
Albacore	IV-V	Pelagic, mesopelagic fish (saury), anchovy, squid		Pinkas et al. 1971
Bonito	IV	Anchovy, squid		Pinkas et al. 1971; SCCWRP[2]
Pacific mackerel	III-IV	Anchovy, euphausiids, squid, young fish		Feder 1974; Miller 1970; SCCWRP[2]
Anchovy	II-III	Zooplankton and phytoplankton		Miller 1976; SCCWRP[2]

[1]Specific to size of fish analyzed.
[2]SCCWRP, unpublished data based on collection during 1978 and 1979.
[3]J.Q. Word, SCCWRP, personal communication.

ample, the median Cs/K ratios for the molly (Levels II-III), the shad (III), the sargo/croaker group (III-IV), and the corvina (IV-V) are 14.3, 17.1, 19.8, and 32.0×10^{-6}, respectively. Thus, the ratio increased by a factor of 2.2 over two trophic level steps. Although this increase is not as large as that observed by Young in 1967 (Table 2), these results nevertheless show a substantial structure in the part of the Salton Sea food web under study.

The manner in which the trace metals and chlorinated hydrocarbons of concern are distributed through this structured food web is of particular interest. As shown in Table 6, there is no evidence of generally increasing muscle tissue concentrations of most of the target trace metals with increase in trophic level or Cs/K ratio. For example, when we compared the median values for seven metals in the highest and lowest trophic levels sampled (the corvina, representing Level IV-V, and the molly, representing Level II-III), we obtained the following overall increase factors for the two trophic level steps:

Silver	<1.5	Iron	0.4
Cadmium	<1.5	Manganese	<0.1
Chromium	0.5	Zinc	0.6
Copper	1.0		

All values for two other metals, nickel and lead, were below the limits of detection and could not be compared.

TABLE 6
Median Concentrations of Cesium, Potassium, Trace Metals, Total DDT, and PCB 1254 in Wet Muscle Tissue of Organisms Collected from the Salton Sea in March 1978.

	Organism and Estimated Trophic Level				
	Corvina, Level IV-V	Croaker, Level III-IV	Sargo, Level III-IV	Shad, Level III	Molly, Level II-III
Number of Samples	4	3	3	3[1]	3[1]
Median weight (kg)	0.84	,0.16	0.48	0.035	0.003
Cesium (μg/kg)	116	84.6	76.8	59.9	43.7
Potassium (g/kg)	3.63	4.05	4.07	3.50	3.06
Cs/K ratio $\times 10^{-6}$	32.0	20.9	18.8	17.1	14.3
Other trace metals (mg/kg)					
Silver	<0.003	0.002	0.002	0.003	0.002
Cadmium	<0.003	0.001	0.001	0.006	0.002
Chromium	<0.016	0.018	0.028	0.024	0.030
Copper	0.30	0.46	0.62	0.56	0.30
Iron	2.1	4.4	8.4	4.8	5.2
Manganese	0.046	0.41	0.23	1.3	0.70
Nickel	<0.04	<0.03	<0.03	<0.03	<0.02
Lead	<0.04	<0.04	<0.03	<0.06	<0.04
Zinc	3.1	3.2	3.5	3.9	5.3
Mercury					
Organic	0.030	0.009	0.012	NA[2]	0.008
Total	0.016	0.009	0.005	0.008	0.005
Chlorinated hydro-carbons (mg/kg)					
Total DDT	0.20	0.064	0.19	0.24	0.040
PCB 1254	0.014	0.002	0.008	0.040	0.000
Weight of samples					
% dry weight	25.0	23.7	27.0	31.3	24.5
% lipid weight	2.0	1.8	8.0	18.8	5.5

[1]Composites containing 10-12 individuals; shad collected March 1979
[2]Not analyzed.

Similar overall increase factors were obtained by combining, where possible, the shad and molly data for Levels II-III and comparing them with the Level IV-V data. The results of this survey provide a substantial argument against increases in concentrations of these particular metals with trophic level in marine ecosystems.

The results for a tenth metal—mercury—were very different (Table 7). Median values for total concentrations of this metal in the molly (Level II-III), shad (III), sargo/croaker (III-IV), and corvina (IV-V) are 0.005, 0.008, 0.007, and 0.016 respectively, suggesting that concentrations tend to increase with trophic level. Application of the nonparametric, one-sided Mann-Whitney U-Test indicated that the difference between the corvina and sargo/croaker concentrations of total mercury were statistically significant (P <0.01). We therefore sought additional information by analyzing these samples for organic mercury. There appeared to be a systematic error in our results in that concentrations of organic mercury were often slightly higher than those for total mercury. However, the same general relationships between median concentration and trophic level were observed (Table 7). Again, the difference between values for Level III-IV and Level IV-V was found to be statistically significant (P < 0.01). Thus, these two sets of independent analyses indicate that, on a wet-weight basis, muscle tissue concentrations of mercury increase threefold with a presumed two-step increase in trophic level in this ecosystem.

The data listed in Table 6 show no apparent relationship between the wet-weight concentrations of total DDT and PCB 1254 in the muscle tissue of the study organisms and their assumed trophic levels. However, these synthetic compounds are often found in higher concentrations in lipid-rich tissues. Therefore, we normalized these parameters in a lipid-weight basis and obtained the median concentrations given in Table 8. With one exception, the muscle tissue concentrations of total DDT and PCB 1254 on a lipid-weight basis increase both with increase in Cs/K value and with increase in estimated trophic level.

NEWPORT BAY STUDY

In contrast to the situation observed in the Salton Sea, the alkali metal results obtained from the Newport Bay survey (Table 9) indicated that there was considerably less structure in the food web of this marine ecosystem. The median Cs/K ratios from small mullet (Level II), topsmelt/yellowfin croaker (Level III-IV), and spotted sandbass/striped bass (IV-V) were quite similar: 3.6, 4.6, and 5.2 × 10⁻⁶, respectively.

We have excluded the large mullet from this comparison because the median weight for these specimens (2.7 kg) was an order of magnitude above those of the other species. However, a comparison of the cesium and po-

tassium data for the small and large mullet does provide useful information regarding the effect of specimen size on the results. Because mullet are primarily herbivorous and do not appear to change their diet as they grow, they are useful organisms with which to evaluate the effect of size alone on muscle concentrations of various trace chemicals. Although the large mullet were four to five times as heavy as the small mullet, the median cesium concentrations and Cs/K ratios for the two groups of fish were similar (Table 9). This suggests that, in the absence of differences in food at different growth stages, values for cesium and the Cs/K ratio in muscle tissue of a fish species are not strongly dependent on size. Concentrations of most of the other metals analyzed also did not

TABLE 7

Variations in Muscle Tissue Median Concentrations of Mercury (mg/wet kg) with Differences in Trophic Position of Organisms from Three Marine Ecosystems.

Area and species-group	Assumed trophic level	Organic mercury	Total mercury
Salton Sea:			
Corvina	IV-V	0.030	0.016
Sargo/croaker	III-IV	0.010	0.007
Shad	III	NA[1]	0.008
Molly	II-III	0.008	0.005
Newport Bay:			
Sandbass/bass	IV-V	0.32	0.28
Topsmelt/croaker	III-IV	0.073	0.050
Small mullet	II	0.014	0.017
Palos Verdes:			
Scorpionfish/bocaccio	IV-V	NA[1]	0.26
Crab/prawn/sanddab	III-IV	NA[1]	0.080
Abalone/scallop	II-III	NA[1]	0.033

[1]Not analyzed.

TABLE 8

Variations in Median Muscle Tissue Concentrations of Chlorinated Hydrocarbons, on Wet and Lipid Weight Bases, with Increase in Trophic Position of Organisms from Three Marine Ecosystems.

Area and species group	Assumed trophic level	Cs/K ratio ×10⁻⁶	Total DDT (mg/kg) Wet weight	Total DDT (mg/kg) Lipid weight	PCB 1254 (mg/kg) Wet weight	PCB 1254 (mg/kg) Lipid weight
Salton Sea:						
Corvina	IV-V	32.0	0.20	10	0.014	0.70
Croaker	III-IV	20.9	0.064	3.6	0.002	0.11
Sargo	III-IV	18.8	0.19	2.4	0.008	0.10
Shad	III	17.1	0.24	1.3	0.040	0.21
Molly	II-III	14.3	0.040	0.7	0.000	0.00
Newport Bay:						
Sandbass/bass	IV-V	5.2	0.62	64	0.24	25
Topsmelt/croaker	III-IV	4.6	0.18	20	0.040	4.7
Small mullet	II	3.6	1.00	25	0.12	3.0
Palos Verdes:						
Scorpionfish/ bocaccio	IV-V	15.1	2.1	270	0.23	31
Crab/prawn/ sanddab	III-IV	11.2	1.5	290	0.19	37
Abalone/scallop	II-III	6.4	0.008	11	0.01	1.1

increase greatly with increase in mullet size; however, the median cadmium concentration for the larger mullet was ten times the value for the small mullet, and the copper and iron values for the larger fish were twice as high.

As was the case in the Salton Sea results, trace metal values for Newport Bay specimens did not generally increase with increase in presumed trophic level. Comparison of median concentrations for the highest and lowest comparable groups (sandbass/bass, Level IV-V, and small mullet, Level II) yields the following overall increase factors for this presumed two-to-three step increase in trophic level:

Silver	1.5	Iron	1.0
Cadium	>1.5	Manganese	1.0
Chromium	>0.6	Zinc	1.4
Copper	1.1		

Because the concentrations of silver and cadmium were very low, the significance of the factors listed for these metals is questionable. Nickel and lead concentrations in Newport Bay specimens also were low, as they were in Salton Sea samples. Another similarity between the two sets of data was that distinct increases of total and organic mercury with increase in presumed trophic level were found in both areas (Table 7). Over the two-to-three step increase in trophic position between Levels II and IV-V, total and organic mercury concentrations increased by about a factor of 20.

As was the case with Salton Sea specimens, there is no apparent relationship between the wet weight concentration of total DDT or PCB 1254 in Newport Bay samples and the presumed trophic levels of the specimens. However, a more distinct pattern is revealed when the data are normalized on a lipid-weight basis, as shown in Table 8. The Group IV-V fishes contained distinctly higher lipid weight concentrations of total DDT and PCB 1254 than did fishes at lower levels. In view of the apparent increase in chlorinated hydrocarbon concentrations with mullet size (Table 9) and the fact that the median weight for the small mullet was two to five times higher than the corresponding weight for the other two groups, the correlation with trophic level might have been clearer if fish specimens of approximately equal weight had been available for study.

PALOS VERDES STUDY

Chemical and size data from the benthic/epibenthic marine ecosystem in the waste-water discharge zone of Palos Verdes Peninsula are presented in Table 10. The median Cs/K ratios for specimens at Trophic Levels II-III, III-IV, and IV-V are 6.5, 11.2, and 15.1 × 10^{-6}, respectively. This represents an increase in the ratio by a factor of 2.3 over the presumed two trophic level steps. Again, with the exception of total mercury, there was no apparent increase in levels of toxic trace metals with in-

TABLE 9

Median Concentrations of Cesium, Potassium, Trace Metals, Total DDT, and PCB 1254 in Wet Muscle Tissue of Organisms Collected from Newport Bay in July 1978.

	Organism and Estimated Trophic Level					
	Striped bass Level IV-V	Spotted sand bass, Level IV-V	Yellowfin croaker, Level III-IV	Topsmelt, Level III	Mullet, Level II	
					Large	Small
Number of specimens	3	3	3	3	3	3
Median weight (kg)	0.25	0.31	0.21	0.05	2.7	0.60
Cesium (µg/kg)	21.7	22.6	19.8	12.4	16.8	16.1
Potassium (g/kg)	4.39	4.10	3.58	3.36	3.76	4.49
Cs/K ratio ×10^{-6}	4.94	5.51	5.53	3.69	4.47	3.59
Other trace metals (mg/kg)						
Silver	0.003	0.003	0.003	0.002	0.002	0.002
Cadmium	0.003	0.003	0.002	0.002	0.020	<0.002
Chromium	<0.009	0.014	0.008	<0.010	0.016	0.018
Copper	0.27	0.26	0.26	0.20	0.55	0.24
Iron	1.7	2.2	2.4	1.9	4.2	2.0
Manganese	0.17	0.093	0.28	0.36	0.068	0.13
Nickel	<0.03	<0.04	<0.03	<0.03	<0.04	<0.03
Lead	<0.04	<0.04	<0.03	<0.04	<0.04	<0.04
Zinc	4.1	4.3	5.8	14	3.3	2.9
Mercury						
Organic	0.36	0.27	0.054	0.092	0.017	0.014
Total	0.41	0.20	0.050	0.051	0.010	0.017
Chlorinated hydro-carbons (mg/kg)						
Total DDT	0.75	0.48	0.20	0.15	4.4	1.00
PCB 1254	0.29	0.19	0.042	0.039	0.47	0.12
Weight of samples						
% dry weight	24.5	23.8	24.4	24.8	28.2	27.3
% lipid weight	0.91	1.07	1.2	0.67	8.6	4.0

TABLE 10

Median Concentrations of Cesium, Potassium, Trace Metals, Total DDT, and PCB 1254 in Wet Muscle Tissue of Organisms Collected from the Palos Verdes Shelf, 1975-77.

	Bocaccio, Level IV-V	Scorpion-fish Level IV-V	Sanddab, Level III-IV	Yellow crab, Level III-IV	Prawn, Level III-IV	Scallop, Level II-III	Abalone, Level II
Number of specimens	3	2	3	2	3	3	3
Median weight (kg)	0.37	0.34	0.073	0.58	0.024	0.095	0.54
Cesium (ug/kg)	77.4	54.4	48.1	21.1	37.3	21.4	24.3
Potassium (g/kg)	4.66	4.01	3.98	3.24	3.33	3.93	3.19
Cs/K ratio × 10^{-6}	16.6	13.6	12.1	6.5	11.2	5.4	7.6
Other trace metals (mg/kg)							
Silver	0.008	0.022	0.005	0.095	<0.004	<0.003	0.028
Cadmium	<0.002	0.004	0.003	0.004	0.032	0.803	0.041
Chromium	<0.010	0.036	0.032	0.080	<0.019	0.255	0.95
Copper	0.15	0.15	0.19	7.84	2.0	0.24	3.35
Nickel	0.058	0.15	0.056	0.26	<0.03	0.046	0.68
Lead[1]	0.08	0.64	0.02	0.14	<0.01	<0.04	<0.12
Zinc	4.7	3.9	3.2	25.2	9.8	19.8	6.1
Total mercury	0.14	0.38	0.081	0.064	0.080	0.056	0.010
Chlorinated hydro-carbons (mg/kg)							
Total DDT	0.61	3.5	6.1	1.5	0.15	0.16	0.001
PCB 1254	0.072	0.39	0.38	0.19	0.058	0.012	0.006
Weight of samples							
% dry weight	28.0	23.0	21.0	20.0	24.0	24.0	25.0
% lipid weight	1.47	0.69	0.88	0.52	1.27	0.76	0.94

[1]Measureable lead values may indicate contamination of sample.

crease in trophic level or Cs/K ratio. Comparison of median concentrations for specimens at Level IV-V and those at Level II-III yields the following overall increase factors:

Silver	1.0	Copper	0.08
Cadmium	<0.01	Nickel	0.3
Chromium	<0.04	Zinc	0.3

However, as in the previous two studies, there was a correlation between wet-weight concentrations of total mercury and trophic level, as shown in Table 7 (organic mercury was not measured in these samples). There also was some indication of a relationship between total DDT and PCB 1254 concentrations, and trophic level and Cs/K ratio (Table 8).

STUDY OF PELAGIC FISHES (SAN PEDRO CHANNEL)

Only the alkali metals were analyzed for the pelagic ecosystem; results are summarized in Table 11 in the same format used to present the 1967 Salton Sea survey results (Table 1). The data indicate distinct structure for both ecosystems. Increase in Cs/K ratios for hypothesized predator/prey relationships in the pelagic ecosystem range from 1.6 to 3.2, with a median value of 2.3. This is in agreement with the corresponding median value of 2.5 (range was 2.0 to 5.5) obtained by Young in the 1967 survey of the inland, quasi-marine ecosystem of the Salton Sea.

CONCLUSIONS

The results of the studies reported here suggest that Cs/K ratios in organisms from a marine ecosystem can indeed provide a useful indication of the degree of trophic structure in the food web of that environment. Although physiological differences between individual species or groups of species considered may cause distinct variations, the information obtained suggests that, in a structured situation, this ratio should approximately double over a single trophic level step. The fact that an increase of this magnitude was not observed over the presumed trophic level steps of the two nearshore marine ecosystems studied to date (Newport Bay and Palos Verdes shelf) is consistent with the hypothesis that such systems experience considerable "homogenization" of energy flow as a result of the opportunistic (i.e. unstructured) feeding patterns of member organisms.

Nevertheless, all four types of "marine" ecosystems investigated (saline lake, back bay, benthic discharge zone, and coastal pelagic community) exhibited measurable food web structure. In the Salton Sea, the Cs/K ratio increased by a factor of 2.2 over two presumed trophic steps. This ratio increased by only about a factor of 1.5 over two to three presumed trophic level steps in upper Newport Bay, and an increase factor of 2.3 was observed over two presumed steps on the Palos Verdes

shelf. This latter value was also the median increase factor measured for several specific predator/prey (single-step) relationships in the coastal pelagic food web of the Bight.

We have completed analyses of trace contaminants in specimens from three of the four study areas. The degree of structure in the food webs of the three systems varied. However, we found no evidence of increase in concentrations of nine of ten trace metals with increase in trophic level within any system. In fact, in the benthic/epibenthic system within the waste-water discharge zone of Palos Verdes Peninsula, concentrations of these metals were considerably lower in the high-level predatory fishes than in the lower level infaunal and filter-feeding organisms. Thus, although the large point-source input of metal wastes from municipal waste-water discharge has previously been shown to result in elevated levels of metals in certain of the invertebrates that occupy the lower trophic levels (Jan et al. 1977), we did not find that this contamination is passed up the food web to fishes situated at higher trophic levels.

In contrast, there were very distinct increases in mercury and total DDT and PCB 1254 concentrations with increase in trophic level in the three ecosystems. Independent measurement of total and organic mercury verified this finding and suggested that most of the mercury in the muscle tissue of the fish specimens investigated was in an organic form. Concentrations increased from the lowest to the highest trophic levels sampled by up to a factor of 20.

There is no question that DDT and PCB 1254 residues are foreign chemicals which occur at significantly higher concentrations in the Palos Verdes marine food web than at distant control sites. However, the results from our control zone surveys (Jan et al. 1977) show that mercury concentrations are normally higher in higher trophic level organisms. We have found no evidence that the waste-water mercury released from the Palos Verdes outfalls is contributing to the increased concentrations of this metal in the marine food web of that region.

TABLE 11

Comparison of the Concentrations of Cesium and Potassium and Cs/K Ratios (on a Wet-Weight Basis) in the Muscle Tissue of Pelagic Fishes from the Southern California Bight with Those in Their Food.

Organism	Major food	Ratio, concentration in organism to concentration in major food		Cs/K ratio ×10⁻⁶
		Cesium	Potassium	
Pacific mackerel	Anchovy	1.90	1.16	1.64
Pacific bonito	Anchovy	2.56	1.26	2.03
Albacore	Anchovy, mackerel	1.77	0.91	1.94
Blue shark	Bonito	2.21	0.89	2.48
Blue shark	Mackerel	2.98	0.97	3.08
Blue shark	Anchovy, mackerel, bonito	3.12	0.99	3.15
Median		2.38	0.98	2.26
Mean		2.42	1.03	2.39

The clearest relationship between total DDT and PCB 1254 concentration and trophic position usually was obtained when the concentrations in wet tissue were normalized to a lipid-weight basis. Order of magnitude increases were observed in several cases.

The increases in mercury, total DDT, and PCB 1254 concentrations with trophic level may well be the result of relatively long biological half-lives of organic mercury and the synthetic organics in muscle tissues of the species analyzed. If a substance has a sufficiently long half-life, the existence of any structure in a food web will result in an increased concentration of the substance with increase in trophic position. Because the resulting increase factors are dependent on the degree to which equilibrium has been reached in any one step and the effect of growth and physiological conditions (such as percent lipid), we are not yet able to quantitatively relate increases in the Cs/K ratios with corresponding increases in the concentrations of trace pollutants that result from the feeding process. However, we believe that the results reported here represent a significant increase in our understanding of trophic position and the problem of food web increases of pollutant concentration in marine ecosystems.

ACKNOWLEDGMENTS

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FREE-FALL PARTICLE COUNTER FOR OCEAN SURVEYS

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ABSTRACT

For a study of particles in the sea as potential food organisms for larval anchovies (Lasker 1975, 1978), a survey method was needed to profile particle concentrations with depth rapidly during California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys.

To do this, a microprocessor-based free-fall particle counter (FFPC) was designed and constructed (Brown 1977) based on the well-known principle that a particle passing into an electrical field in an electrolyte causes a change in electrical properties if resistivity of the particle differs from that of the electrolyte. The widely used Coulter Counter® is an example of an instrument based on this principle.[1] In this report, laboratory calibration and a field test of the FFPC are described as well as modifications to the instrument that permit fast deployment of the probe, shipboard display, and printing of the data.

RESUMEN

Para un estudio de partículas en el mar como organismos potenciales de alimentación para larvas de anchoveta (Lasker 1975, 1978), se necesitaba un método rápido para poder perfilar concentraciones de partículas con la profundidad, durante los cruceros de reconocimiento de CalCOFI.

Para hacer ésto, un contador de partículas de caída libre basado en un microprocesador fue diseñado y construido, basado en un principio bien conocido de que una partícula, al pasar por un campo eléctrico en un electrolito, causa un cambio en las propiedades eléctricas si la resistividad de la partícula difiere de la del eléctrolito. Un ejemplo de un contador que está basado en este principio y que se usa mucho es el Coulter Counter®[1]. En este trabajo, se describe la calibración en el laboratorio y la prueba práctica del contador, así como modificaciones del instrumento que facilitan el despliegue rápido de la sonda, una muestra a bordo, y la imprenta de los datos.

INTRODUCTION

In a series of recent papers, Lasker (1975, 1978, 1979) described the importance of particle size and concentration with depth and area in relation to particulate feeding by anchovy larvae. These studies showed that information on the distribution of particles of about 20-40 μm in "effective diameter"[2] could be related to survival of anchovy larvae and thus to the size of future year classes. The usual technique for obtaining particle size and concentration data has been by overside deployment of a hose and submersible pump. This required considerable ship time and manpower. Using a pump, particle size and concentration could only be obtained by retrieving some of the water from specific depths and by counting particles suspended in the water with a Coulter Counter in the shipboard laboratory. This tedious procedure provides very few data points in vertical transects, nor does it give information on patchy distribution of particles. It became evident in our work that a method was needed that could provide for a continuous record of particle size and concentration with depth quickly and at finer depth intervals. A microprocessor-based system with a free-fall probe was designed by Brown (1977) to collect this information. This paper describes recent engineering innovations of the system, a field test under sea-going conditions, and laboratory calibration.

OPERATION

We have called this instrument a free-fall particle counter (FFPC), although it is tethered with a conducting cable to relay information to a dedicated microprocessor aboard the ship. The instrument is designed to resolve particle layers of at least 0.2 m thick in a vertical profile to 100 meters. In operation, the entire procedure, including deployment of 100 m of conducting cable and retrieval, takes about three to four minutes, although the actual data collection occurs in a pre-set 100 seconds during the fall of the probe. If the probe sinks too slowly, it provides more information for each depth interval, but because the pre-set 100 seconds may have elapsed too soon, it will not collect data to the desired depth. Sinking speed is a function of the amount of lead weight added to the bottom of the probe and a variety of uncontrollable ocean-related factors, e.g. drift and currents. In practice, a winch (Figure 1), designed specifically for the sensor probe (Figure 2) and its cable, is attached to the ship's bucket. As the sensor falls and the cable is payed out, the information obtained by the falling sensor is relayed to the microprocessor where it is stored on tape and displayed on a video screen as particle concentration by size of particle and depth in addition to a time and date record

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[1]Mention of trade names does not imply endorsement by the National Marine Fisheries Service.
[Manuscript received 17 January 1980.]

[2]Particles, regardless of shape, are counted as if they were spherical, hence sizes are recorded as "effective diameters."
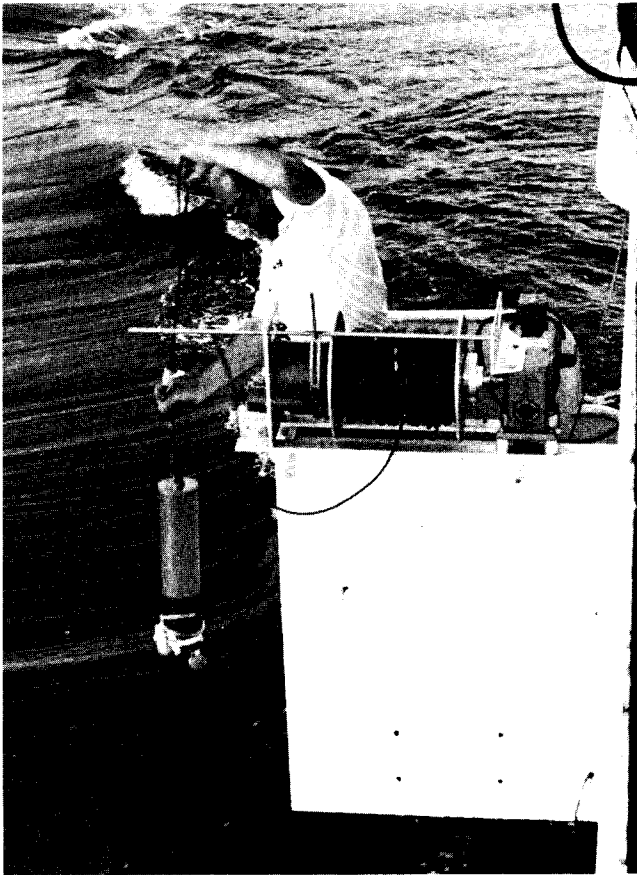
Figure 1. Sensor probe and winch for free-fall particle counter (FFPC). Winch is equipped with manual level wind and clutch. Operator is standing in ship's bucket.
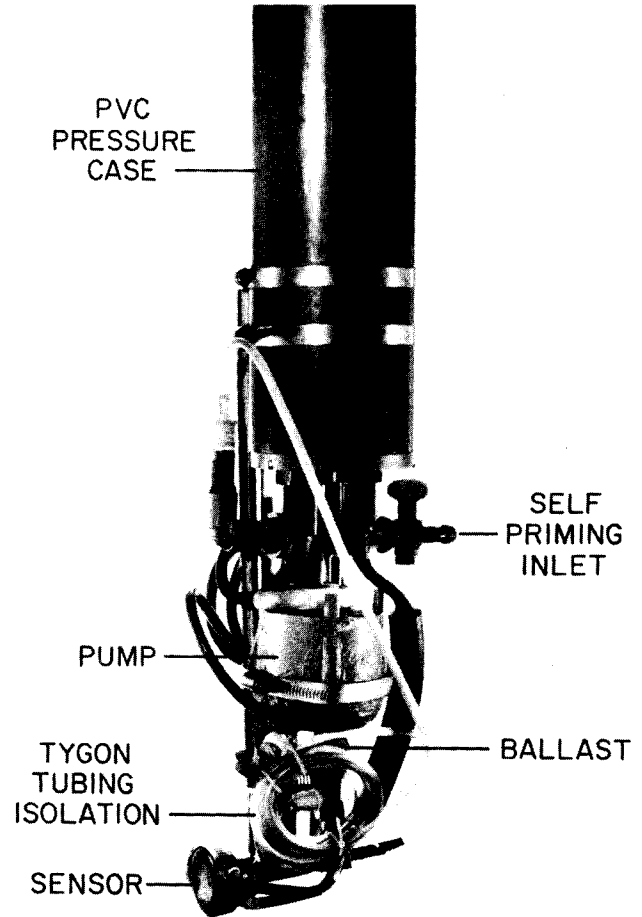

Figure 2. Free-fall particle counter (FFPC) sensor probe (after Brown 1977).

(Figure 3). The video display provides an immediate assessment of the drop and informs the operator whether or not the cast needs to be repeated. The microprocessor is programmed to accept and record the data on a cassette tape, then to relay the information from each cast to a Hewlett Packard 9825 mini-computer, which in turn is programmed to print the information in graphic form by size concentration and depth. For each cast, as many as seven particle size ranges and concentrations can be obtained with depth, and each size range and concentration can be printed on a separate graph aboard ship. Similarly, a digital output is available either of all the data collected or averaged for specified depth intervals (e.g. 1 m, 5 m, etc.).

A fine hole drilled into a fiberglass disk suffices for the sensor pore intake. We have found that a pore of 400-μm diameter can provide information on particles ranging in size from 20 to 100 μm in effective diameter. Other size pores can be used but have not yet been tested and are not reported on here. Clogging of the 400-μm pore is rarely a
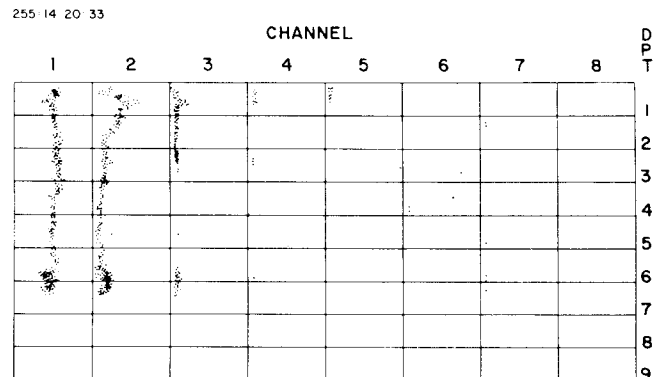
Figure 3. Diagram of a typical video display. Depth (DPT) is given on the ordinate. Day of the year (255) and time of day are shown on the screen at the upper left hand corner. Each dot is an indication of the number of particles of a particular size class sensed by the probe for 0.2 second. Channel 1 is not used because of electrical interference. With a 400 μm pore, Channel 2 receives impulses from particles ranging in effective diameter from 20.2-25.3 μm; Channel 3, 25.4-31.9 μm; Channel 4, 32.0-40.2 μm; Channel 5, 40.3-50.7 μm; Channel 6, 50.8-63.9 μm; Channel 7, 64.0-80.5 μm; Channel 8, 80.6-100.0 μm. The data from this cast are shown as a cumulative curve, third from the left in Figure 6.

problem since the amount of water pulled through the pore during any one descent is about 50 ml and usually has very few large particles in it.

CALIBRATION

Figure 4 illustrates a laboratory calibration of the sensor probe against the Coulter Counter model T_A using a mature culture of the dinoflagellate, *Gymnodinium splendens*, or 30-40 μm polystyrene beads. When particle concentrations are below 250-300 particles/ml, there appears to be no coincidence of counts, and particle concentrations can be obtained directly without resorting to a calibration curve. There is an obvious coincidence problem above 300 particles/ml, and corrections must be made whenever this is encountered. However, rarely are such high concentrations of particles >20 μm diameter found in California waters.

FIELD TEST

A typical series of casts were taken about 10 miles off the coast of San Diego on 12 September 1979 in rapid succession. Each cast and retrieval took about five minutes with the ship drifting slightly southeast. The positions of the ship are shown in Figure 5, top. There was a

sharp thermocline between 7 and 18 m and a strong pycnocline at 12 m (S = 33.5 °/oo, T = 15.5°C; Figure 5, bottom). Figure 6 is a summary of total particles from 20-100 μm in effective diameter with depth taken at approximately 5-minute intervals. Note that the pycnocline at 12 m effectively marks the lowest boundary of a broad particle layer in the surface water. Reproductions of the computer printout are given in Figure 7. With slight changes
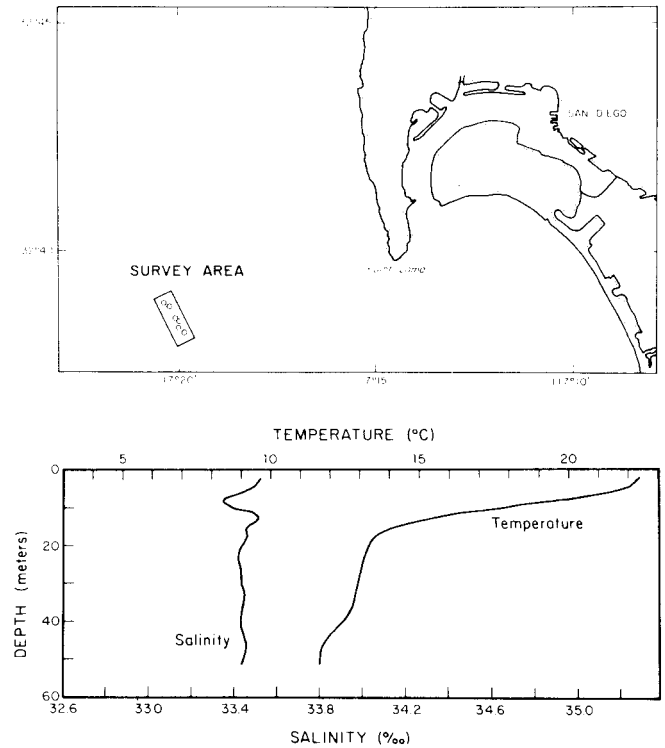
Figure 5. Top, ship positions for repetitive free-fall particle counter (FFPC) sampling; bottom, salinity and temperature profiles taken at first station.

Figure 4. Calibration of free-fall particle counter (FFPC) with 400 μm pore against Model T_A Coulter Counter, 280 μm pore. Microscope counts were used to verify Coulter Counter output.
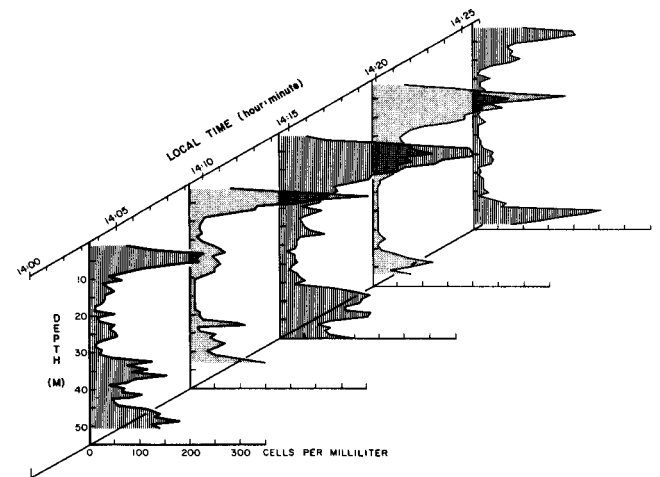
Figure 6. Total particles from 20-100 μm effective diameter with depth taken at approximately 5-minute intervals. Ship positions are shown in Figure 5.
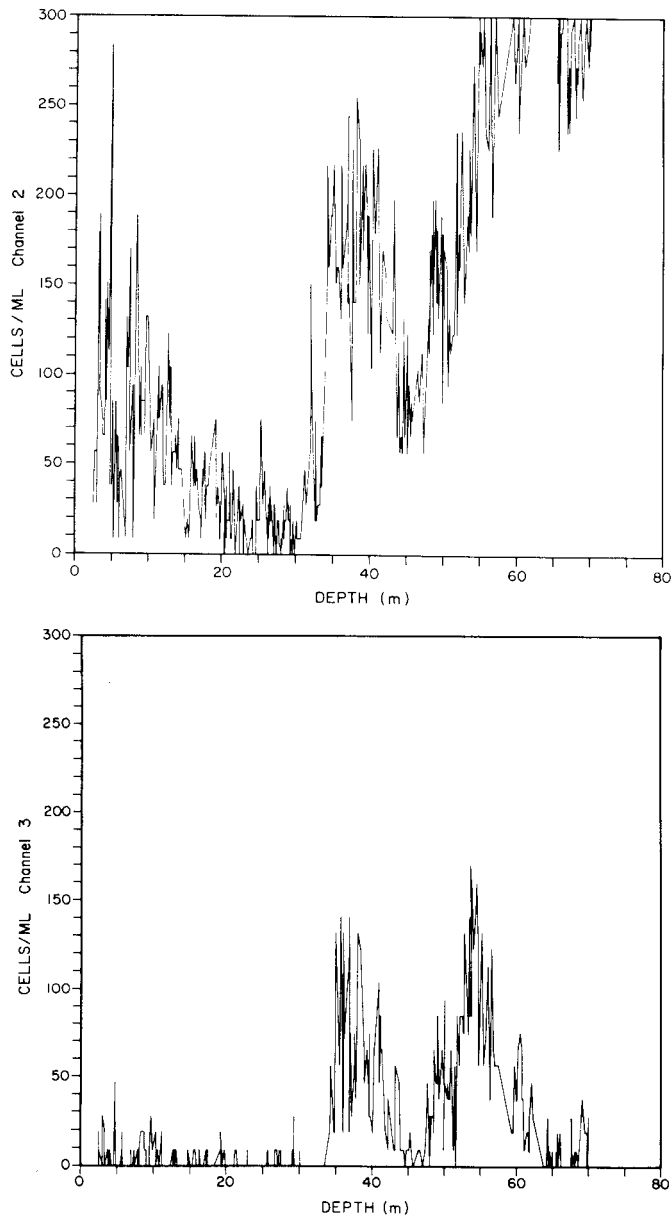
Figure 7. Graphic output from a single cast using the Hewlett Packard 9825 mini-computer and peripheral unit: Top, Channel 2, 20.2-25.3 μm; bottom, Channel 3, 25.4-31.9 μm particles.

in the Hewlett Packard 9825 program, specific size ranges can be printed separately or summed to give cumulative size ranges and concentrations with depth.

DISCUSSION

There are several operational advantages unique to this instrument. These are 1) each profile of particle concentration with depth to 100 m can be made in less than five minutes; 2) particle sizes may be differentiated by seven usable electronic channels; the size displayed in each channel may be varied by using different pore sizes; 3) an immediate plot of particle concentration by size and depth is available on shipboard by interfacing the micro-processor with a mini-computer (Hewlett Packard 9825) and its peripheral plotter and printer; 4) the submersible portion of the unit is portable and replaceable; and 5) the water drawn through the pore (about 50 ml) can be retrieved from the intake tube and preserved for later study.

Two major disadvantages to the instrument are evident: 1) species of phytoplankton and microzooplankton cannot be assigned to a particular depth; and 2) intake volumes with pores to 400 μm are small for any single cast, thus large particles (>100-μm diameter) are sampled too infrequently for statistical treatment.

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EUPHAUSIIDS IN THE GULF OF CALIFORNIA—THE 1957 CRUISES

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ABSTRACT

Euphasiid crustaceans in the Gulf of California were examined from four bimonthly CalCOFI grid cruises during February through August of 1957. Of the nine species found to regularly inhabit the Gulf, *Nematoscelis difficilis* and *Nyctiphanes simplex* are common to the warm-temperate California Current. These have the broadest ranges in the Gulf, peaking in abundance and reproducing maximally during February-April and February-June respectively, before intense August heating takes place in the Gulf. *Euphausia eximia*, a species having high densities at zones considered marginal to the eastern tropical Pacific, also varies little in range during the year, consistently occupying the southern half of the Gulf. Tropical *Nematoscelis gracilis* shows a range complementary to that of *N. difficilis*; these species overlap in the southern Gulf. Three *Euphausia* species of the tropical Pacific occupy the southern Gulf in February-April, expanding northward during June-August but, like the cool-water species, scarcely reproducing in the Gulf during the warm season. The distributions and abundances of the species and their life stages, particularly the youngest larvae, are described in relation to seasonal variation in flow and temperature in the Gulf.

RESUMEN

Se examinaron crustáceos eufáusidos del Golfo de California tomados durante cuatro cruceros bimensuales de CalCOFI entre febrero y agosto de 1957. De las nueve especies encontradas que regularmente habitan en el Golfo, *Nematoscelis difficilis* y *Nyctiphanes simplex* son comunes en las aguas templada-cálidas de la Corriente de California. Estas especies presentan una distribución amplia en el Golfo, alcanzando una máxima abundancia y reproducción durante febrero-abril y febrero-junio, respectivamente, antes de llegar el calor intenso de agosto. *Euphausia eximia*, una especie de altas densidades en las zonas consideradas marginales al Pacífico tropical oriental, también varía poco en su amplitud de distribución durante el año, ocupando consistentemente la mitad sur del Golfo. *Nematoscelis gracilis*, es tropical y muestra una distribución complementaria con *N. difficilis*; estas especies concurren en el sur del Golfo. Tres especies de *Euphausia* del Pacífico tropical ocupan el sur del Golfo en febrero-abril, extendiéndose hacia el norte durante junio-agosto, pero, como las especies de agua fría, escasamente se reproducen en el Golfo durante la estacion cálida. Las distribuciones y abundancias de las especies y de sus etapas de vida, en particular las de las larvas más juveniles, se describen en relación con las variaciones estacionales en el flujo y las temperaturas de las aguas del Golfo.

INTRODUCTION

The Gulf of California is inhabited by dense stocks of plankton (Osario-Tafall 1946; Zeitzschel 1969). This appendix of the North Pacific Ocean communicates with the eastern boundary circulation at the northern limit of the eastern tropical Pacific, which is characterized by its distinctive oxygen-deficient layer. The 1000-km axis of the Gulf extends from the mouth at the tropic, 23°27'N, to latitude 32°N, which is within the belt of the warm-temperate Californian Transition Zone, discussed most recently by Newman (1979). The Gulf parallels the terminal part of the California Current, which meanders southward on the other side of the Baja California peninsula.

Little attention has been paid to ways in which the Gulf's nearly enclosed planktonic populations range along this stretch of water, which is recognized on the basis of the fish fauna to be one of temperate-tropical transition (Walker 1960). Indeed, only sparse information exists as to the zooplankton species presently occupying the Gulf or to their distribution. Data are best for Foraminifera (Bradshaw 1959; Parker 1973), Chætognatha, Siphonophora, and Scyphomedusæ (Alvariño 1969), and pontellid Copepoda (Fleminger 1967, 1975). Hyperiid Amphipoda are presently under study by Siegel-Causey, whose first findings (in press) presage description of a diverse amphipod fauna. Existing knowledge of the plankton of the Gulf of California has been reviewed by Brinton et al. (in press).

Euphausiids sampled across the mouth of the Gulf (Brinton 1979) were grouped as 1) residual from the main stream of the California Current to the north (e.g. *Nematoscelis difficilis*, *Euphausia pacifica*, and *Thysanoessa gregaria*), 2) species proliferating at the productive margins of the eastern tropical Pacific (e.g. *Euphausia eximia* and the associated, more coastal *Nyctiphanes simplex*), 3) endemic equatorial vertical migrators adapted to the oxygen-dificient regions (*Nematoscelis gracilis*, *Euphausia diomedeae*, and indistinctly associated *E. distinguenda* and *E. lamelligera*), and 4) non- or short-distance migrating warm-water cosmopolites that avoid the oxygen deficiency (e.g. *Stylocheiron affine*, *S. carinatum*).

The Gulf deepens into basins with depths up to 1,000 m

in the north and 3,500 m in the south. Hence, there is sufficient vertical space for occupancy by the *Euphausia* and *Nematoscelis* species which undergo vertical migrations of 300 or 400 m. The extent to which euphausiids penetrate the Gulf had been known previously only on the basis of a September-October 1952 CalCOFI cruise along the southernmost part of the western side (Brinton 1962; these 1952 distributions are detailed here along with the 1957 distributions).

Half of the area of the Gulf is neritic, with the broadest shelf in the northern end and along the eastern side (Figure 1). Although most euphausiids have oceanic rather than neritic ranges, nevertheless there is a species with neritic affinities (Brinton 1962; Figures 113, 114) corresponding to each, but one, of the Pacific's ten littoral provinces recognized by Ekman (1953). Two of these occur in the Gulf. *Nyctiphanes simplex*'s range corresponds with Ekman's American Temperate Tropical Zone and *Euphausia lamelligera*'s with the Pacific Tropical American.

Ships of the National Marine Fisheries Service and the Scripps Institution of Oceanography occupied a standardized grid of stations in the Gulf during 1956 (three cruises) and 1957 (four cruises). All employed the Cal-COFI techniques regularly used at that time for sampling zooplankton; that is, oblique tows to 140 m, using a 1-m net of 0.55-mm-mesh width, following Ahlstrom (1948). The 1957 cruises provided the most seasonal and geographical coverage and were selected for this study. Net tows generally strained 300 to 400 m^3 of water and were standardized to 1,000 m^3. Samples were aliquoted and counted using methods described in Brinton (1979).

A biogeographical analysis of fish eggs and larvae in the Gulf (Moser et al. 1974) was based on samples from three of the four cruises discussed here and from three 1956 cruises. Hence, the 1957 fish distributions can be strictly compared with these euphausiid distributions.

Interest in examining biology of Gulf plankton in relation to oceanographic processes has heightened due, in part, to the importance to Mexico of understanding regenerative cycles in these productive coastal waters and also to emerging awareness among oceanographers of the Gulf's distinctive topography, its unique climate, and the substantial containment of its biota. Ayala-Castañares (1979) has characterized it as a natural laboratory.

THE PHYSICAL ENVIRONMENT

Upwelling and Mixing

The climate and circulation of Gulf waters are influenced by seasonally reversing winds and changes in incident heat. Upwelling, determined by the divergence of the Ekman transport, is expected to be strongest along the eastern side of the Gulf during the northeasterly winds
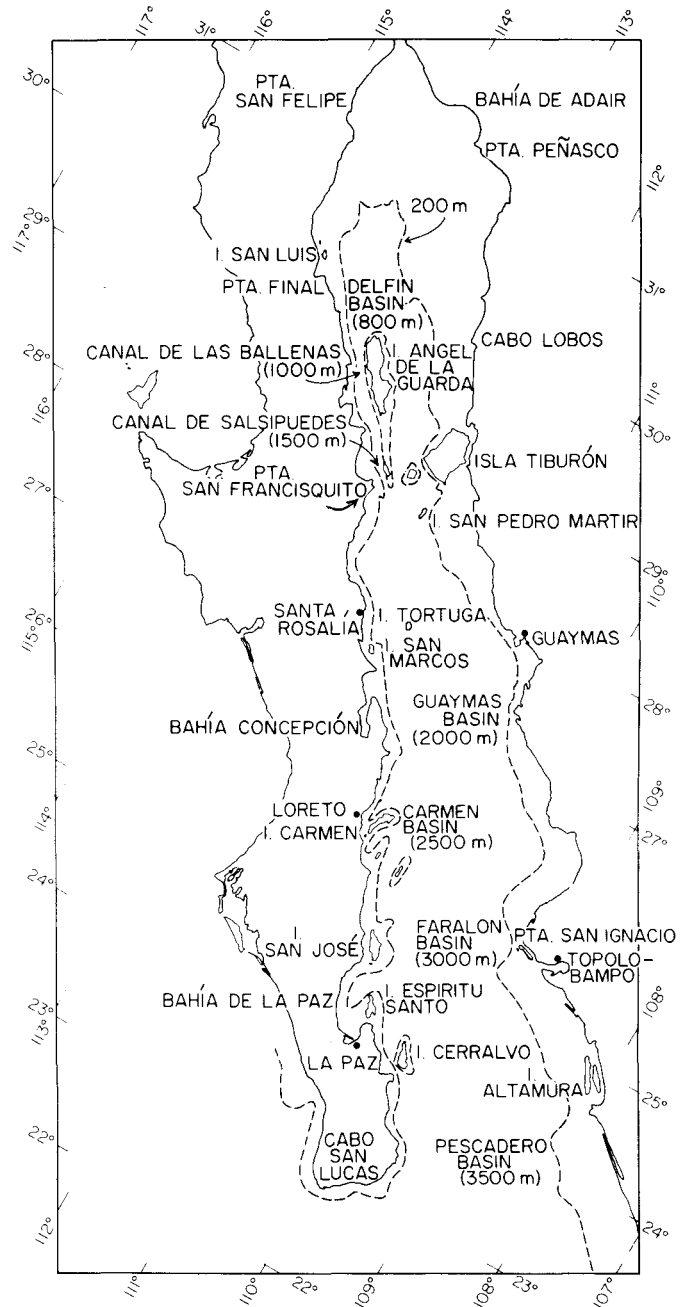
Figure 1. The Gulf of California. Edge of shelf and maximum depths of principal basins are indicated.

of winter and spring and then to shift to the western side during southwesterly winds of summer and early fall (Roden 1971). This is illustrated by the temperature distributions in Roden and Groves (1959) and in Figures 2 and 3 of the present paper; these distributions are based on the 1957 cruise measurements.

The many islands, particularly along the western Gulf, provide much extra coastline which augments the extent of mixing processes and upwelling: 1) in channels between islands or between islands and the coast, tidal mix-
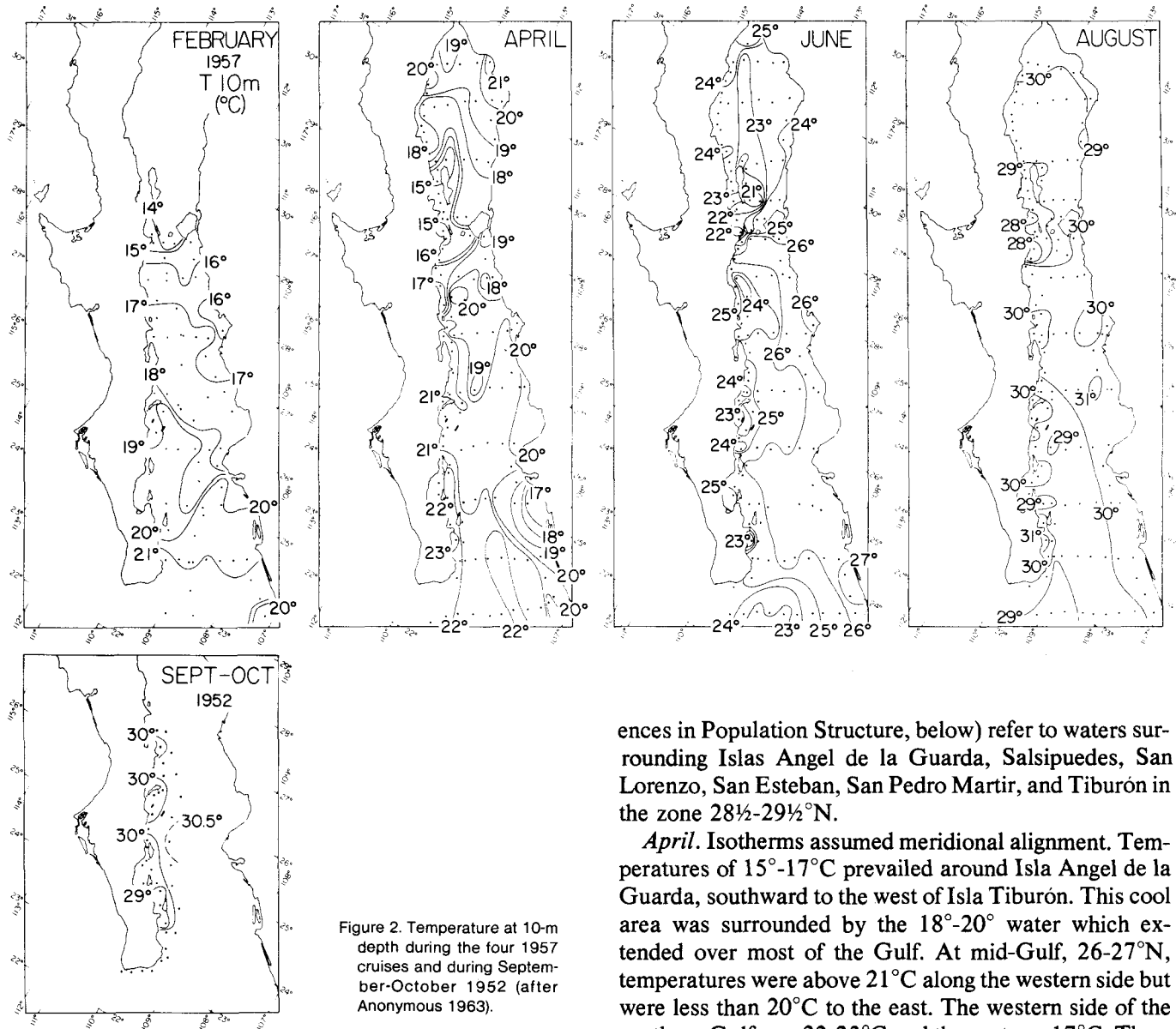
Figure 2. Temperature at 10-m depth during the four 1957 cruises and during September-October 1952 (after Anonymous 1963).

ing can be as intense as it is over the northern shelf and 2) island topography may be optimal for persistent upwelling because there is always some coastline normal to the shifting wind. Such diverse features preclude generalized explanations of nutrient renewal, plankton production, and hence, the distribution of plankton in the Gulf.

Temperature at 10-m Depth (Figure 2)

These temperatures are representative of the mixed layer into which the older life stages of most vertically migrating euphausiid species occurring here usually ascend in the nighttime. Larvae live only in this layer and the upper part of the thermocline (Brinton 1979).

February. Isotherms were roughly zonal, ranging from 14°C in the island channels to 20-21°C at the mouth of the Gulf. The "island channels" (cf. Regional Differ-

ences in Population Structure, below) refer to waters surrounding Islas Angel de la Guarda, Salsipuedes, San Lorenzo, San Esteban, San Pedro Martir, and Tiburón in the zone 28½-29½°N.

April. Isotherms assumed meridional alignment. Temperatures of 15°-17°C prevailed around Isla Angel de la Guarda, southward to the west of Isla Tiburón. This cool area was surrounded by the 18°-20° water which extended over most of the Gulf. At mid-Gulf, 26-27°N, temperatures were above 21°C along the western side but were less than 20°C to the east. The western side of the southern Gulf was 22-23°C and the eastern, 17°C. Thus, the eastern side was cooler in the southern Gulf than farther north.

June. The advance of seasonal warming continued, reaching 23-26°C over most of the Gulf. Only in the mixed waters of the northwestern island channels were temperatures as low as 21-22°C. Along the western side of the mid- and southern Gulf, temperatures responded to effects of the southerly winds and were 2 to 3°C cooler than to the east, thus differing from the condition in April.

August. Temperatures of 29-31°C now prevailed almost throughout the Gulf, with lowest values, to 28°C, again only in the northwestern island channels.

September-October. Temperatures observed in 1952 in the southern Gulf agreed with those of August 1957, indicating that summer conditions may persist into October.
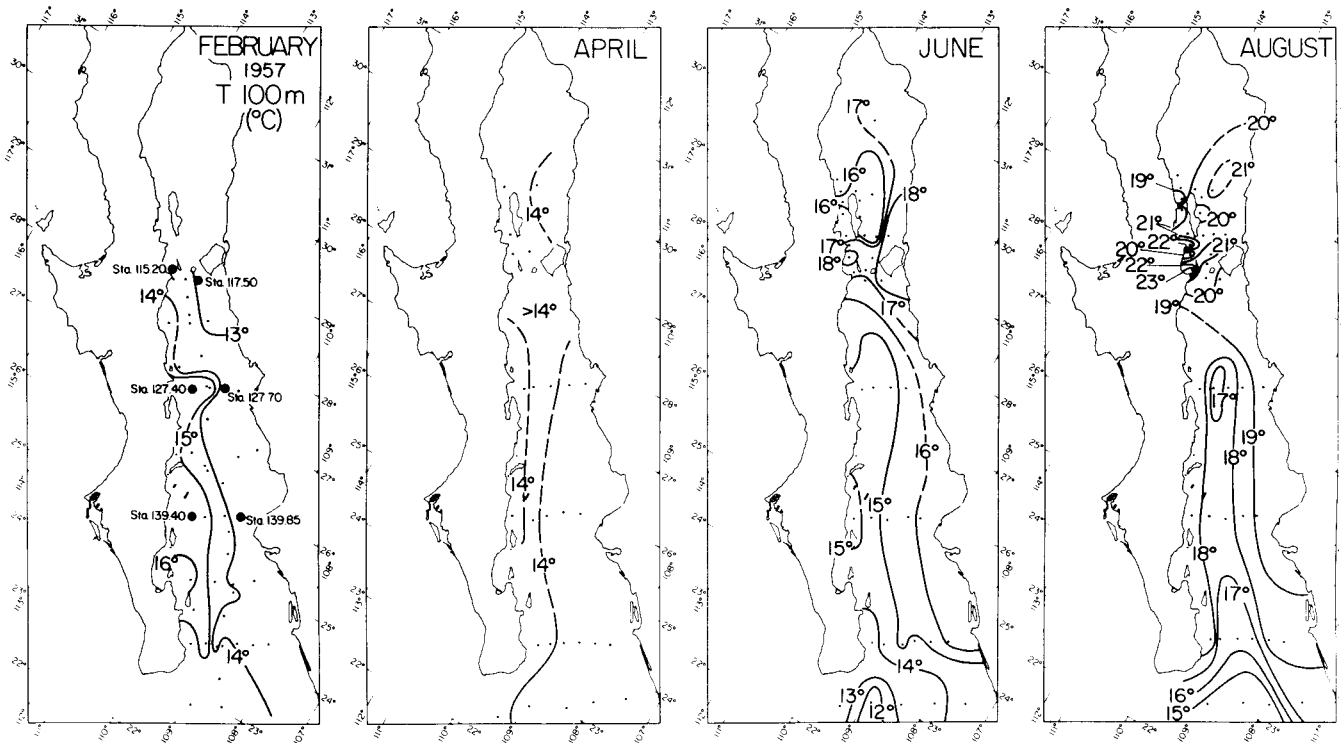
Figure 3. Temperature at 100-m depth (data from Reid et al. 1965). Positions of hydrographic casts are indicated as small dots. Stations for temperature profiles in Figure 4 are indicated by large dots.

Temperature at 100-m Depth (Figure 3)

At 100-m depth, temperature varies seasonally in the Gulf, whereas at 200 m, change is insignificant (Figure 4). At the deep mouth of the Gulf, 100-m temperature remained nearly constant, 14-16°C, throughout the year, whereas in the northern, shallower half of the Gulf, water at this depth warmed from 13-14°C in February-April to 19-23°C in August. In the sector of the island channels (Zone B, Figures 4, 18), this variation reflected the appearance of a summer thermocline following intense winter and spring mixing through the water column. In the mid- and southern Gulf the summer increase was evidently caused both by convection and downward conductive transfer from a surface subjected to progressively intense heating.

Seasonal variation at 100 m was greatest in the eastern Gulf (Figures 3, 4), evidently due to more penetrating June-August warming than took place along the western side where upwelling had become relatively stronger.

One hundred meters approximates the deep limit of the nighttime level of most euphausiids considered here (except the somewhat deeper living adults of *Nematoscelis difficilis*) and is near the upper limit of the levels to which migrating juveniles descend in the daytime, whereas adults of most species go deeper.

February. Upward bending of subsurface isotherms was conspicuous toward the eastern side of the Gulf. This was not evident in the 10-m temperature distribution,

indicating that upwelled water was not reaching the surface layer.

April. At mid-Gulf (26-28°N) there was <14°C water on both sides, but the eastern half was still generally a little cooler than the western.

June. The April situation was now reversed, as also in the surface layer. Isotherms now emerged toward the west.

August. The progression of summer warming was conspicuous, particularly over the broad shelf of the northern Gulf and along the eastern side. Ridging of subsurface isotherms along the Gulf's axis was evident toward the south.

Oxygen

The oxygen-deficient layer in the eastern tropical Pacific lies between the thermocline and about 700 m. The [O_2] in this layer may be as low as 0.05 ml/liter, which is near the limit of measurability. Water having this extreme minimum extended from 21°N off Cabo Corrientes at the mouth of the Gulf, southward to 11°N during June of 1974 (Brinton 1979). During 1957 this layer was diluted when it entered the Gulf. For example, at 23°N [O_2] of 0.1 ml/liter was unusual at any season and never occurred in water above 300 m except near the western side in April (Roden and Groves 1959). Moreover, the lowest [O_2] found half-way up the Gulf, at 27°N, was 0.2 ml/liter at 500-m depth.
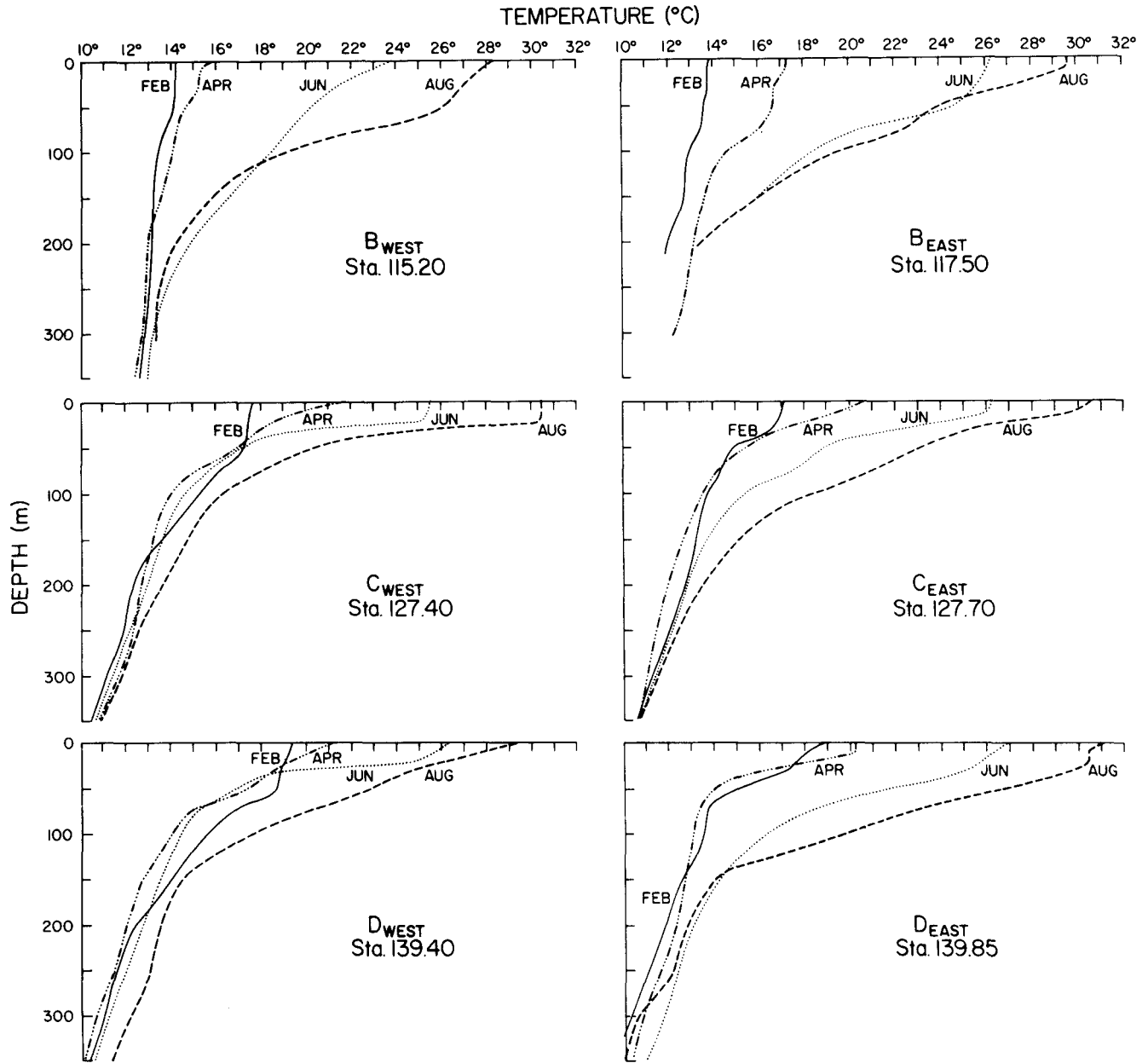
TEMPERATURE (°C)

Figure 4. Temperature profiles for February, April, June, and August of 1957 at localities on eastern and western sides of Gulf of California. Zones (B, C and D) and localities are shown in Figure 18 (data from Reid et al. 1965).

Oxygen deficiency has much to do with creating an environment for endemism among euphausiids in the eastern tropical Pacific and 2) with sharply restricting subtropical species and warm-water cosmopolites there. However, it appears not to be sufficiently shoal, extreme, or widespread in the Gulf to have had the same dominating role in the selection of which species are present.

Nevertheless, the depth of a given low-[O_2] surface may be used to show the spread within the Gulf of this salient property of eastern equatorial water as it relates to the 0-300-m range of depth in which most euphausiids are

expected to live. In the basins of the northern Gulf, the 1.5 ml/liter [O_2] surface is below 200-300 m during all seasons (Figure 5). It is deepest during April-June in the strongly mixed waters of the western island channels. By mid-Gulf it shoals to 100-200 m, and at the mouth, to 70-100 m. This surface tilts upward toward the east during the northeasterly winds of February-April, then upward toward the west in June.

Least [O_2] within the 0-300 m layer is at localities where the 1.5 ml/liter surface shoals to 70 m or less. Roden and Groves showed that low values of 0.1-0.5
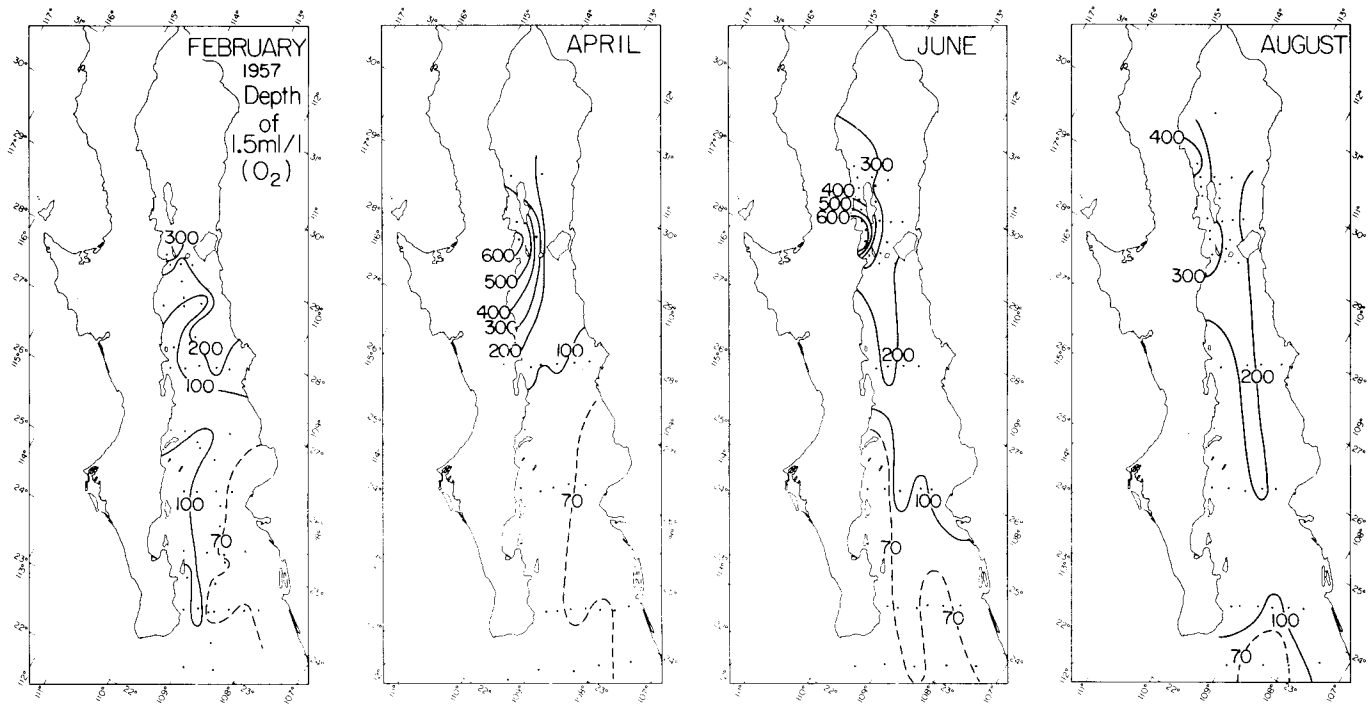
Figure 5. Depth of 1.5 ml/liter concentration of oxygen (data from Reid et al. 1965).

ml/liter are at 100-300 m in the southern Gulf, with the upper limit of the 0.5-ml/liter layer shoalest in February (40-80 m) and deepest in August (150-250 m).

Salinity

Seawater evaporation exceeds freshwater runoff into the Gulf (Roden and Groves 1959), but surface salinity beyond embayments ranges between 34.4 and 35.9 °/oo. This compares with a maximum salinity of about 34.0 °/oo in the open sea to the west (Love 1973). Therefore salinity per se is not expected to influence the distribution and abundance of plankton in the Gulf. Estuaries and lagoons along the southeastern coast may nevertheless contribute nutrients to the Gulf, as indicated by the primary productivity maxima, which were observed seaward of that coast during August of 1972, associated with relatively low surface salinities of 34.4-34.5°/oo (Gilmartin and Revelante 1978).

Currents

The geostrophic flow diagrammed in Figure 6 (after Wyllie 1966) shows mean surface flow to have been out of the Gulf during February and April. Flow at 200 m—the daytime depths of many migrating euphausiids—was then generally consistent in direction with surface flow. According to Roden and Groves this upper level outflow is compensated by inflow at greater depths.

By June, surface flow had reversed, entering the Gulf across most of the mouth and persisting toward the north as a stream which shifted toward the eastern side by August. Flow at 200 m was opposite to surface flow during the summer.

Direct observations supplemented by computations of geostrophic flow have been made of cyclonic cells of circulation extending across the width of the Gulf during August 1978 (Emilsson and Alatorre in press). Such a cell in the 0-50-m layer in the southern Gulf provided inflow along the eastern shelf and outflow near the tip of Baja California not unlike that described for August 1957. A similar eddy farther inside the Gulf was also indicated. This is pertinent in discussing exchange between the Gulf and the adjacent Pacific and how planktonic stocks may be maintained in the Gulf.

GEOSTROPHIC FLOW AT THE SURFACE
(RELATIVE TO 500 DECIBARS)

GEOSTROPHIC FLOW AT 200m DEPTH
(RELATIVE TO 500 DECIBARS)
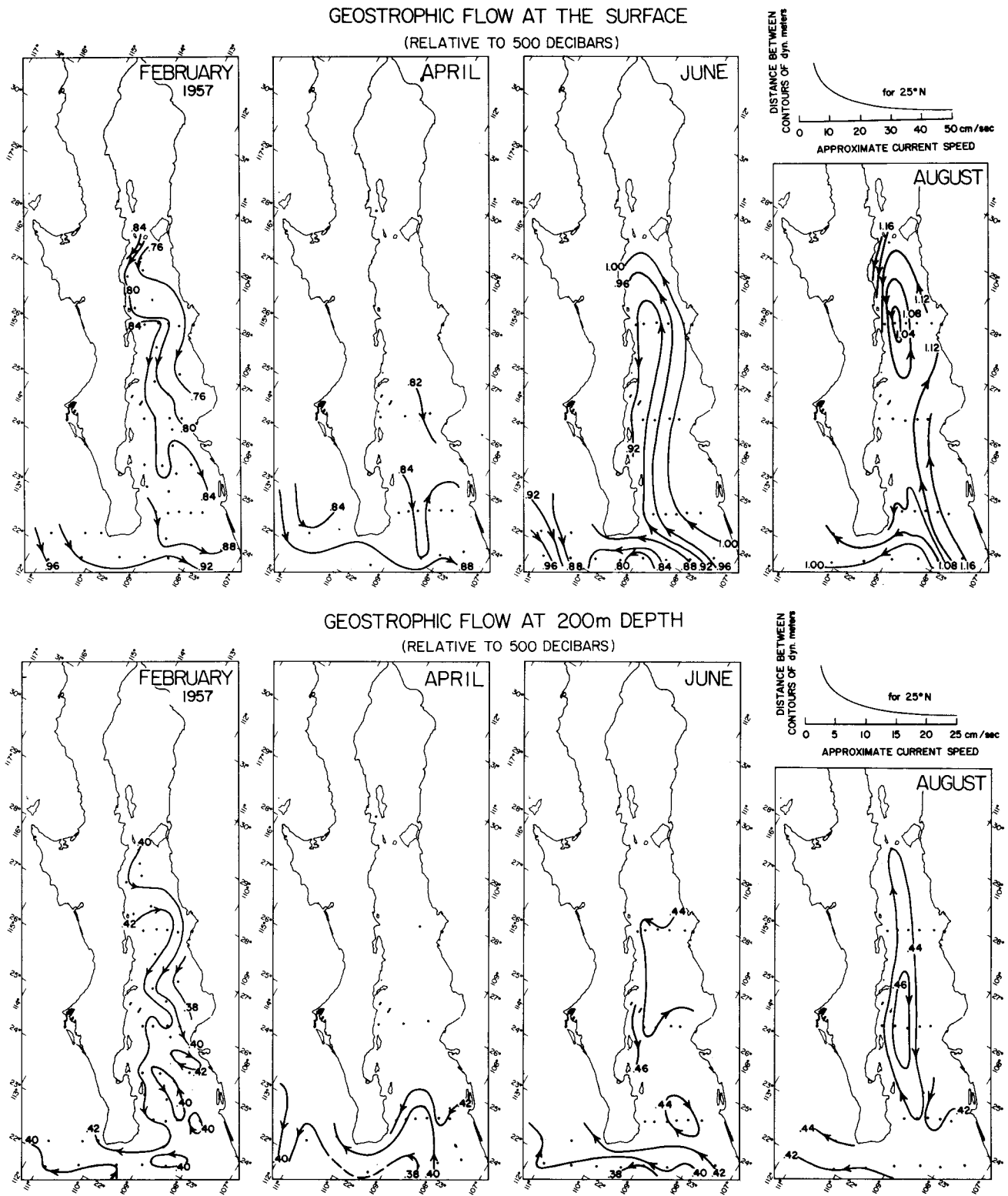
Figure 6. Geostrophic flow at surface and 200 m, relative to 500 decibar surface, inferred from casts at indicated localities (after Wyllie 1966).
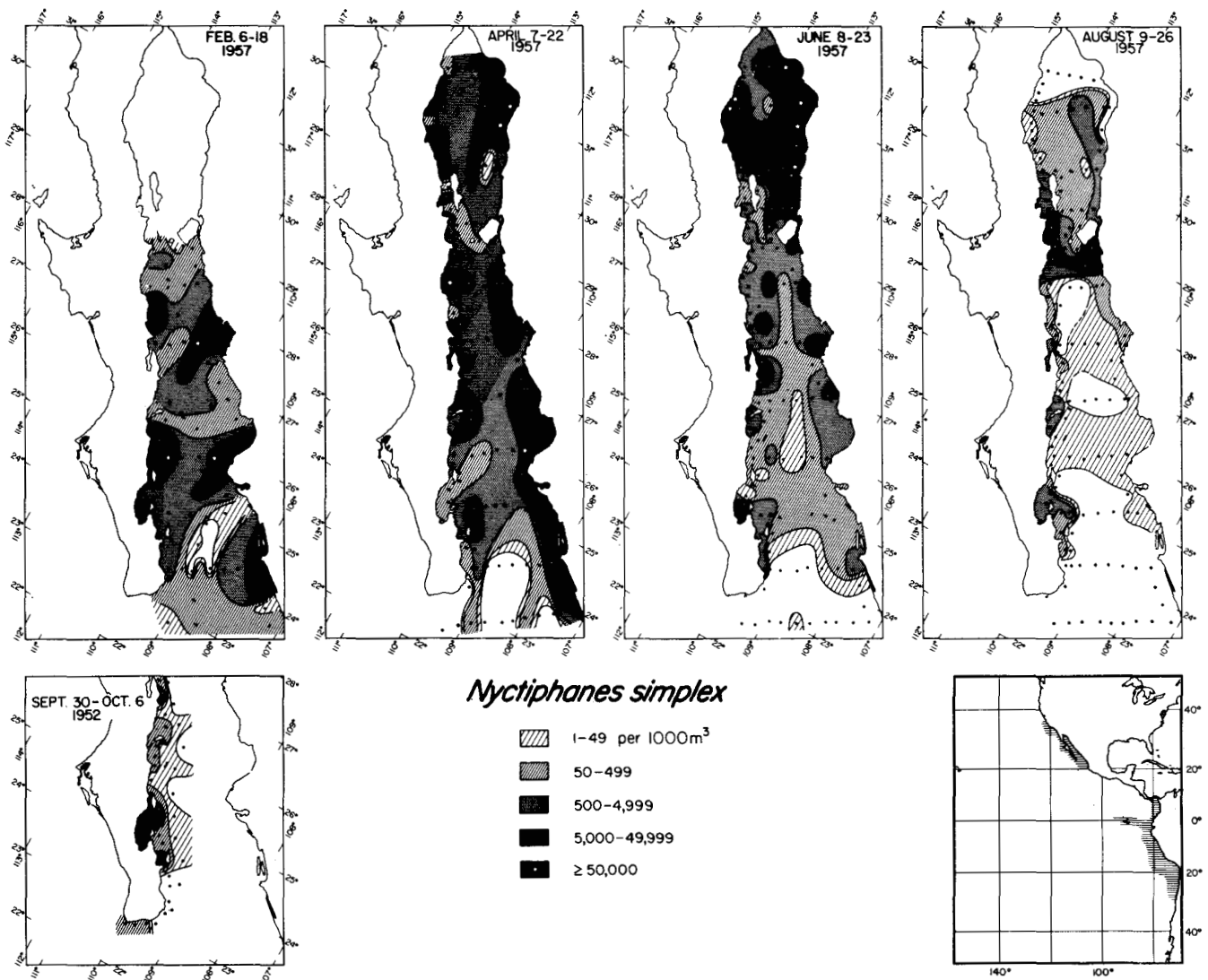
Figure 7. The coastal neritic species, Nyctiphanes simplex.

THE SPECIES DISTRIBUTIONS

Nyctiphanes simplex *(Figure 7)*

This euphausiid has the strongest neritic ties of those inhabiting the subtropical Californian region. Its range typically extends along Baja California northward to southern California, 34°N. During the warm year 1958, it reached 40°N off northern California.[1] *N. simplex* is the most abundant and widespread euphausiid in the Gulf of California during all seasons and has been observed in dense swarms by day (Steinbeck and Ricketts 1941) and in fields of luminescence at night (authors' personal observation), as *"Nyctiphanes"* (night shining) implies.

The vertical range of *N. simplex* seems to vary with

[1]Published reports on the distributions of the Gulf species outside of the area of this study will not be cited repeatedly in the text to follow. These references are, for the California Current, Brinton (1967a, b, 1973); for the eastern tropical Pacific and its transition with the California Current at the mouth of the Gulf, Brinton (1979); for the overall Pacific, Brinton (1962); and for the global picture, Mauchline and Fisher (1969) and Brinton (1975).

locality (Brinton 1967a, 1979). Clearest evidence of diurnal migration has been found seaward of the shelf. Species of *Nyctiphanes* in other oceans have been described as descending close to the shelf in the daytime where they may feed in the superficial sediments (Mauchline and Fisher 1969; Gros and Cochard 1978). High densities ($>5,000/1,000$ m³) in the Gulf were found in both day and night samplings.

During 1957, maximum numbers were generally nearshore or over the shelf. In February, when surface isotherms were oriented in an east-west direction (Figure 2), there were three zones with high densities, 27-28°N, 25-26°N, and 24-24½°N on the eastern side. These were located alternately with zones in which densities were moderate, generally $<500/1,000$ m³. The February distribution extended to the southernmost part of the Gulf, associated with southerly flow in the upper levels (Figure 6).

Figure 8. The warm-temperate species, *Nematoscelis difficilis*.

In April, high densities were along the Gulf's margins, particularly the eastern side. These extended as far south as the mouth, 24°N, where surface temperatures of 17-20°C persisted, now due to upwelling. Except for low numbers at the mouth, densities of *N. simplex* were >500/1,000 m³ almost everywhere in the Gulf, as the overall population peaked.

By June the upper water masses of the Gulf were warmer by 3-6°C than in April, and mean flow in the southern half of the Gulf was northerly. Highest densities were then general to the northern Gulf but were infrequent south of the island channels, diminishing to zero at the mouth.

When temperatures increased to 28-31°C in August, the population became reduced. The overall range of *N. simplex* remained unchanged except for retraction from the northernmost shelf region. Highest densities were

now around the island channels where temperatures were lowest, to 28°C. Peak numbers had been outside of these channels during the previous months. Pockets of moderate density were present on the western side of the Gulf to 24°S, evidently associated with summer mixing processes along that coast. The 1952 data on *N. simplex* suggest that those processes persist into October.

Nematoscelis difficilis *(Figure 8)*

In the oceanic North Pacific *Nematoscelis difficilis* inhabits the temperate-subtropical transition zone of the North Pacific Drift, 40-45° N (= Subarctic-Central in water mass terms). It is also prominent throughout the California Current from southern Oregon to Baja California but is known from the Gulf of California on the basis of three low-density records near Bahía Concepción, September-October 1952 (Figure 8). This popula-
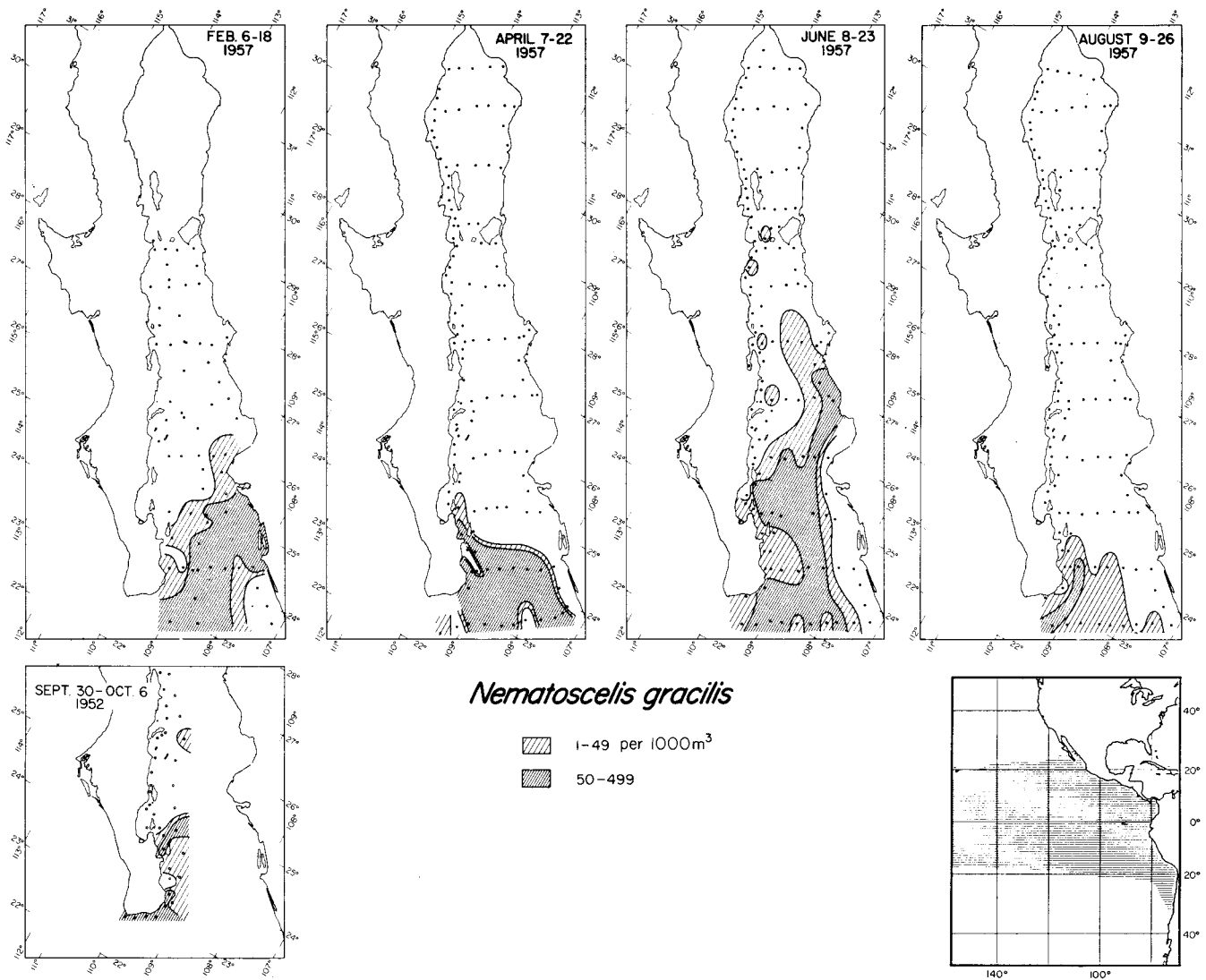
Figure 9. The tropical *Nematoscelis* species, *N. gracilis*.

tion was interpreted (Brinton 1962) as relict—isolated by tropical water at the mouth of the Gulf. However, the range of *N. difficilis* in the Gulf during 1957 nearly overlapped that of *Nyctiphanes simplex*, and this species was second in abundance of the Gulf euphausiids. These were altogether unexpected findings.

It is safe to state that *N. difficilis* lives deeper than *Nyctiphanes simplex*, though their vertical ranges overlap. The profiles for those species to the west of California and Baja California showed *N. simplex* tending to stay above approximately 100 m and adult *N. difficilis* below the mixed layer, except where stratification had broken down, as with upwelling (Brinton 1967a, 1979). (Weibe and D'Abramo [1972] showed that most *Nematoscelis megalops*, a close sibling and geographical analogue in the Atlantic of *N. difficilis*, are below 100 m at night in the Mediterranean Sea. Wiebe and Boyd [1978]

showed that *N. megalops* was spread through the upper 600 to 800 m in Gulf Stream cold core rings and apparently did not engage in diurnal vertical migrations.)

The February 1957 distribution showed *N. difficilis* concentrated toward the western side of the Gulf. High densities extended to the mouth. Though February data were lacking for the northern Gulf, this month is seen to be generally optimal for *N. difficilis*. Penetration into the southeastern Gulf of the 20°C isotherm at 10 m is associated with fewest numbers, but the presence of *N. difficilis* this far south assures exchange with the California Current population (cf. February 1957 distribution to west of Baja California in Brinton 1967b).

In April, instances of >5,000/1,000 m³ were fewer than in February in the southern half of the Gulf but did occur along both coasts to about 26°S.

From June to August, the diminishing population
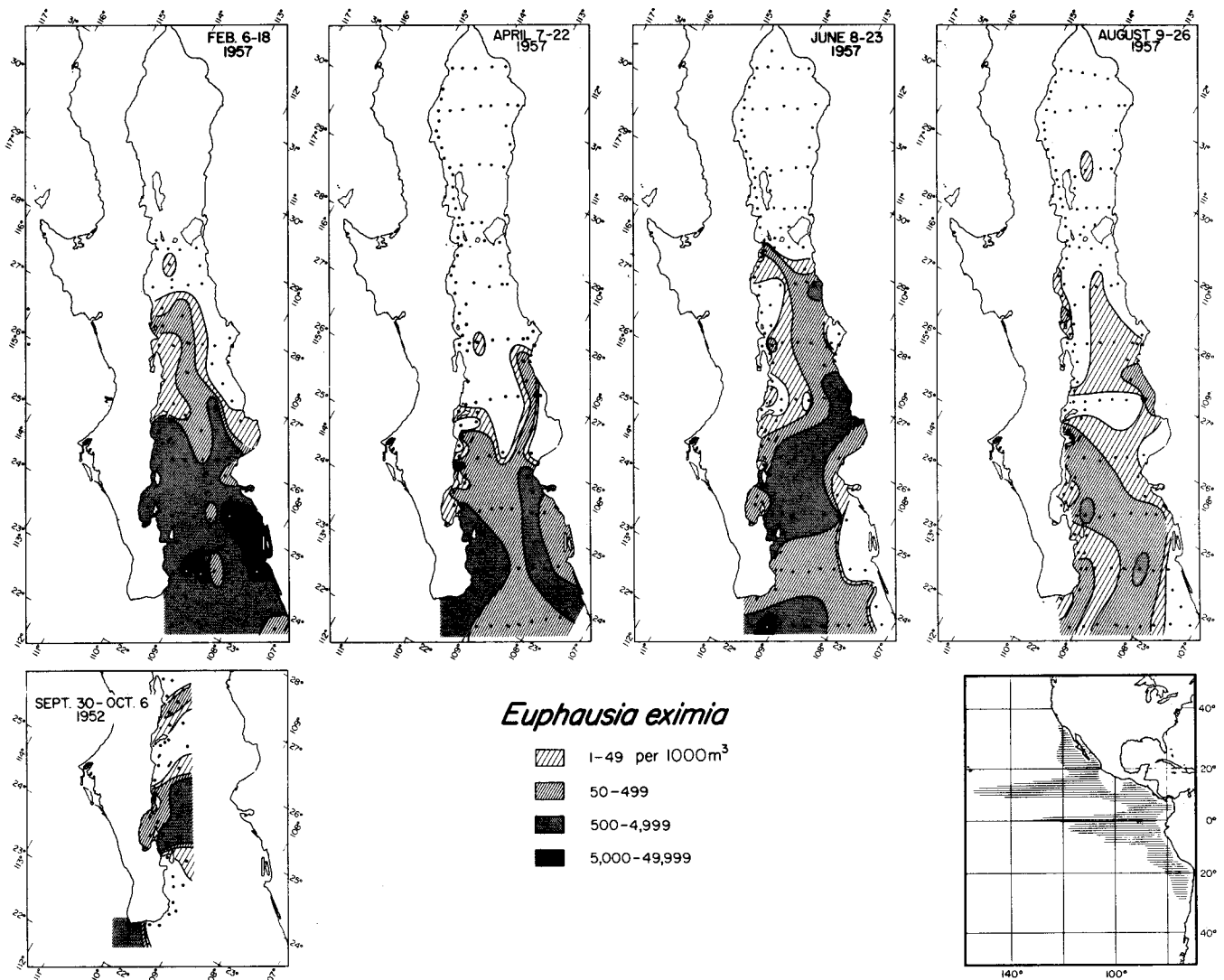
Figure 10. *Euphausia eximia*, which proliferates at margins of the eastern tropical Pacific.

tended to concentrate toward the west where coolest temperatures prevailed. Heated shelf waters to the north and east evidently provided limited refuge there, with occurrences primarily in or near the northern island channels and in the eastern zone south of Bahía Guaymas, 27-28°N. Tropical water entering the mouth of the Gulf— particularly to the east—appears to have compressed the distribution toward the north and west. Larvae, which customarily occur in the upper layer now warmed to 28-30°C, were represented by a single specimen, a furcilia, in the August catches.

If the vertical range of adult *N. difficilis* in the Gulf is greater than 200 m, as was supposed to be the case off southern California, this might induce mortality when the euphausiids are carried into neritic waters. However, in the terminal part of the California Current off Baja Califoria, 23°N, adults migrated through less than 200 m,

apparently limited to strata where [O_2] was greater than about 1.5 ml/liter. Such a vertical range in the Gulf could help to explain the extensive presence of *N. difficilis* shoreward of the basins.

During June and August in the mid- and southern sectors of the Gulf (Figure 3, 4), high temperatures in the upper 100 m would be expected to limit *N. difficilis* to below that depth, and shoaling of the 1.5-ml/liter oxygen surface to less than 100 m could further narrow the vertical range, thereby all but eliminating this organism from the southern Gulf by August.

Nematoscelis gracilis *(Figure 9)*

This species belongs to the euphausiid assemblage of the eastern tropical Pacific, while also ranging along the equatorial Indo-Pacific belt. The June 1974 data from the mouth of the Gulf of California (Brinton 1979) showed
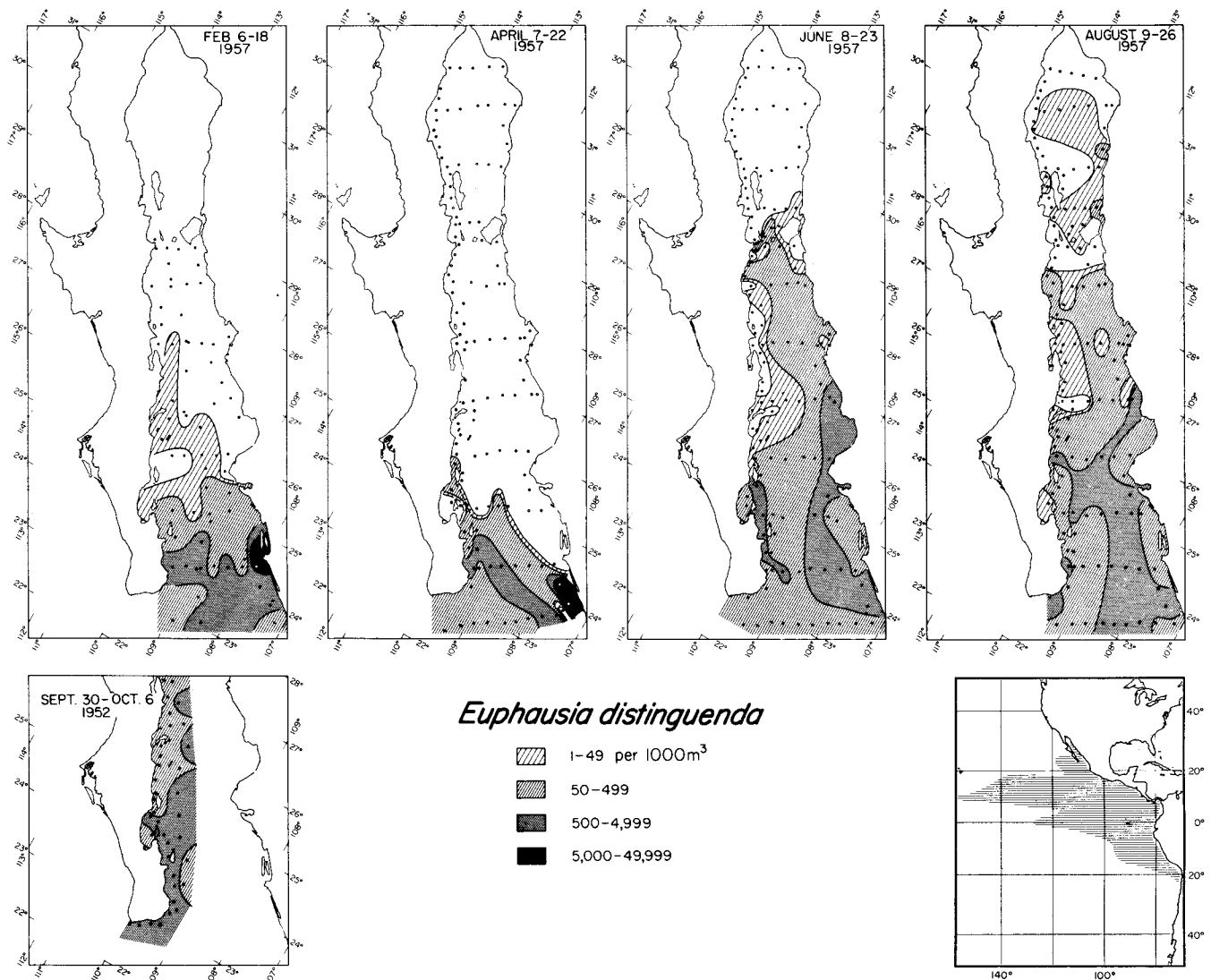
Figure 11. *Euphausia distinguenda*, endemic to the eastern tropical Pacific.

that the northern limit of *N. gracilis* abuts the southern limit of congener *N. difficilis* there. Adults of both species were beneath the 0-40-m layer at night, except at an upwelling locality to the west of Cabo San Lucas. In the daytime *N. gracilis* was within the extreme [O_2] minimum layer, 300-400 m, while *N. difficilis* was above 200 m, apparently limited by the 1.0- or 1.5-ml/liter [O_2] surface. Larvae and juveniles of both species ranged within or into the mixed layer, day and night.

During February of 1957, *N. gracilis* was present only in the southern Gulf. Its most northern presence was to the east where the oxygen minimum was shoalest (Figure 5) and where *N. difficilis* was sparse. Flow at 200-m depth shows this distribution to be within a system of slow eddy circulation. Elsewhere, where *N. difficilis* was dominant, flow was southerly (Figure 6).

The April distribution extended farthest north on the western side, as far as Isla Espíritu Santo, 24½°N. This was within the warmest waters in the Gulf—>21°C at 10 m (Figure 2) and >14°C at 100 m (Figure 3).

June warming and strong northerly flow in the upper levels (Figure 6) brought *N. gracilis* to the northern island channels, 29°N, though its uninterrupted geographical distribution extended only to the Guaymas Basin, 27½°N.

By August, northerly transport to mid-Gulf was reduced. There, eddy circulation developed, and the range of *N. gracilis* retracted southward. The high temperatures general to the Gulf in August should be suitable for this species, in keeping with its distribution across the eastern tropical Pacific. Hence, a southerly trend in flow within the subsurface habitat of the bulk of *N. gracilis* may be limiting.

Euphausia eximia *(Figure 10)*

E. eximia is abundant in the California Current to the west of Baja California, 21-30°N. The range extends
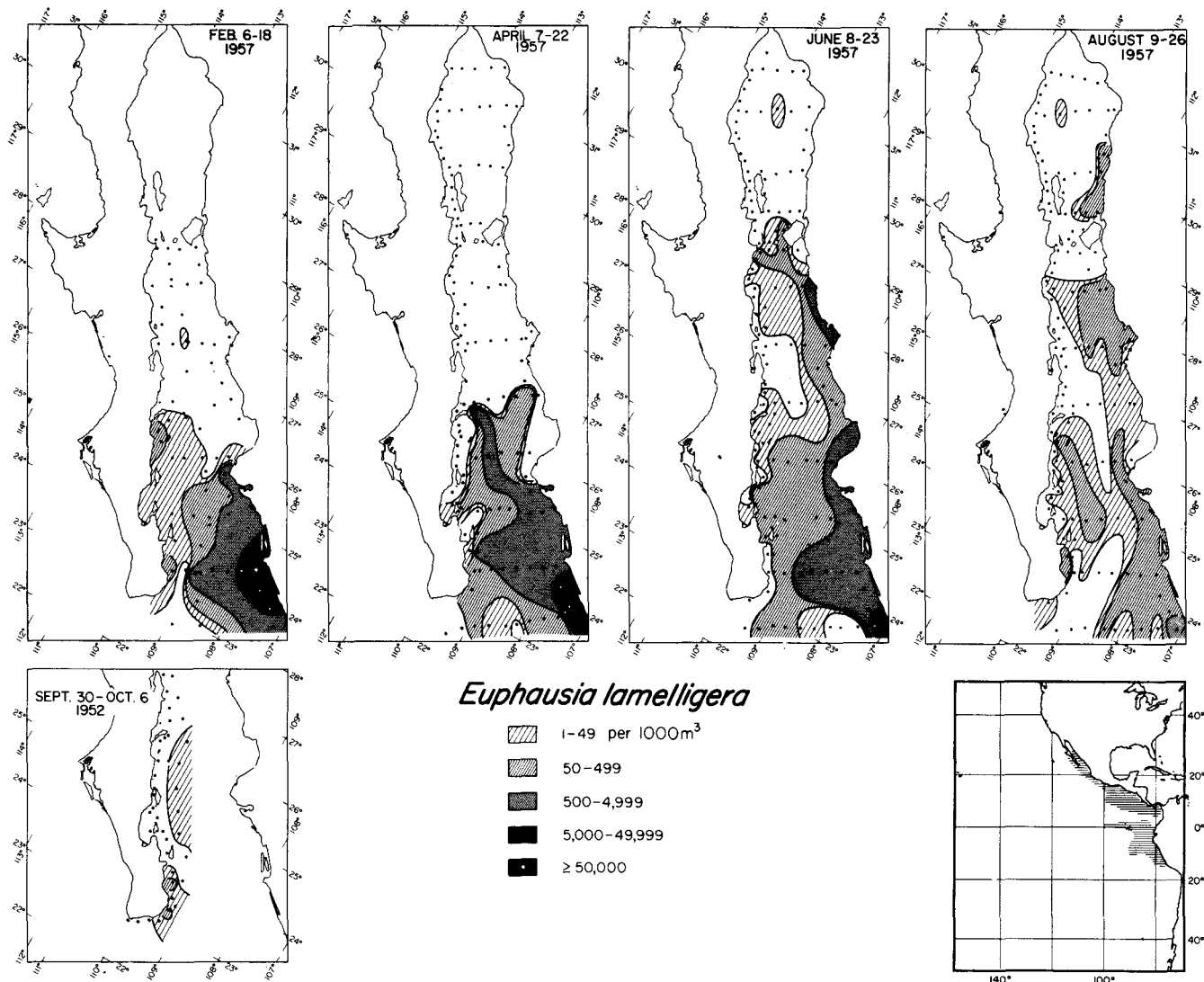
Figure 12. *Euphausia lamelligera*, coastal to the eastern tropical Pacific.

across the eastern tropical Pacific, but the species is sparse, nonreproductive, and avoids the mixed layer in waters where surface temperature exceeds 26°C and/or [O_2] in the minimum layer is <0.1ml/liter (i.e. low). This includes the region between the equator and 21°N at the mouth of the Gulf.

E. eximia in the Gulf shifted little with season, appearing as a resident population from 28°N southward. As with the two warm-temperate species, *Nematoscelis difficilis* and *Nyctiphanes simplex*, highest densities of *E. eximia* were during February. Maxima for *E. eximia* were in a region of sluggish circulation in the southern Gulf. The most northern presence of significant numbers was in June when upper level flow was strongly toward the north, particularly on the western side. Lowest densities were in August when temperatures >26°C extended to 25-60-m depth (Figure 4).

Euphausia distinguenda *(Figure 11)*

E. distinguenda is endemic to the eastern tropical Pacific where it is widespread and is the most abundant euphausiid. The vertical range extends up into the warmest layer there and it is also tolerant of lowest [O_2], 0.05 ml/liter, at daytime depths. In both respects, *E. distinguenda* differs from *E. eximia*. It also differs from *E. eximia* in that its distribution in the Gulf fluctuates greatly with season.

In February, *E. distinguenda* was as far north as 27°N off Bahía Concepción. This may be a residual tongue; the August range showed that *E. distinguenda* is distributed nearly throughout the Gulf late in the year. Also, this mid-Gulf presence is to the west of the southerly flow at both the surface and 200 m (Figure 6).

As during February, high densities in April were at the mouth of the Gulf, with maxima over the eastern shelf.

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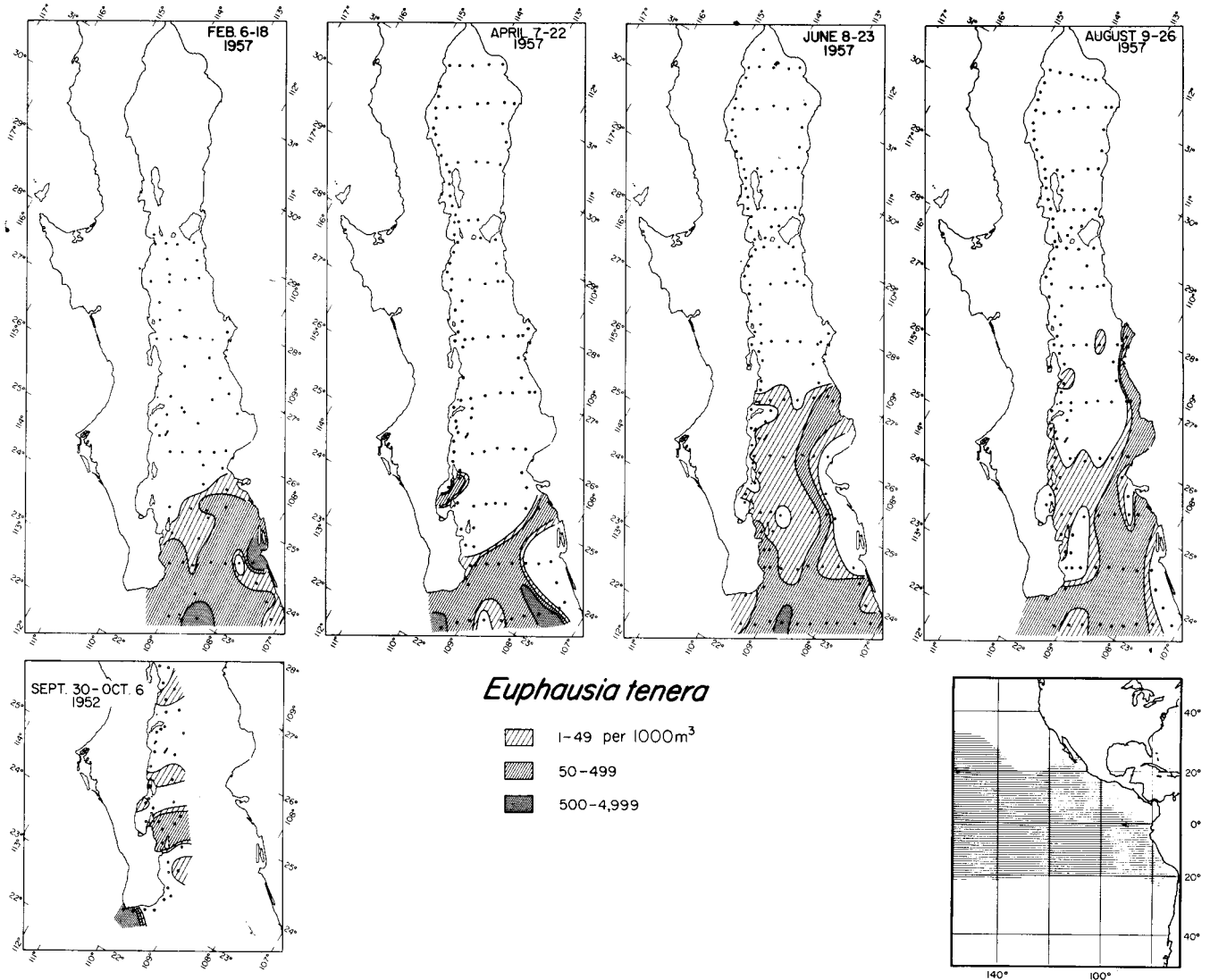
Figure 13. *Euphausia tenera*, oceanic in tropical seas.

E. distinguenda moved up the Gulf during June-August when northerly flow developed, mainly on the western side. Upper level temperatures now exceeded 22°C at 10 m and 15°C at 100 m. Presence of this organism in shelf waters of the northern Gulf in August must have resulted from northward flow through the island channels, followed by branching flow toward the east.

Euphausia lamelligera *(Figure 12)*

E. lamelligera is more coastal than *E. distinguenda* in the eastern tropical Pacific where both are endemic. The two species are particularly closely related (Brinton 1975, 1979), but their overlapping coastal-versus-oceanic ranges within the tropics indicate incomplete habitat separation.

There appears to be even less separation in the Gulf than farther south. Here there is much shelf and slope area

in relation to basin, and a population having basic affinities with one system could readily be mixed with the other. Thus, the overlapping of *E. distinguenda* and *E. lamilligera* in the Gulf parallels the similarity between the distributions of the Gulf's two warm temperate euphausiids—typically oceanic *Nematoscelis difficilis* and coastal *Nyctiphanes simplex*.

Whereas the February-April range of *E. lamelligera* scarcely reached mid-Gulf, 27°N, the June-August period of northerly flow brought it to the northern shelf, mainly along the eastern slope. Breaks in continuity appeared in the zone of the island channels, near 29°N (cf. *E. distinguenda*). Highest densities were regularly in eastern waters at the mouth of the Gulf.

Euphausia tenera *(Figure 13)*

E. tenera has a broadly tropical distribution around the globe. It is the smallest *Euphausia* species—slender,
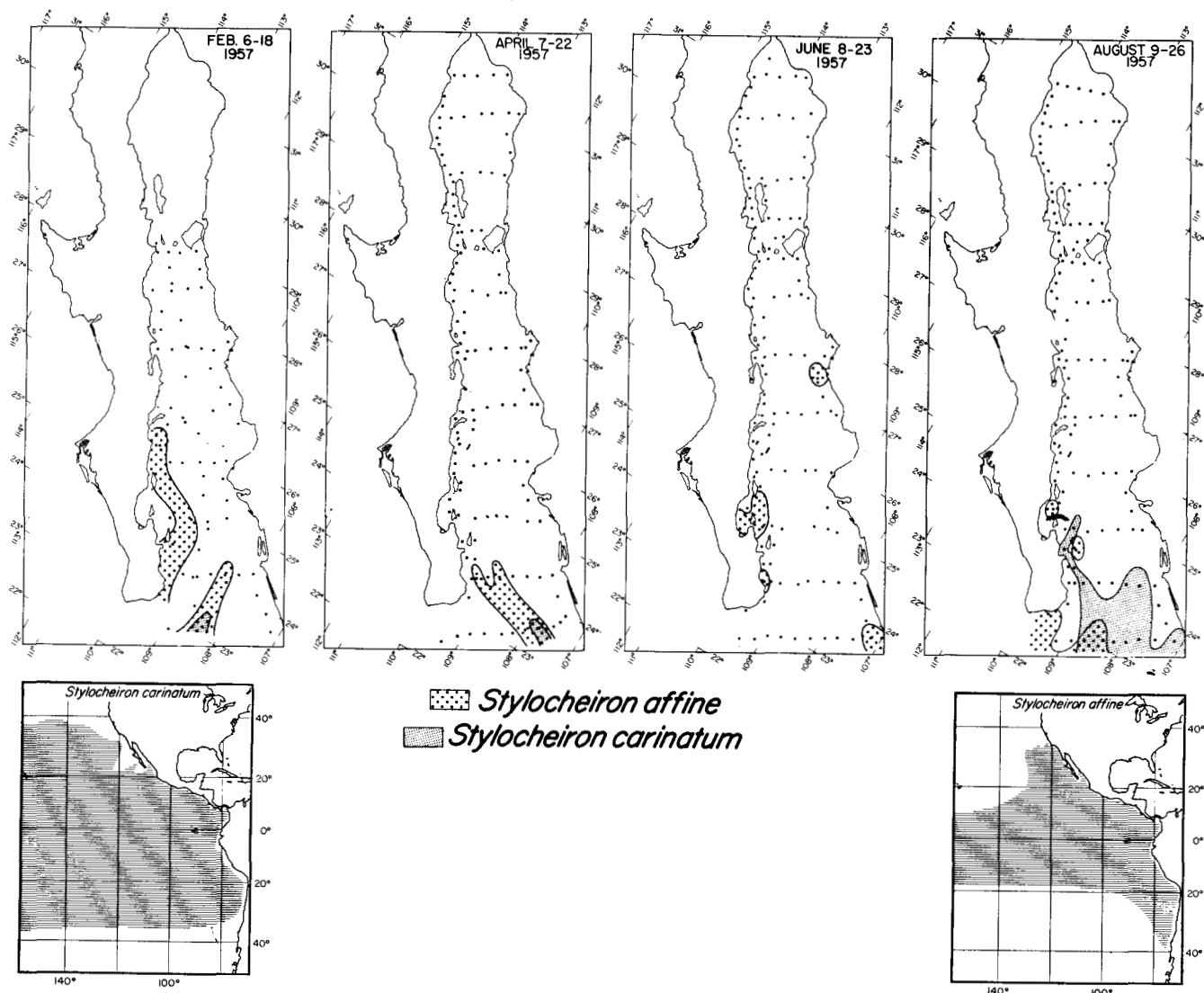
Fiogure 14. The two *Stylocheiron* species found in the Gulf of California. *S. affine* is present here as the East Equatorial Form. The overall range shown for *S. affine* excludes the relatively divergent Central Form.

rarely reaching 11 mm in length, compared with 12 and 14 mm for the more robust *E. lamelliggera* and *E. distinguenda* or with as much as 25 mm for *E. eximia* in the Gulf. However the diurnal vertical migration of *E. tenera*, as determined in the eastern tropical Pacific, is as extensive as that of the others, about 0-300 m for the adult.

During February and April, *E. tenera* was limited to the southern Gulf. During the June and August periods of warming and inflow, the distribution extended barely to mid-Gulf, mainly within the northerly current near the eastern side. This, together with *E. tenera*'s consistently low density over much of the southeastern shelf at the mouth, 24-26°N, contributed to this being the *Euphausia* species at lowest density in the Gulf. These characteristics attest to the midocean, though not necessarily bluewater, affinities of *E. tenera* (Brinton 1962, 1979), relative to the eastern boundary current affinities of the predominant species in the Gulf.

Stylocheiron affine *and* S. carinatum *(Figure 14)*

During 1957, these euphausiids were few, patchy in occurrence, and restricted to the southern Gulf. They were not present in the September-October 1952 samples. The intrusions show no significant pattern of seasonal change.

S. affine is represented in the general area by a "California Current Form" and an "East Equatorial Form," which have been observed to merge off the mouth of the Gulf (Brinton 1962). These, together with a "West Equatorial Form," are the basis for the composite range shown in Figure 14, inset. There were few adult specimens in the 1957 material, and no analysis of "Form" was attempted.

S. carinatum has been described as particularly sparse off the mouth of the Gulf and, when present there (Brinton 1962, 1979), as derived from tropical water to the south.

S. affine is a nonmigrator, living mainly within the thermocline. *S. carinatum* appears to be a short-distance

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migrator, between the mixed layer at night and the thermocline in the day. Thus, both are distributed by upper level flow, being unable to avail of the deep countercurrents which often serve the strong vertical migrators in maintaining range stability.

Nematobrachion flexipes *and* Euphausia diomedeae

Two other euphausiid species (distributions not shown here) were recorded at or near the mouth of the Gulf. Young of *Nematobrachion flexipes* were at 23°N, near the tip of the Baja California peninsula in June (one record) and August (two records). These specimens evidently came from the southernmost part of the California Current, inasmuch as *N. flexipes* has been found lacking in the most oxygen-deficient part of the eastern tropical region to the south.

The virtual absence from the Gulf of the widely tropical species *Euphausia diomedeae* was unexpected. Single specimens were found at 23°N, south and southeast of Cabo San Lucas, in April and June. In August there were two records at the mouth of the Gulf and one at 27°N in the northerly stream on the eastern side.

E. diomedeae is related to *E. eximia* (e.g. their larvae are almost indistinguishable), more so than to *Euphausia lamelligera, E. distinguenda,* or *E. tenera.* Evidently the Gulf is habitable by *E. eximia*, which "proliferates at the margins of the eastern tropical Pacific" (Brinton 1979), and not by its more tropical relative, *E. diomedeae.*

EUPHAUSIID BIOMASS

In tropical and subtropical seas, the proportion of euphausiid biomass to total zooplankton biomass (wet displacement volume) retained by our nets varies between about 3% and 50% among localities. However, within oceanographic regions there is less variability. This is seen in the June 1974 values from three regions of the eastern Pacific (Brinton 1979): 1) southernmost California Current, $\bar{x} = 12\%$, range 7-15%; 2) outer Gulf (Cabo San Lucas to Cabo Corrientes), $\bar{x} = 8\%$, range 7-13%; 3) eastern tropical zone (Acapulco to Galapagos Islands), $\bar{x} = 21\%$, range 9-49%.

These means of euphausiid biomass are higher than the 3 to 7% obtained inside the Gulf during 1957 (Figure 15). However, an annual mean of the four monthly means of total zooplankton biomass in the Gulf in 1957 is close to 300 cc/1,000 m³. This compares with the regional 1974 means outside the Gulf of 258, 312, and 305 cc/1,000 m³ for regions 1), 2), and 3) above, respectively. These latter values for total biomass were obtained in June 1974. The June 1957 mean inside the Gulf agreed with the mean of the four 1957 cruises. This indicates that biomass in the Gulf, at least in June, may be of the same order as that in the subtropical-tropical ocean outside.

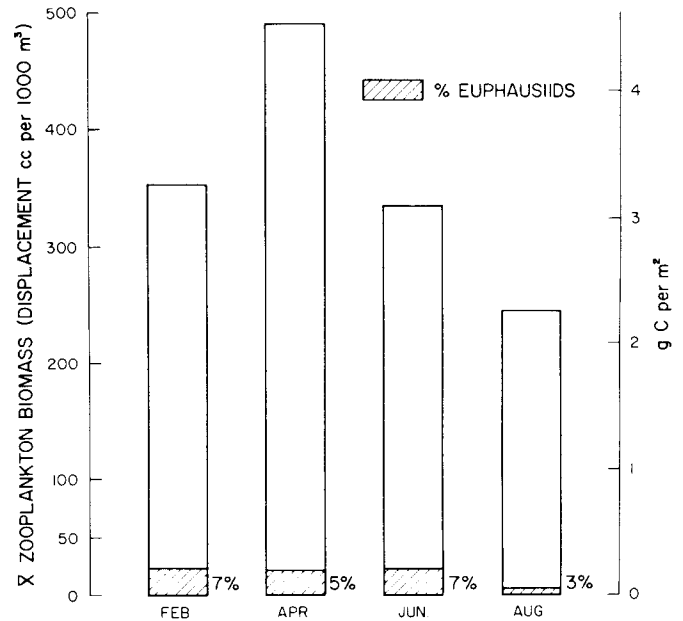However, the June 1974 data outside of the Gulf were

Figure 15. Mean euphausiid biomass shown as a percentage of the mean total biomass for each Gulf of California cruise in 1957.

obtained using a Bongo net, which differs in design from the 1-m ring net used in the Gulf in 1957. The Bongo net has no anterior bridle to signal a warning to the plankton. Bongo nets are proving to be more effective than the 1-m net in catching euphausiids of >8-mm length; smaller sizes are caught in equal number (authors' unpublished observations from California Current samples). Biomass of specimens 7-14 mm (which includes juveniles of all Gulf species + adults of all except *Euphausia eximia* and *Nematoscelis difficilis*) is underestimated by about two times when the 1-m net is used; of specimens 15-20 mm (includes adults of *E. eximia* and *N. difficilis*) by about four times. Hence, most Gulf species may have been substantially undersampled, leading to underestimation of euphausiid biomass by a mean of three times. The estimates of total numbers of euphausiids are much less affected by difference in the kind of net than are estimates of biomass because specimens >8 mm—mostly adults—are few compared with young stages.

Comparisons of biomass among the Gulf cruises and between the Gulf cruises and samplings outside the Gulf may nevertheless aid in placing the Gulf's plankton in perspective with that of the adjacent ocean. Euphausiid biomass in the Gulf was nearly constant at 20 cc/1,000 m³, or 0.2 g carbon/m², during February to June (means for all stations of each cruise; Figure 15). However, expressed as a percentage of the total, euphausiids were most, 7%, in February and June, and down to 5% in April when total biomass peaked.

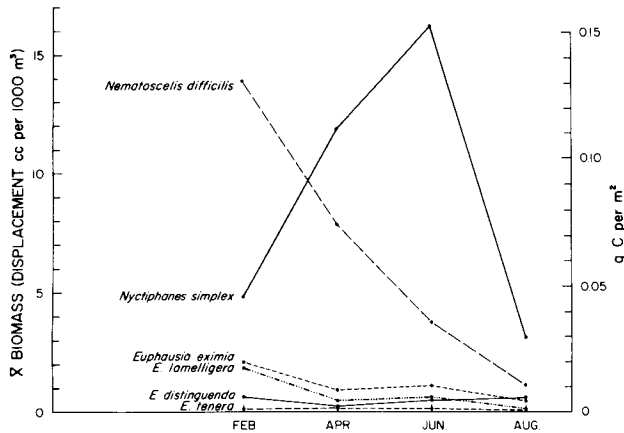This nearly uniform euphausiid biomass during February to June resulted from the simultaneous buildup in

Figure 16. Biomass of six euphausiid species, each determined as a mean of values for all stations of each of the Gulf of California cruises in 1957.

Nyctiphanes simplex and decline from February onwards in *Nematoscelis difficilis* (Figure 16). February peaks in biomass for *Euphausia eximia* and *E. lamelligera* contributed little to the overall euphausiid biomass at that time, through certainly being significant in the southernmost part of the Gulf.

Euphausiids decreased to 3% in August, when the two bulk species were much diminished.

THE DEVELOPMENTAL PHASES—
ABUNDANCES AND DISTRIBUTIONS

During 1957 in the Gulf, euphausiid recruitment and survivorship developed in an interpretable way in the three species that appear to be resident—those sufficiently numerous and geographically stable to show some independence from the populations outside the Gulf. These species are *Nyctiphanes simplex, Nematoscelis difficilis,* and *Euphausia eximia.*

The tropical species entering the Gulf are centered either 1) in the eastern tropical Pacific to the south (*Euphausia distinguenda* and *E. lamelligera*) or 2) in the ocean-wide equatorial belt to the south and west (*Nematoscelis gracilis* and *Euphausia tenera,* and *E. diomedeae* of which one specimen was found north of the mouth, 23° 30′N). *E. distinguenda* and *E. lamelligera* reproduced substantially in the southern Gulf. Few larvae of *N. gracilis* and *E. tenera* (see below, Proportions of Life Phases), and none of *E. diomedeae,* were found in the Gulf.

The calyptopis is the youngest larval phase retained by our nets, and its abundance will be used as a measure of recruitment to the populations of the species considered resident. Only general trends in survivorship and growth may be derived from the four bimonthly sets of samples.

There is some information on life-span of species of euphausiids similar to those living in the Gulf. Jörgensen and Matthews (1975) gave one year as the probably life-

span of *Nematoscelis megalops* in a Norwegian fjord. *N. difficilis* is very closely related to *N. megalops* and has the same life-span, or a little longer, based on Brinton and Wyllie's (1976) data from the California Current. Gros and Cochard (1978) interpreted *Nyctiphanes couchii,* a northeastern Atlantic relative of *N. simplex,* as living approximately two and a half years in the Bay of Biscay. *Euphausia pacifica,* in the California Current off southern California, lives to one and a half years, according to Brinton (1976); there is no information on the life histories of the tropical *Euphausia* species.

Nyctiphanes simplex

In the Gulf, *Nyctiphanes simplex* produced most calyptopes in February (Figure 17), the mean being 3,600/1,000 m³, which accounted for 80% of the total for the four 1957 cruises. Calyptopes declined in numbers as the year progressed. However, *N. simplex* was the only species to produce these larvae in significant numbers as late as August. High variances (Appendix I) are associated with these means, and with those below, in the discussion of regional variation in the occurrences of life stages. However, means will nevertheless be used here as indications of seasonal and regional trends in abundances.

Furcilia larvae increased during February-June, while calyptopes decreased, indicating improving larval survivorship as spring progressed. Youngest *N. simplex* calyptopes of 1-mm length (Boden 1951) must grow to oldest furciliae of 5- or 6-mm length in about a month (cf. *N. couchii;* Le Roux 1973)—certainly in less than the two-month interval between the Gulf cruises. Hence, the June peak in furciliae derives from calyptopes produced somewhat after the apparent peak in February.

Juvenile *N. simplex,* like the furcilia larvae, were most numerous during April-June, whereas adults showed a steady increase during February-June, with scarcely a decline in August.

Nematoscelis difficilis

Ninety percent of the February-August crop of calyptopes of *Nematoscelis difficilis* were produced in February when the mean density was 900/1000m³ (Figure 17). The coinciding February peak in the older larvae (furciliae) indicates that maximum recruitment was earlier than February. (Gopalakrishnan [1973] found the larval life of *N. difficilis* to be of the order of 30 days.) Calyptopes declined during April to June and ceased to be produced by August. Adults and larvae were both most numerous in February. Whereas *Nyctiphanes simplex* adults increased through the year, those of *N. difficilis* decreased, though in both species the adult stock remained nearly constant. It appears likely that the numerous larvae of February, or somewhat earlier, led to the April-June peak in juveniles and then to a substan-
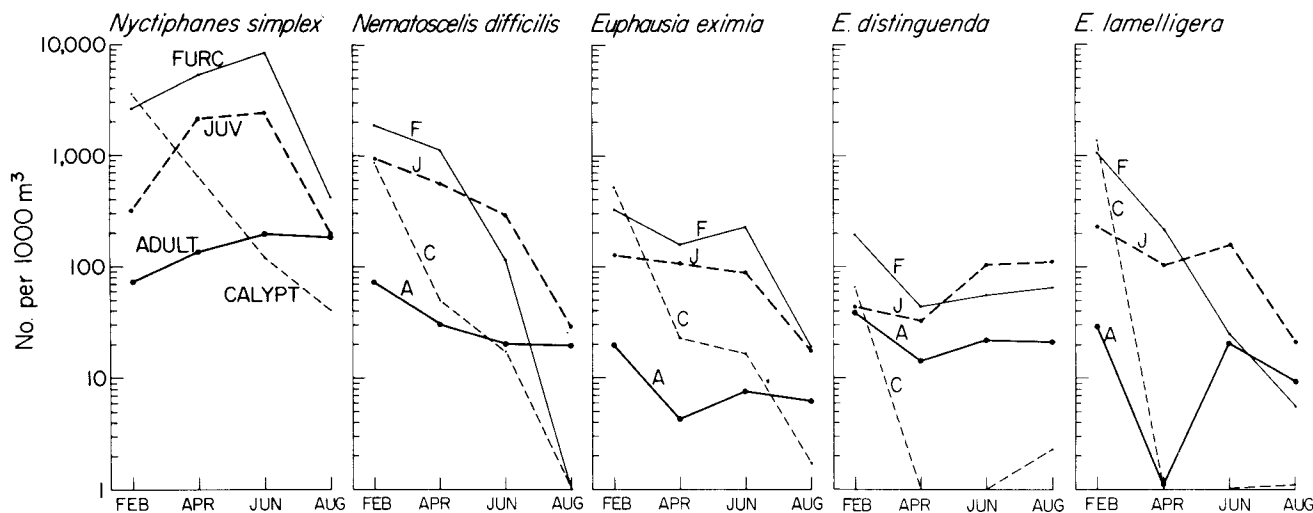
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Figure 17. Seasonal variation in abundances of life phases of five predominant euphausiids. Values are means of all values, each Gulf of California cruise in 1957. See Appendix I for data on *Nyctiphanes simplex* and *Nematoscelis difficils*.

tial stock of young adults in August, clearly the most stressful period for *N. difficilis*. These adults would be expected to reproduce during the ensuing winter.

Euphausia eximia

This species followed nearly the same pattern as *Nematoscelis difficilis*. Ninety-five percent of all calyptopis larvae were observed in February, with their production decreasing nearly to zero by August. In *E. eximia* there were relatively more furciliae entering the population as late as June. Adults were then at a second peak, following a February maximum. Adults held their numbers into August, evidently receiving input from the June juveniles, whereas the younger phases were much reduced.

Euphausia distinguenda

Of the tropical species, *E. distinguenda* showed the most stability through the year, with furciliae, juveniles, and adults nearly constant in numbers. However, the youngest larvae (calyptopes) were significantly present only in February inside the Gulf. Substantial recruitment from the south may have occurred during the June-August period of northerly flow.

Euphausia lamelligera

The distribution of *E. lamelligera* (Figure 12) shows that the center of distribution of this coastal species is at the mouth of the Gulf and southward. As in the other species, peak recruitment in the Gulf was in February. Furciliae steadily declined thereafter. Adults remained nearly constant in numbers, except for a near absence in April at the end of the spring period of outflow.

Regional Differences in Population Structures

The Gulf is considered here to consist of four zones (Figure 18), which roughly reflect common limits of seasonal shifts in zonation of the euphausiids (Figures 7-14).

These zones are modified from those proposed by Gilbert and Allen (1943) that corresponded with differences in diatom abundances and are like those proposed by Round (1967) for phytoplankton floras. Round's northern and southern zones apply to euphausiids. His central zone is subdivided here to separate the distinctive "island channels," 28½-29½°N, from "mid-Gulf."

Although scarcely 100 km apart, the two sides of the Gulf nevertheless differ with respect to 1) extent of continental shelf, hence of neritic mixing through the water column, and 2) nutrient renewal through upwelling in a given season. In the northern Gulf, in the zone of island channels and in the mid-Gulf, mean temperatures (10-m depth) are somewhat lower on the western side throughout the year (except in mid-Gulf in February; Figure 19). In the southern Gulf, the eastern side is cooler during February-April, and the western side during June-August.

Nyctiphanes simplex and *Nematoscelis difficilis*, the two species that utilize most of the area of the Gulf, were examined for east-west differences in population characteristics in the four zones.

Nyctiphanes simplex (Figures 18A, 20A). In the northern Gulf and in the island channels (zones A and B), calyptopis larvae were more abundant on the eastern side throughout the year, except in August when the western island channels became the principal refuge for the presence of calyptopes.

In the southern half of the Gulf (zones C and D) calyptopes were commonest on the eastern side in February, with the maximum shifting to the west during April-August. However, the dominance of zones A and B in the production of calyptopes is seen in Figure 20A, in which the mean value for the eastern Gulf during all of February-June (four zones combined) is well above that for the western side.
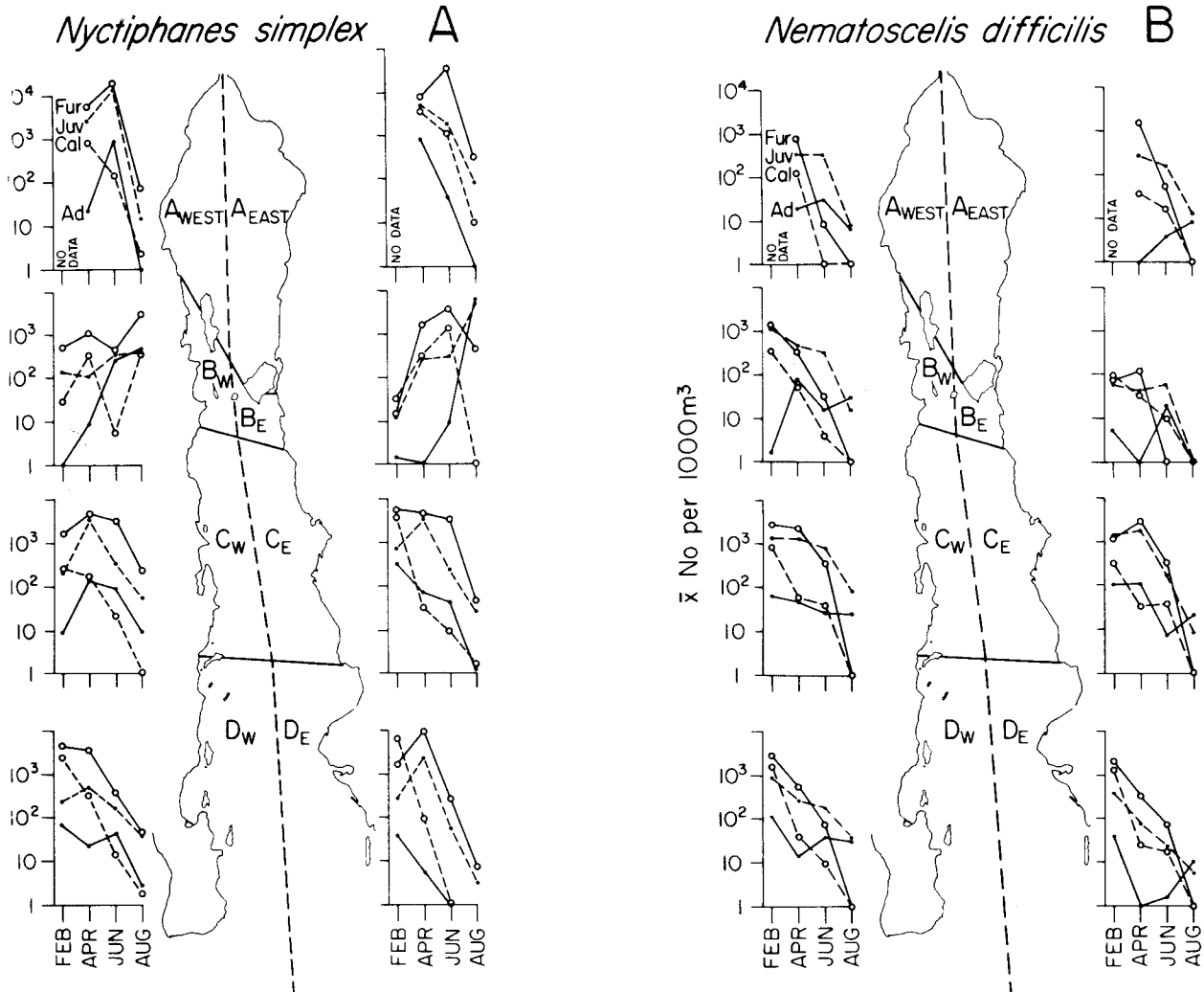
Figure 18. Seasonal changes 1957 in abundances of life phases of a) *Nyctiphanes simplex* and b) *Nematoscelis difficilis* on eastern and western sides of Gulf of California. (See Appendix I for data.) Zones are approximated from characteristics of euphausiid distributions: A, northern Gulf; B, zone of island channels; C, mid-Gulf; D, southern Gulf.

Furcilia larvae averaged a little more numerous to the west in February and August (Figure 20A), largely because of higher numbers in the western island channels than in the eastern, zone B (Figure 18A). During April-June the overall maximum moved to the east, affected largely by the distribution in the upper half of the Gulf (zones A and B).

Like calyptopes, juveniles and adults were more concentrated to the east during February-April. The difference was more significant in the adults, due 1) in February to high numbers to the west in zone C, though most adults were then in zone D, and 2) in April to high numbers to the west in zone A, to which zone the maximum for adults had then shifted.

By June the maxima for juveniles and adults had moved toward the west, with the abundances in the northern Gulf (zone A) most strongly affecting the mean values shown in Figure 20A. By August, maxima for both of these older life phases had shifted back to the eastern side; however, Figure 18A again shows that the easterly shift only took place in the north, though in both zones A and B.

Nematoscelis difficilis (Figures 18B, 20B). In the nothern Gulf with its extensive shelf, zone A, most calyptopes were on the western side in April, with the maximum shifting to the east in June (Figure 18B). Somewhat more furciliæ were to the east in zone A during both April and June. Juveniles declined almost equally on both sides of the northern Gulf as the year progressed. More adults were to the west during April-June, but by August there was no east-west difference.

In zone B, mixing is to considerable depths in channels between islands and between islands and the mainland. To the west, where the deep Canal de las Ballenas and Canal de Salsipuedes are generally cooler than surrounding waters (Figure 19), larvae were more abundant
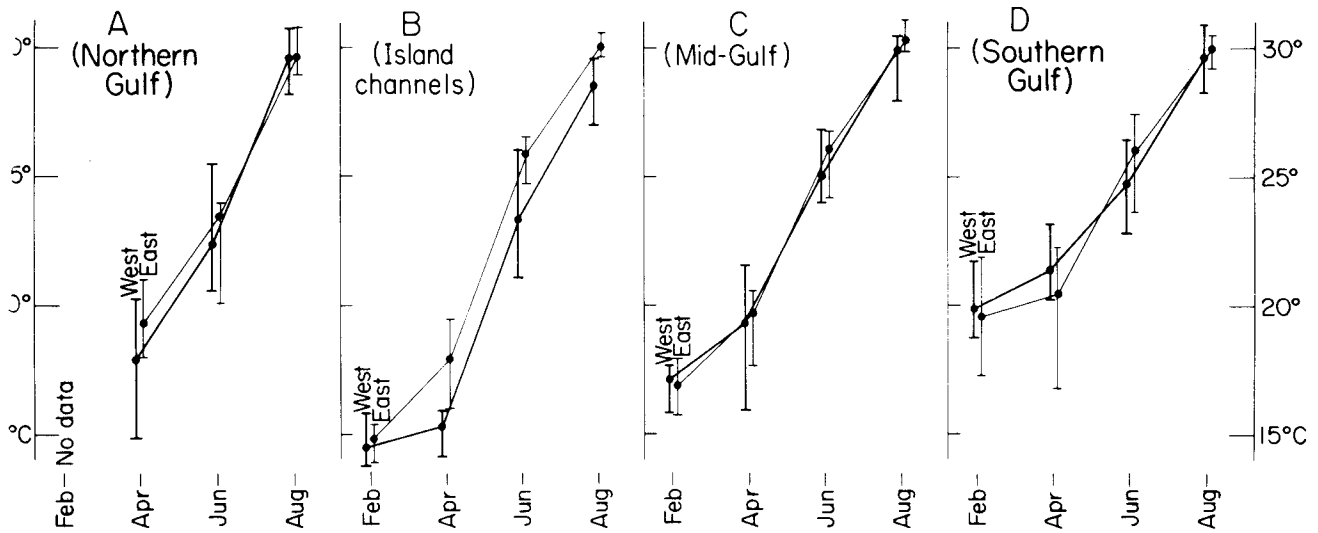
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Figure 19. The 1957 10-meter temperatures for eastern and western halves of each zone of the Gulf of California, plotted as means and ranges.
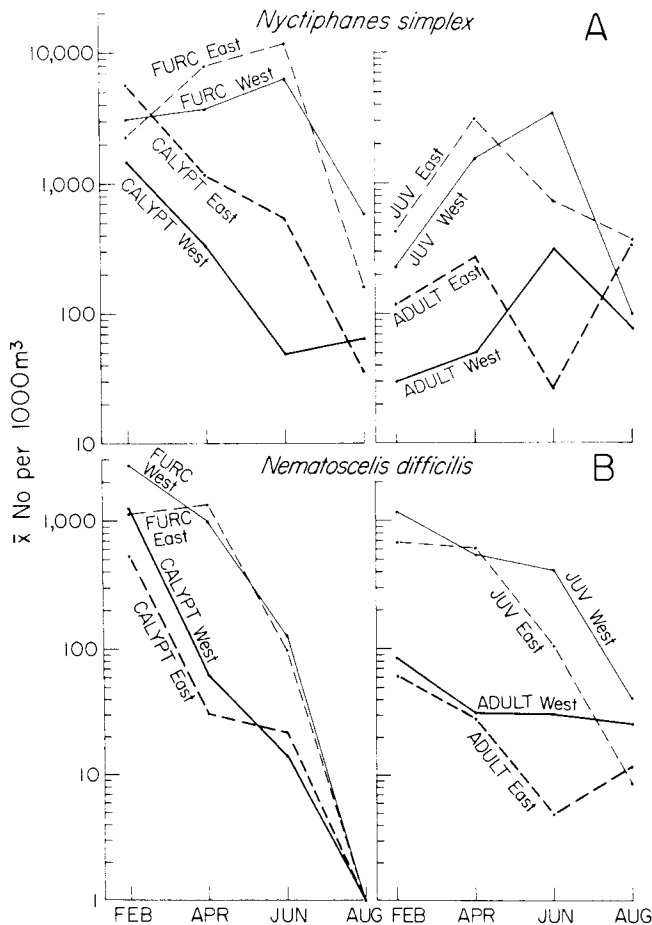

Figure 20. The 1957 seasonal abundances of life phases of the two predominant warm-temperature species, comparing eastern and western sides of the Gulf of California. A. *Nyctiphanes simplex*, B. *Nematoscelis difficilis*. (See Appendix I for data).

throughout the year than to the east, off Isla Tiburón. Juveniles declined progressively through the year on both sides of the zone, while numbers of adults fluctuated.

In zone C, mid-Gulf, there were more calyptopes to the west than to the east during the reproductive period, February-April. Juveniles were more numerous in this zone than to the north, and adults were more consistent in numbers through the year than elsewhere.

On both sides of zone D, the southern Gulf, calyptopis and furcilia larvae steadily decreased to zero as the year progressed. Juveniles and adults were regularly more abundant on the more oceanic, western side.

Thus, significant east-west differences in *N. difficilis* were few:

1) Calyptopes averaged somewhat higher to the west during February-April (Figure 20B), a consequence of higher abundances to the west in all four zones. During June, they were more abundant to the east in three of the zones and were equally distributed in the fourth.

2) Furcilia were more abundant to the west during February, particularly in zones B and C, but were equally distributed during April-June.

3) Juveniles and adults were about four times more abundant on the western side during June-August, with the least such difference in the shallow northern Gulf, zone A.

TEMPERATURES AT WHICH YOUNGEST LARVAE OCCURRED

Temperature at 10-m depth in the Gulf ranged between 13 and 32°C during February-August 1957. The youngest larvae sampled (calyptopes) of one or another euphausiid species were found across the full range of

temperature, except the maximum, >31°C (Figure 21). However, it was evident (Figure 17) that in all species most reproduction was in the winter.

In this discussion, a given °C includes all increments between that °C and the next, i.e. "14°C" includes 14-14.9°C.

February temperatures were the lowest observed, 13-20°C, and in April the range was 15-22°C. General warming had begun by June.

Nyctiphanes simplex produced 80% of its calyptopis larvae in the mid- and southern Gulf (zones C, D) in February at localities where temperatures were 17-18°C (Figures 2, 21). Most of the smaller April crop was where temperatures were 14, 17, and 20°C, with the highest mean at 14°C. These low temperatures no longer prevailed in the upper layers in June when the small number of calyptopes were found mostly at 23-24°C, near the lower limit of temperature found for that cruise. In August most of the relatively small maximum of calyptopes were found at 27°C—again the lowest temperature encountered.

From the lowest to the highest temperatures there is a declining trend in the percentage of stations at which calyptopis larvae of *N. simplex* were found, regardless of numbers. This trend (Figure 21) is punctuated by spikes at 14°C, 23°C, and 27-28°C, corresponding to the April, June, and August maxima in absolute numbers.

In *Nematoscelis difficilis* the February and April temperatures at which calyptopis larvae peaked were 17-19°C (Figure 21). This range was general to mid-Gulf in February and mainly on the western side in April. The few larvae produced in June were scattered across the full available range of temperature of 22-27°C. Percentages of stations at which calyptopes were found tended to be highest toward the lower end of the temperature range.

In the three principal *Euphausia* species living in the southern half of the Gulf during their main period of reproduction, February-June, calyptopis larvae were found concentrated at 20°C during the February maximum, again at 20°C in April in the case of *E. eximia*, at 24-26°C in June, and at 29-30°C in August. These were essentially the prevailing temperatures in the Gulf during the respective seasons. We know nothing of the extent to which these larvae might be at somewhat greater depths as the year progressed, so as to occur at more nearly constant temperatures. However, the simple reduction in numbers of larvae after February in the cases of *E. distinguenda* and *E. lamelligera* and after April in *E. eximia* indicates that the warmer months are not conducive to substantial recruitment in the Gulf.

PROPORTIONS OF LIFE PHASES

For each of seven euphausiid species, the annual proportion of the total made up by each of the four life phases

sampled here is similar. Catch curves, in which means for the four cruises are averaged (Figure 22), show furcilia larvae to be the most numerous phase and adults the least.

There are fewer calyptopes than furciliae due, in part, to the relative duration of these phases. Data obtained from rearing *Nematoscelis difficilis* (Gopalakrishnan 1973), *Nyctiphanes couchii* (Le Roux 1973), and *Euphausia eximia* (M. Knight personal communication) all indicate that the calyptopis phase lasts about 10-12 days and furcilia phase about twice as long, 18-24 days. Thus, even without considering interphase mortality, mean numbers of calyptopes should be half those of furciliae. However, calyptopes were found to average about one quarter the number of furciliae. There is clearly substantial escapement by calyptopes through the 0.55-mm meshes of the net. (Smallest calyptopes of *Nematoscelis difficilis* and
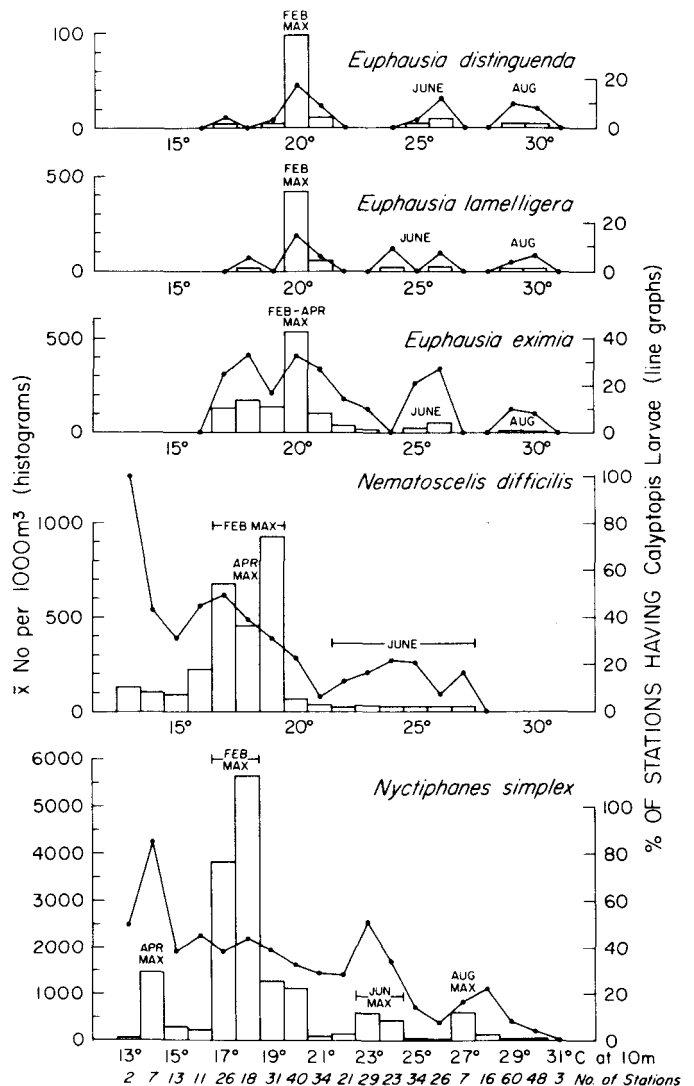

Figure 21. The youngest larvae sampled (calyptopes), all four 1957 cruises of the Gulf of California, plotted as a function of temperature (10-m depth).
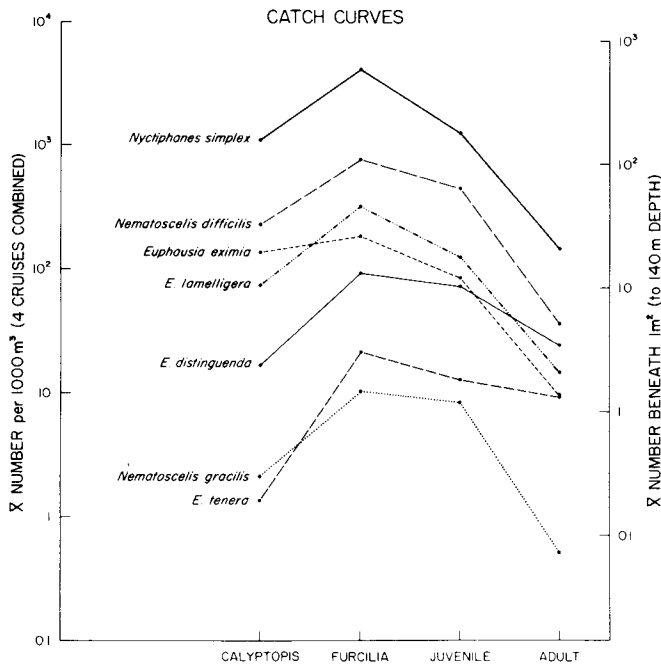
Figure 22. Abundances of life phases, all of the 1957 Gulf of California cruises combined.

Nyctiphanes simplex are about 1.0-1.3 mm in length and about one-half of that in depth or width.)

The juvenile and adult phases in warm-temperate euphausiids are expected to be of the order of six months each, with some adults living to one and one-half or two years of age (Brinton 1976; Gros and Cochard 1978).

The shapes of the curves in Figure 22 reflect a combination of 1) recruitment intensity, 2) duration of life-phase, and 3) survivorship. A rough mean for the ratio of calyptopis:furcilia:juvenile:adult for all seven species is 1:4:3:0.5. *Euphausia eximia* has relatively most calyptopes, indicating both high recruitment and high larval mortality in this largest of the Gulf species. *E. distinguenda* and *E. tenera* have proportionately more adults than the other species, indicating either a relatively long adult phase or a greater influx of adults to the Gulf. The similarities among the curves suggest similarities in life-span—possibly one year in this strongly seasonal regime.

Whereas *Nyctiphanes* and *Nematoscelis* incubate their externally attached eggs for a time, *Euphausia* sheds its eggs directly into the water. This means that the nauplii (not retained by our nets) of *Euphausia* swim freely but those of *Nyctiphanes* and *Nematoscelis*, whose eggs hatch as metanauplii and then develop into calyptopes, are protected. The difference in rearing strategy does not lead to a difference, here, in the ratio of calyptopes that survive to the next phase.

SUMMARY AND DISCUSSION

The mouth of the Gulf of California is located almost exactly on the tropic, 23°27'N. To the west, this line

approximates the zone of mixing of the California Current with the Equatorial Water mass of the eastern tropical Pacific. Hence, through recent time, most tropical euphausiid species and those of the southern part of the California Current have had access to waters of the Gulf. Present-day colonization by species from the California Current system has been made by only three species, representing three genera, whereas tropical species appear as transients, except in the southernmost part of the Gulf.

Nematoscelis difficilis, *Nyctiphanes simplex*, and *Euphausia eximia* are established in much of the Gulf, and their ranges there varied little with season. *Euphausia pacifica* and *Thysanoessa gregaria* are distributed like *N. difficilis* in the California Current, and both may occur as far south as the mouth of the Gulf (Brinton 1979). Their absence in the Gulf is evidently due to inability to accommodate to summer extremes in temperature and to a lack of flow into the Gulf in winter-spring when conditions there might be within their ranges of tolerance. *E. pacifica* is a vertical migrator which enters the surface layer at night in all regions where the species has been observed. This characteristic could be a disadvantage for residence in the Gulf. *N. difficilis* tends to avoid the surface layers where a thermocline is developed, as in the summer in the Gulf. *Thysanoessa gregaria* is a nonmigrator or short-distance migrator inhabiting the depth range of the thermocline itself. Evidently such a stratum is insufficiently stable or constant in temperature to have permitted *T. gregaria* to occur here.

Nyctiphanes simplex and *Euphausia eximia* are logical inhabitants of the Gulf because their ranges are centered in these latitudes. In addition, the extensive shelf in the Gulf is particularly suitable for *N. simplex*.

Many euphausiid species occupy different depths, both in the course of their life histories and diurnally as migrating juveniles and adults. These depths may span hundreds of meters. Distributions of these species are certainly affected by the conservative conditions beneath the sea surface. However, the generally more variable upper level phenomena—currents, temperature, food—may act in a critical way at any stage of an animal's development. Variation in some, if not all, of these parameters is more extreme in the Gulf, particularly the northern half, than in most oceanic regions. The August warming to 29-31°C in the Gulf is more extreme than in the open ocean, and the Gulf euphausiids then enter a resting phase with respect to reproduction, though the ranges of most species are then most expanded.

The biogeographical accommodations that euphausiids in the Gulf of California have made to seasonal changes in temperature and direction of flow include both reciprocal and common responses among the warm-temperate and the tropical species in this partly closed system. Reciprocal responses include the relationships of the ranges of *Nematoscelis difficilis* and *N. gracilis* in the
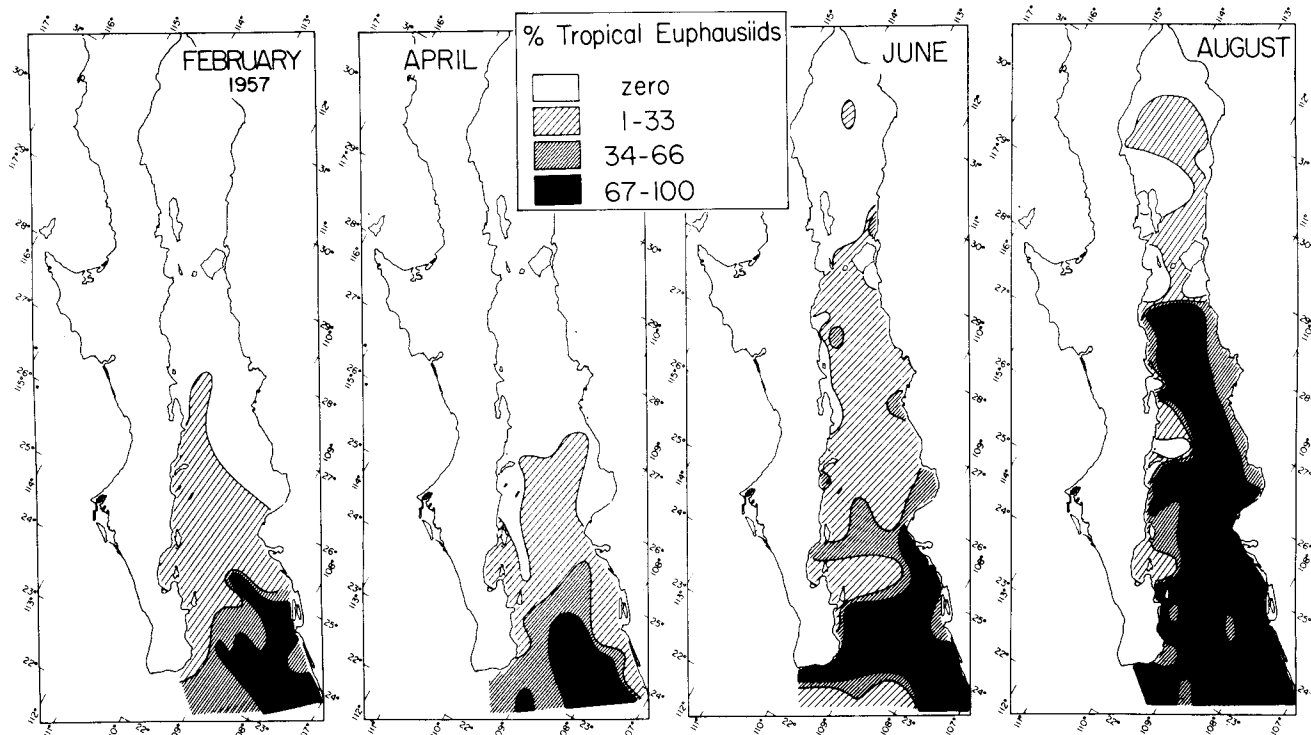
Figure 23. The tropical euphasiids (four species: *Euphausia distinguenda, E. lamelligera, E. tenera,* and *Nematoscelis gracilis*) shown as % of total euphausiids occuring in the Gulf of California.

southern half of the Gulf during February-April, with tropical *N. gracilis* occupying areas where warm-temperate *N. difficilis* was absent or at low density and moving northward on the eastern side in June as *N. difficilis* receded from there. Both species of *Nematoscelis* showed lowest density and diminished range during the heat of August (Figures 8, 9).

Although the range of *Euphausia eximia* extended northward into mid-Gulf during all seasons, the composite range of the strictly tropical species showed northern range extension after April, reaching the zone of the island channels in June and the northern Gulf in August where their dominance extended northward through mid-Gulf (Figure 23).

The dominant Gulf species, *Nyctiphanes simplex* and *Nematoscelis difficilis*, although both occupying most of the Gulf during all seasons, nevertheless showed certain complementary characteristics. *N. difficilis* was at its peak in mid-Gulf in February, while *N. simplex* was then building for April (western Gulf) and June (northern Gulf) maximum abundances. By June *N. difficilis* was sparse in the northern Gulf (Figures 7, 8). In August, *N. simplex* was most dense in the zone of the island channels, where *N. difficilis* was, for the first time, sparse or absent.[2]

Though there were distinct zonal irregularities in the presence of larvae (Figure 18), there were trends showing that *N. simplex* calyptopes and, to a lesser extent, furciliæ were more abundant along the shallower eastern side of the Gulf during their periods of peak production, whereas maxima for *N. difficilis* were in the generally deeper waters of the western side (Figure 20B). However, the shallow northern Gulf was an important nursery area for both species.

The strong warm-temperate zooplankton community in the Gulf includes, together with the euphausiids *Nematoscelis difficilis* and *Nyctiphanes simplex*, the copepod *Calanus pacificus californicus* Brodskii which bulked as the dominant organism in the Gulf during February-April.

Moser et al. (1974) emphasized the widespread occurrence in the Gulf of two fishes of commercial importance having cold-water affinities. The Pacific mackerel, *Scomber japonicus*, averaged fifth in abundance in the Gulf, and the Pacific sardine, *Sardinops sagax caeruleus*, varied between third and sixth in abundance, depending on the cruise.

According to A. Fleminger (personal communication), most *Calanus* submerge to greater depths than the 0-140m sampled during these 1957 cruises. Evidence that this is not the case with *N. difficilis* consists of the fact that

[2]An unpublished report by Mundhenke (1969: The relationships between water masses and euphausiids in the Gulf of California and the eastern tropical Pacific, masters thesis, U.S. Naval Postgraduate School, 115 pages) has come to our attention since this paper went to press. This discusses euphausiids from 54 Tucker Trawl samples obtained by R/V *Te Vega* in the Gulf during September 22-November 14, 1967. As in our August samples, *Euphausia eximia* and *E. distin-*

guenda occurred northward to the island channels, but *Nematoscelis gracilis* was in mid-Gulf, 27°N, as in our June samples. *E. lamelligera, E. tenera,* and the *Stylocheirons* were not recorded, but *E. gibboides* and *Nematobrachion flexipes* were reported inside the Gulf to 28°N, differing significantly from our findings. *Nematoscelis difficils* was found in all zones, but *Nyctiphanes simplex* only from mid-Gulf northward.

numbers of adult *N. difficilis* did not decrease significantly in August in the 0-140 m layer sampled during the 1957 cruises (Figure 17). Younger stages were then much reduced, but this is consistent with the pattern in all species.

The values in the Gulf for biomass of euphausiids were 25 cc/1,000 m³ during February to June, dropping to 7 cc in August. The higher means are like those in the richer part of the California Current off central California, San Francisco to Point Conception (Isaacs et al. 1969; Fleminger et al. 1974). There, 30-80 cc/1,000 m³ were measured along different lines of stations between San Francisco and Point Conception during April 1956. Mean values of biomass for different east-west transects of the California Current were then 4-9 cc from Point Conception southward along Baja California. During April in the warm year 1958, values were 3-6 cc/1,000 m³ all the way from San Francisco southward.

Summer (July) values for euphausiid biomass during 1955-56 in the California Current were 10-15 cc/1,000 m³ north of Point Conception and 3-10 cc to the south. Values in 1957-59 were slightly lower. The mean proportion of total biomass made up by euphausiids was also nearly the same on opposite sides of the Baja California peninsula. In the southern part of the California Current during 1956-59 it was 10% (January), 7% (April), 6% (July), 10% (October), comparing with 7% (February), 5% (April), 7% (June) and 3% (August) in the Gulf. The richer places along western Baja California for both euphausiids and total biomass are near Punta Banda (31°N), Vizcaino Bay (28-29°N), and Punta Eugenia (29°N) southward along the coast. In the eastern tropical Pacific (Brinton 1979), euphausiids were at maxima of 13 cc and 26 cc beneath 1 m², or 20% and 50% of total volume, at the equator and the northern edge of the North Equatorial Countercurrent. Off the mouth of the Gulf they were 2-7 cc/1,000 m³, or 3-6% of total biomass. The values for cc beneath 1 m² approximately convert to cc per 1,000 m³ by doubling. Longhurst's (1976) data indicated that euphausiids comprise about 5% of total biomass at 14°N in the eastern tropical Pacific, agreeing with proportions observed at the mouth of the Gulf.

Thus, euphausiid biomass and its proportion of the total biomass in the Gulf is intermediate between that found in the richest and poorest parts of either the California Current or the eastern tropical Pacific. Parts of the Gulf having the largest standing stocks correspond to places and times where *Nyctiphanes simplex* and *Nematoscelis difficilis* are most abundant. At such localities, values of 50-200 cc/1,000 m³ for euphausiids and > 1,000 cc for total biomass are as high as any reported from mid- to low latitudes in the Pacific.

Could *Nyctiphanes simplex* be economically harvested in the Gulf? Several localities having densities of >50,000/

1,000 m³ were encountered in the northern Gulf during April-June. Such densities of euphausiids are rare in the California Current, although *N. simplex* has been found in such numbers in Bahía Sebastián Vizcaíno, 28°N. In the northern Gulf, the mean biomass of this species was at a maximum of 77 g/1,000 m³ in the western sector in June (data converted from Figure 18A). This is somewhat higher than April and June values of 35 g and 48 g from the eastern sector of the northern Gulf.

As stated in the section on euphausiid biomass, a factor of 2 may be applied to these values for *N. simplex* from CalCOFI 1-m net catches so as to equate them with those obtained using an unbridled net. This gives mean biomass values in the range of 70-150 g/1,000 m³ in the sectors in which *N. simplex* is most abundant. Higher local densities would, of course, be encountered.

The range 70-150 g compares with 100-300 g/1,000 m³ for *Euphausia pacifica* in the vicinity of the Strait of Georgia in the inland waterway of British Columbia. There, *E. pacifica* and *Calanus plumchrus* have been the objects of a modest fishery, which expanded from 10 tons/year in 1970 to >100 tons in 1974 (Heath 1977). Midwater trawls were used.

A next step in addressing the question of practicability of harvesting *N. simplex* would be exploratory fishing in the northern Gulf by means of plankton trawls, possibly in conjunction with acoustic reconnaissance (e.g. Sameoto 1972), and a study of population dynamics of the species.

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APPENDIX I Population Data for the Two Principle Euphausiid Species from the Four 1957 Gulf of California Cruises

NYCTIPHANES SIMPLEX

Area		Feb W N	Feb W X̄	Feb W SD	Feb E N	Feb E X̄	Feb E SD	Apr W N	Apr W X̄	Apr W SD	Apr E N	Apr E X̄	Apr E SD	Jun W N	Jun W X̄	Jun W SD	Jun E N	Jun E X̄	Jun E SD	Aug W N	Aug W X̄	Aug W SD	Aug E N	Aug E X̄	Aug E SD
A	Calypt	4	33	23	3	56	46	15	908	2542	13	4165	9913	19	164	366	15	1290	3270	17	2	7	16	10	25
	Furc	4	571	804	3	15	9	15	6358	8033	13	8970	12846	19	21430	36265	15	37578	58417	17	83	106	16	365	693
	Juv	4	150	226	3	12	16	15	2973	4125	13	4485	6368	19	14154	24557	15	2041	2619	17	20	57	16	94	156
	Adult	4	0		3	5	2	15	11	20	13	928	2199	19	986	1924	15	45	83	17	1	2	16	0	0
B	Calypt	10	269	588	11	5736	18103	10	371	568	3	308	405	11	6	12	4	1456	2500	13	403	960	3	0	0
	Furc	10	1677	2352	11	3881	7440	10	1298	2206	3	1732	1867	11	480	265	4	3860	4904	13	3130	2517	3	462	238
	Juv	10	266	400	11	786	1094	10	121	310	3	288	281	11	392	602	4	313	476	13	417	364	3	5671	6365
	Adult	10	9	15	11	325	693	10	10	23	3	0	0	11	261	413	4	9	10	13	470	1610	3	6116	6517
C	Calypt	17	2484	6563	19	1693	2189	19	171	571	13	32	110	22	21	37	13	10	25	22	1	3	13	2	5
	Furc	17	4451	13016	19	6308	18719	19	4951	5128	13	4845	4796	22	3358	7149	13	3457	5904	22	243	777	13	49	95
	Juv	17	247	462	19	274	567	19	3049	3749	13	3341	2930	22	363	442	13	256	291	22	56	138	13	28	39
	Adult	17	50	152	19	13	32	19	171	358	13	74	161	22	94	342	13	47	143	22	9	27	13	1	5
D	Calypt	31	1453	5003	33	5547	17723	32	148	453	48	94	173	30	15	33	18	1	5	31	2	7	19	0	0
	Furc	31	3055	9862	33	2270	4768	32	2451	7369	48	9890	16442	30	398	724	18	257	700	31	47	109	19	7	14
	Juv	31	228	420	33	421	810	32	510	1211	48	2472	6038	30	166	661	18	58	99	31	40	110	19	2	7
	Adult	31	30	115	33	116	427	32	11	35	48	6	25	30	43	217	18	0	0	31	2	6	19	1	2
All Areas	Calypt							76	333	1254	48	1193	5471	82	50	189	50	506	2030	83	64	407	51	4	15
	Furc							76	3695	6783	48	7765	12842	82	6076	19780	50	12574	36122	83	592	1537	51	156	432
	Juv							76	1579	3032	48	3116	5379	82	3490	13202	50	725	1689	83	99	223	51	371	2037
	Adult							76	50	194	48	274	1215	82	305	1036	50	26	89	83	77	660	51	360	2137
East+West	Calypt	64	3564	13352				124	666	3568				132	122	582				134	41	322			
	Furc	64	2651	7680				124	5270	9796				132	8538	27335				134	426	1256			
	Juv	64	327	658				124	2174	4170				132	2443	10543				134	197	1274			
	Adult	64	75	320				124	137	779				132	199	830				134	185	1424			

NEMATOSCELIS DIFFICILIS

Area		Feb W N	Feb W X̄	Feb W SD	Feb E N	Feb E X̄	Feb E SD	Apr W N	Apr W X̄	Apr W SD	Apr E N	Apr E X̄	Apr E SD	Jun W N	Jun W X̄	Jun W SD	Jun E N	Jun E X̄	Jun E SD	Aug W N	Aug W X̄	Aug W SD	Aug E N	Aug E X̄	Aug E SD
A	Calypt		NO DATA					15	130	294	13	38	131	19	0	0	15	17	45	17	0	0	16	0	0
	Furc							15	770	994	13	1565	2124	19	8	27	15	56	141	17	0	0	16	0	0
	Juv							15	345	986	13	263	833	19	333	661	15	158	376	17	8	15	16	14	51
	Adult							15	20	42	13	0	0	19	31	94	15	4	14	17	7	29	16	8	32
B	Calypt	4	358	252	3	98	82	10	53	93	3	33	46	11	3	9	4	10	17	13	0	0	3	0	0
	Furc	4	1445	1562	3	72	72	10	330	217	3	112	158	11	32	55	4	0	0	13	16	25	3	0	0
	Juv	4	1421	1733	3	58	74	10	443	528	3	38	53	11	318	273	4	57	65	13	30	61	3	25	61
	Adult	4	2	3	3	5	8	10	75	102	3	0	0	11	16	22	4	20	34	13	0	0	3	32	61
C	Calypt	10	809	934	11	319	584	19	59	250	13	33	115	22	39	56	13	37	76	22	0	0	13	0	0
	Furc	10	2787	2431	11	1125	1499	19	2244	1587	13	2824	2939	22	348	307	13	217	312	22	1	2	13	2	2
	Juv	10	1386	1351	11	1359	1295	19	1385	1057	13	1839	1480	22	817	783	13	166	143	22	87	212	13	9	212
	Adult	10	62	77	11	101	94	19	48	110	13	104	216	22	27	48	13	6	9	22	26	42	13	20	42
D	Calypt	17	1694	2031	19	694	1791	32	38	97	19	25	78	30	9	22	18	18	72	31	0	0	19	0	0
	Furc	17	2887	6066	19	1307	3320	32	527	1233	19	334	603	30	75	152	18	70	270	31	40	94	19	6	14
	Juv	17	931	1298	19	386	595	32	261	493	19	73	153	30	184	253	18	23	67	31	30	90	19	10	43
	Adult	17	115	228	19	49	144	32	14	30	19	0	0	30	36	106	18	2	4	31			19		
All Areas	Calypt	31	1236	1681	33	515	1717	76	63	197	48	31	104	79	14	36	50	22	64	83	0	0	83	0	0
	Furc	31	2668	4756	33	1134	2686	76	978	1421	48	1330	2193	79	127	233	50	98	251	83			83	0	0
	Juv	31	1162	1385	33	681	1001	76	546	868	48	601	1169	79	406	604	50	104	232	83	42	128	83		128
	Adult	31	84	180	33	62	126	76	32	75	48	28	122	79	30	83	50	5	14	83	25	65	83	12	65
East+West	Calypt	64	864	1592				124	50	168				132	17	49				134	0	0			
	Furc	64	1878	3907				124	1114	1769				132	117	240				134	<1	<1			
	Juv	64	914	1226				124	567	996				132	292	519				134	29	103			
	Adult	64	73	155				124	30	96				132	20	67				134	20	59			

N = numbers of stations; X̄ = mean; SD = standard deviation

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> Scripps Institution of Oceanography, A-027
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> La Jolla, CA 92093

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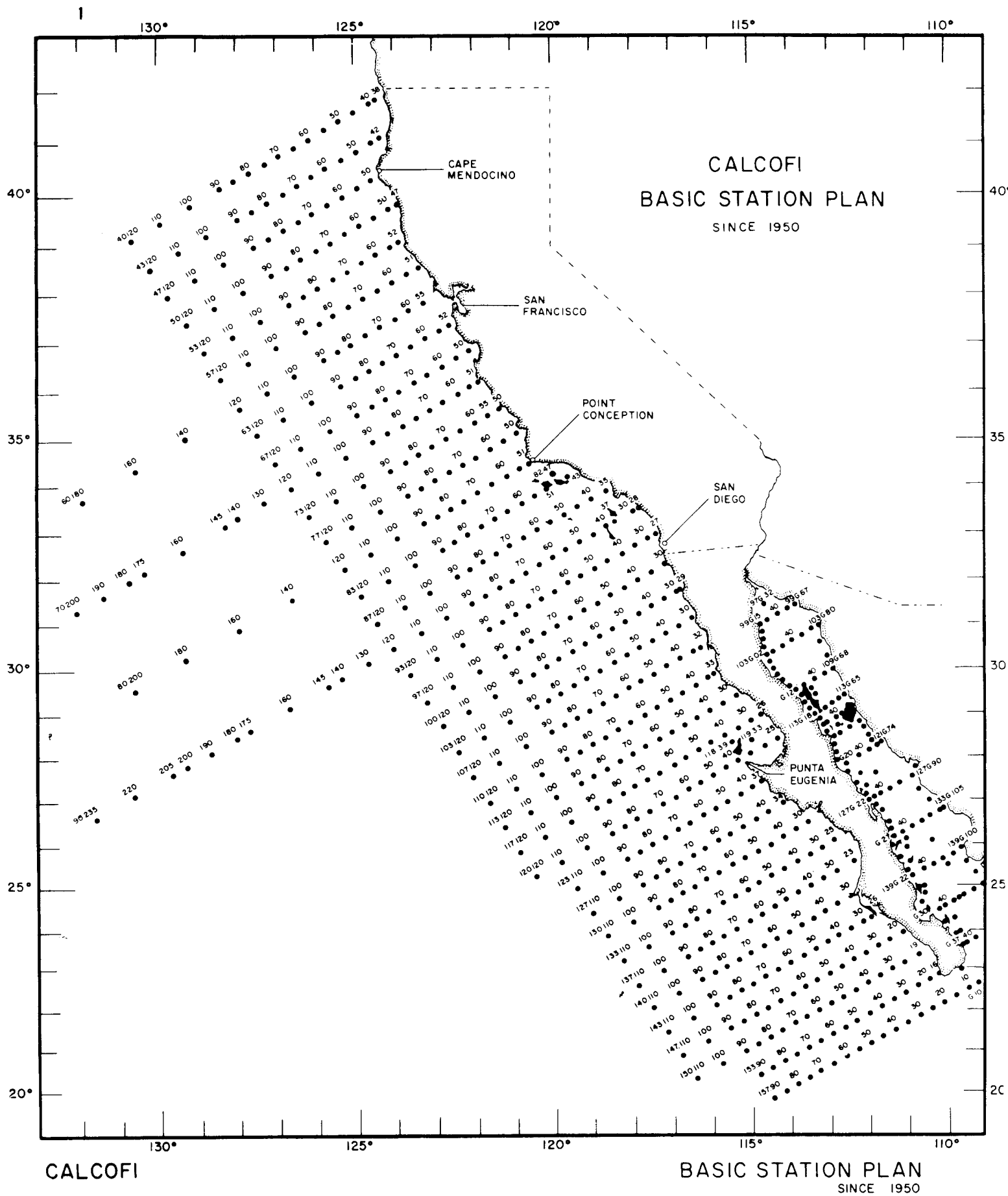
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