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In Memoriam

John Dove Isaacs
28 May 1913—6 June 1980



John Isaacs, a most distinguished colleague, died 6 June 1980 at the age of 67.

As Director of the Marine Life Research Group at Scripps Institution from 1957 to 1975, he was an active participant in CalCOFI. His published contributions to these studies are a matter of record and need no listing here.

His work and reputation extend far beyond the range of our shared activities. He was a member of the National Academy of Sciences, the National Academy of Engineering, and the American Academy of Arts and Sciences.

His contributions to the CalCOFI program, his presentations, and his many comments upon the other

papers at our meetings have been vigorous and perceptive. His insight into all of the fields represented here has been inspiring.

I remember John Isaacs in many ways and for many things, but I believe there is one event that represents his breadth and vision, and indeed, himself, well enough to stand as an introduction to those who did not know him. This is the concept that led him, with Elton Sette, to convene our Symposium on the changing Pacific, held more than 20 years ago, which dealt with the remarkable oceanic events of 1957-58. It was the beginning of much of the work done nowadays in the World Ocean and in climatology.

I would like to quote a little from the introduction to the Symposium.

“By the fall of 1957, the coral ring of Canton Island, in the memory of man ever bleak and dry, was lush with the seedlings of countless tropical trees and vines.

“Two remarkable and unprecedented events gave rise to this transformation, for during 1957 great rafts of sea-borne seeds and heavy rains had visited her barren shores.

“Elsewhere about the Pacific it also was common knowledge that the year had been one of extraordinary climatic events. Hawaii had its first recorded typhoon; the seabird-killing *El Niño* visited the Peruvian Coast; the ice went out of Point Barrow at the earliest time in history; and on the Pacific’s Western rim, the tropical rainy season lingered six weeks beyond its appointed term.” *CalCOFI Reports, Vol. VII, 1960.*

The results of that Symposium have been to make us take longer, broader, and better looks at our problems. Many major programs that are active today have sprung from the concepts engendered at that meeting.

I have cited this work not as John’s greatest accomplishment, which it may not be, but more as a typical product of his mind and energy.

None of us should try to model himself closely upon any particular person. In any case John Isaacs’ wide-ranging paths would be among those hardest to follow. But his imagination, perception, and tremendous breadth and depth of interest, will surely remain in our memory as examples of what constitutes a great scientist and a great man.

Joseph L. Reid

PART I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE—1981

The CalCOFI Committee is pleased to announce three new atlases in press or in preparation. These are Atlas Number 28, "Distributional Atlas of Fish Larvae in the California Current Region: Northern Anchovy, *Engraulis mordax* Girard, 1966–1979," by Roger Hewitt; Atlas Number 29, "Teleconnections of 700 mb Height Anomalies for the Northern Hemisphere," by Jerome Namias; and Atlas Number 30, "Vertical and Horizontal Distribution of Seasonal Mean Temperature, Salinity, Sigma- t , Stability, Dynamic Height, Oxygen and Oxygen Saturation, 1950–1978 in the California Current," by Ron Lynn, Kenneth Bliss, and Larry Eber. These new atlases and the papers in this volume of reports by Bernal and by Chelton again remind us of the tremendous importance of long time series in the understanding of oceanic ecosystems. CalCOFI Data Report Number 29 (CDFG Sea Survey Cruises 1979) has been distributed, and CalCOFI Data Report Number 30 (CDFG Sea Survey Cruises 1980) is in preparation.

Recent changes in the economics and methodologies of marine and fisheries research have caused the Committee to examine the past work of CalCOFI and to begin to examine its future role. At the request of the Committee, Paul Smith has undertaken a preliminary reexamination of Oscar E. Sette's 1942 model for fisheries research. Additionally, the Committee intends to convene, in the spring of 1982, a workshop on the future of CalCOFI.

Some new methods or approaches to research are being employed or examined. The discovery by Hunter and Goldberg in 1980 that the ovaries of spawning female anchovies could be categorized as to spawning condition permitted the execution in 1980 of a plan by Parker that would permit biomass estimation directly from estimates of daily egg production, fraction of female anchovies spawning daily, sex ratio, and fecundity. Tests of the efficacy of this "egg production method" are being conducted during the triennial CalCOFI survey cruises of 1980–81.

With a view toward reducing ship time while maintaining the integrity of the CalCOFI time series at the level of resolution of low-frequency, large-scale

events, Hayward and Venrick are testing the efficacy of "indicator stations." They are collecting full suites of biological, chemical, and physical data from the entire CalCOFI grid, but they are occupying four stations for 48 hours each; thus they will be able to perform within-station, between-station, and large areal statistical comparisons. If these stations prove to represent larger areas adequately, it may permit CalCOFI to reduce the scale of its ship operations with respect to some time-series-dependent questions.

Also offering the potential to reduce the areal scope of CalCOFI ship operations is the California Coastal Fronts program. Simpson and Haury are examining the characteristics of frontal systems in the California Current using traditional and state-of-the-art techniques, such as satellite radiography, time series analyses, and numerical modelling. These frontal systems may be significant in the survival of fish of commercial importance.

The members of the Committee extend their thanks to George Hemingway who has served as Coordinator from July of 1979 through June of 1981. During his term as Coordinator, CalCOFI Reports became a reviewed annual journal with a publication date only a few months after the final deadline for the submission of papers. We appreciate George's dedicated service to CalCOFI and wish him well in his future endeavors.

Since 1979, the Coordinator's duties rotate among the three principal agencies: Scripps Institution of Oceanography, University of California San Diego; the Southwest Fisheries Center, National Marine Fisheries Service; and the California Department of Fish and Game. From July 1981 through June 1983, the CalCOFI Committee will be in excellent hands as we welcome Reuben Lasker of the Southwest Fisheries Center as its new Coordinator.

We wish to thank all the reviewers and the editorial staff for their excellent work on this volume.

The CalCOFI Committee
Joseph L. Reid
Izadore Barrett
John Radovich

ESTIMATE OF THE SPAWNING BIOMASS OF THE NORTHERN ANCHOVY CENTRAL SUBPOPULATION FOR THE 1980-81 FISHING SEASON

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ABSTRACT

The spawning biomass of the central subpopulation of northern anchovies off the Pacific coast of the State of California and Northern Baja California was surveyed by four ichthyoplankton cruises during the period, February-May 1980. The extent of the 1980 coverage was about half of the four cruise surveys conducted in previous years. Using a modified larva census method, the estimate of the 1980 spawning biomass was calculated at 1,775,000 tons. The optimum yield (OY) for the 1980-81 fishing season within the U.S. Fishery Conservation Zone was 179,000 short tons as determined by the OY formulation adopted by the Pacific Fishery Management Council's Anchovy Plan. The 1980-81 U.S. reduction quota for the northern anchovy was set at 166,400 short tons. In the fall of 1980 the California Fish and Game Commission established an 80,000 short ton limit on the amount of anchovy that could be processed by shore-based reduction plants in California.

RESUMEN

La biomasa del desove para la subpoblación central de anchovetas del norte frente a la costa Pacífica del estado de California y de Baja California Norte fue estudiado durante cuatro cruceros de reconocimiento de ictioplancton durante febrero-mayo de 1980. El área cubierta en 1980 era aproximadamente la mitad de ésta cubierta en los cuatro cruceros de reconocimiento efectuados en años previos. Usando un método de censo de larva modificado, la estimación de la biomasa del desove para 1980 se calculó en 1,775,000 toneladas cortas. El rendimiento óptimo para la temporada de pesca 1980-81 dentro de la Zona de Conservación de Pesquería de los EE.UU. fue de 179,000 toneladas cortas, determinado por la formulación del rendimiento óptimo adoptada por el Pacific Fishery Management Council en su Plan para Anchoveta. La cuota de reducción de los EE.UU. para 1980-81 para la anchoveta fue fijada en 166,400 toneladas cortas. En el otoño de 1980 la Comisión de Pesca y Caza de California estableció un límite de 80,000 toneladas cortas para la cantidad de anchoveta

que podía ser procesada por las plantas de reducción basadas en las costas de California.

INTRODUCTION

Catch quotas for the U.S. anchovy fisheries are established each year on July 1 using the current estimate of the anchovy spawning biomass as specified by the formulation in the Fishery Management Plan (FMP) for the Northern Anchovy Fishery (Pacific Fishery Management Council 1978). This paper is the third in a series of reports that document the annual estimate of spawning biomass of the central subpopulation of northern anchovy from which the optimum yield for the coming season is established (Stauffer and Parker 1980; and Stauffer 1980). The 1980 estimate is based on anchovy larva abundance data collected on the 1980 California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larva survey of four cruises that only partially surveyed the seasonal and areal range of the northern anchovy spawning period. This survey was conducted under the direction of the La Jolla Laboratory, Southwest Fisheries Center (SWFC), National Marine Fisheries Service. Other research institutions cooperating in this survey were the Scripps Institution of Oceanography, Instituto Nacional de Pesca, Mexico, and Pacific Research Institute of Fisheries and Oceanography, Soviet Union.

LARVA SURVEY

Anchovy spawning biomass was estimated from anchovy larva abundance using a modification of the larva census method developed by Smith (1972) and further documented in Appendix I of the FMP (PFMC 1978). The incomplete larva census estimates for winter and spring quarter, which resulted from the partial coverage of the survey, were expanded to an annual larva census based on a regression analysis of the historical CalCOFI data. The four cruises on the egg and larva survey were conducted within the geographic range of the central subpopulation of the northern anchovy (Vrooman et al. 1980) as outlined by the eight regions shown on the CalCOFI station plan given in Figure 1.

The regions of southern California and Baja

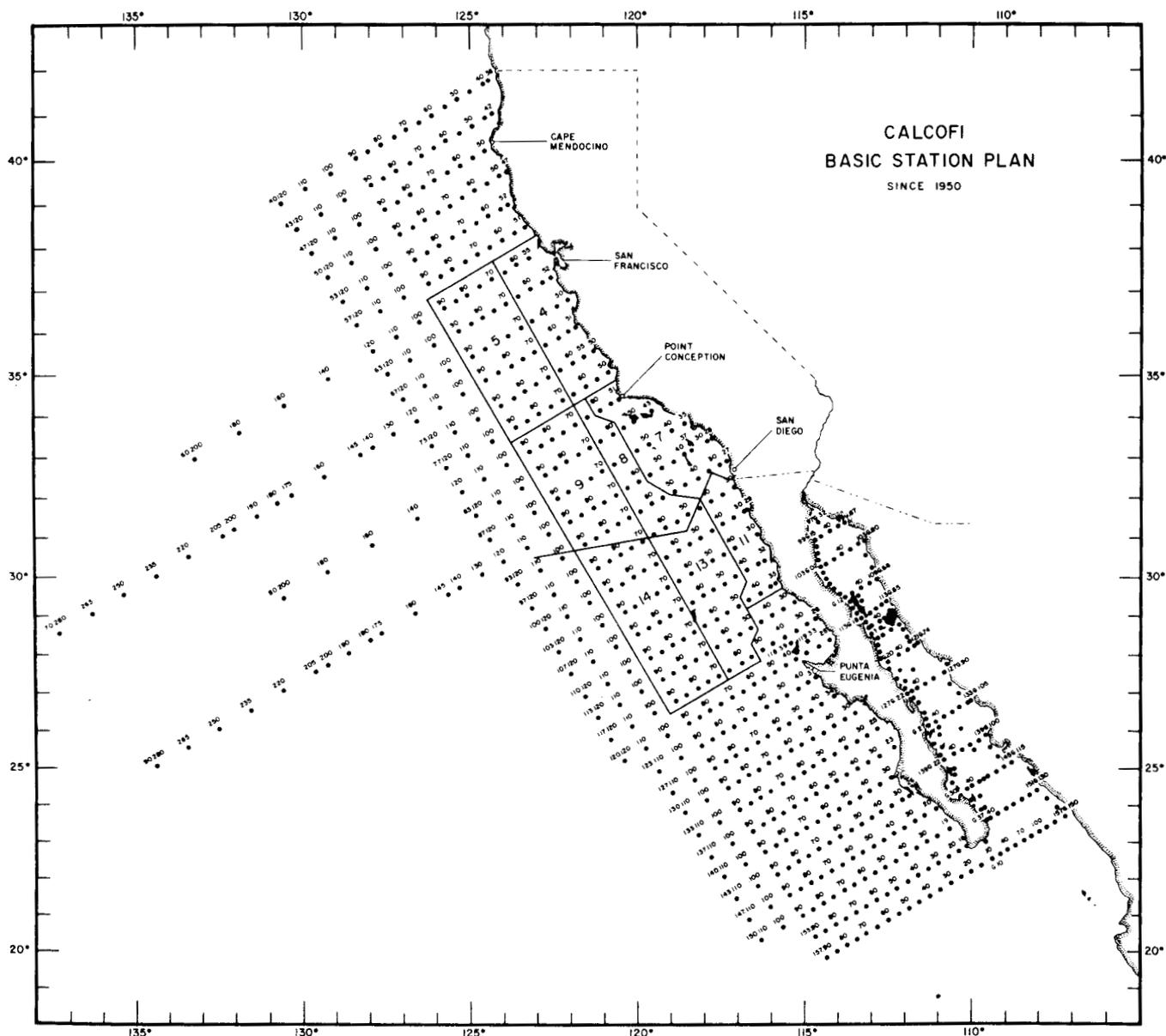


Figure 1. CalCOFI basic station plan. Geographic range of the central subpopulation of northern anchovy is within the light-numbered regions.

California were redefined so that the boundaries between the region group 7, 8, and 9 and the region group 11, 13, and 14 coincided with the U.S.-Mexico border as in 1979 (Stauffer 1980). The four cruises were 1) 8003 TK, February 21-March 17; 2) 8003 JD, March 20-April 10; 3) 8004 JD, April 11-19; and 4) 8005 JD, May 16-30. The first cruise was conducted by the Soviet R/V *Tikhookeanskiy* and the other three by the U.S. R/V *David Starr Jordan*. The stations occupied by each cruise are shown in Figure 2. The occupied stations off central California for cruises 8004 JD and 8005 JD are not shown. Only one cruise 8003 JD received a permit to conduct fishery research within Mexico's 200-mile zone.

Collection and processing of anchovy larva samples in 1980 were the same as for the 1979 CalCOFI survey as reported by Stauffer (1980). Plankton samples were collected with the paired CalCOFI bongo net. The data and samples were brought back to the Southwest Fisheries Center (SWFC) for processing and sorting. All of the plankton sample from the starboard net 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 sample was sorted. The 1980 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.

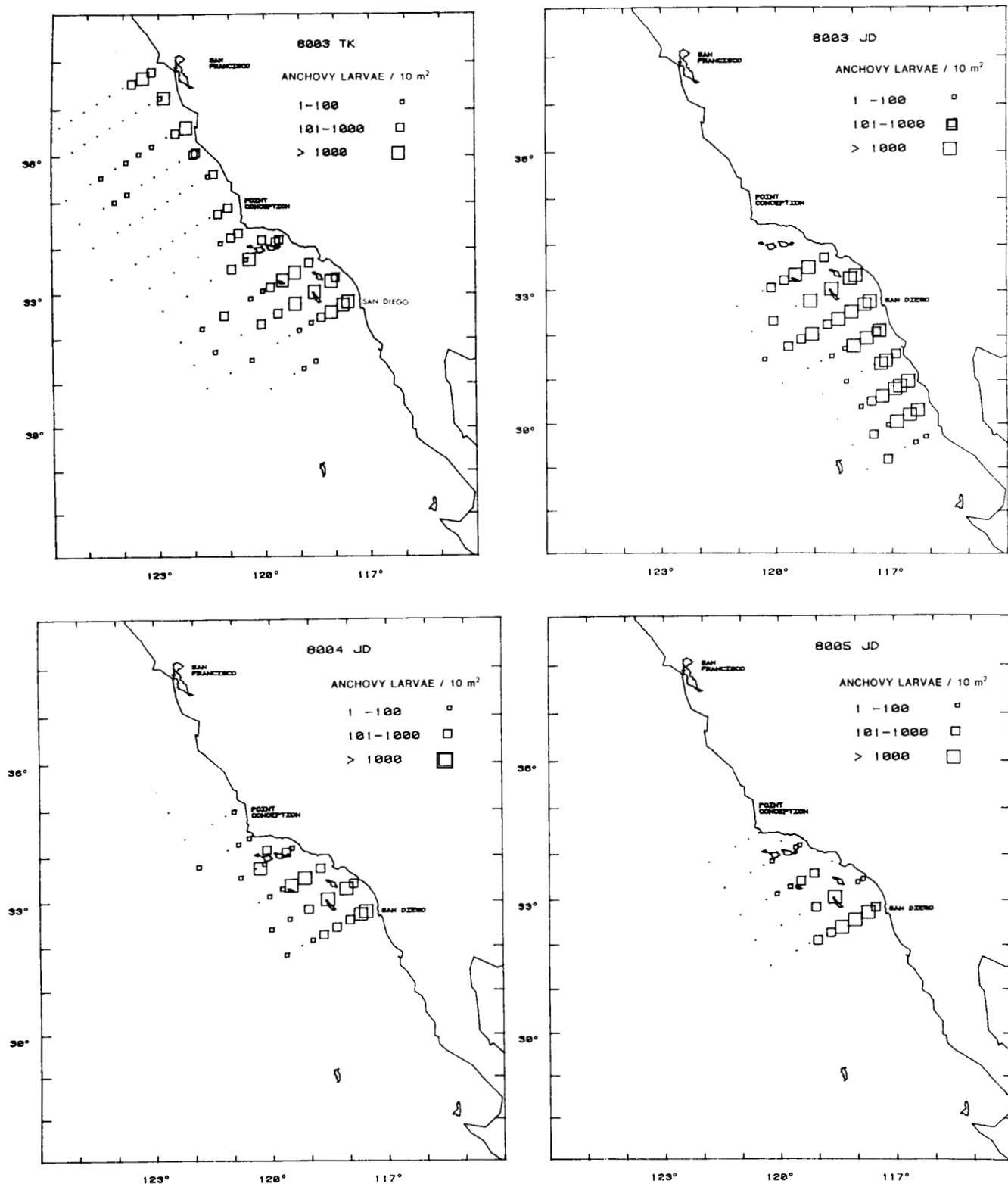


Figure 2. Pattern of occupied stations and geographic distribution of anchovy larvae for four CalCOFI cruises conducted during February-May period in 1980.

A decision was made in early winter 1980 to estimate spawning biomass also by the egg production method (Parker 1980) because of the limited coverage

of the CalCOFI cruises. To accomplish the task, the 8003 JD and 8004 JD cruises were designed to include the collection of anchovy egg samples and adult fish

with a midwater trawl net. Processing these samples in the laboratory was given first priority. There was insufficient time to process all bongo plankton samples to meet the July 1 deadline for announcement of the biomass estimate. As a result CalCOFI stations north of line 80 for cruises 8004 JD and 8005 were excluded from the processing and analysis.

In general the distribution of anchovy larvae for the central subpopulation was similar to that observed in 1979 for comparable regions and months (Stauffer 1980). The distribution of the standardized number of anchovy larvae per 10 M² sea-surface area is summarized in Figure 2 for the four 1980 CalCOFI cruises. For the Southern California Bight regions of 7, 8, and 9, larvae were within 140 nautical miles of the coast. The larva densities were highest in the Southern California Bight region 7 for the March and early April 8003 JD cruise with larva density tapering off by May similar to prior years. For central California regions samples were sorted for only the 8003 TK cruise conducted in early March. At this time anchovy larvae were distributed within 50 nautical miles of the coast. Examination of the anchovy egg samples from 8004 JD for central California regions found only a few anchovy eggs in Monterey Bay, suggesting that anchovy spawning had ceased in that area by the time of the 8004 JD cruise (Stauffer and Picquelle 1980). The distribution of anchovy larvae off northern Baja California extended about 100 nautical miles offshore, although the spawning apparently was concentrated

within 40 nautical miles of the coast (Stauffer and Picquelle 1980).

Because the 1980 egg and larva survey lacked a January cruise and samples for CalCOFI northern Baja and central California regions in the spring quarter were not sorted, the 1980 annual larva census estimate was derived from a regression analysis of the historical CalCOFI anchovy larva data recompiled to generate larva census numbers that matched the coverage of the 1980 egg and larva survey (Table 1). The historical larva data were summarized for CalCOFI regions 7, 8, 9, 11, and 13 (southern California and northern Baja California regions) for the second half of the winter quarter (15 February to 31 March) and for regions 7, 8, and 9 for the spring quarter. These regions and time periods corresponded to areas in which 1980 CalCOFI larva samples were collected and sorted. These winter and spring totals were summed to provide a modified larva census (L_m) for the CalCOFI time series which was comparable to the incomplete larva census for the 1980 survey. To expand L_m to an equivalent annual larva census values (L_a) as given in Appendix I of the FMP, the difference between these values, L_u (i.e. $L_u = L_a - L_m$) was regressed on L_m for the historical CalCOFI years in which there were sufficient data (see Table 1). The analysis excluded the 1979 census data which was also an expanded estimate from a partial survey. This regression is

$$L_u = 3.043 - 0.0107 L_m \quad (1)$$

TABLE 1
 Larva Census Data (10⁹ Larvae) for Estimating 1980 Spawning Biomass

Year	(1) 2nd half of winter (Region 7,8,9,11,13)	(2) Spring quarter (Region 7,8,9)	Sum (1)+(2)	Annual larva census ¹	Estimated biomass ¹ (1,000 tons)
1951	455	458	913	1,841	180
52	353	257	610	1,600	156
53	1,705	144	1,849	5,208	510
54	3,730	410	4,140	7,838	768
55	5,644	1,047	6,691	8,618	846
1956	3,506	816	4,322	4,944	485
57	4,192	4,027	8,219	11,960	1,172
58	5,203	3,620	8,823	15,087	1,479
59	3,825	4,843	8,668	15,440	1,514
60	10,527	4,804	15,331	15,713	1,540
1966	14,170	17,212	31,382	36,452	3,572
1969	32,852	3,496	36,348	30,594	2,998
1972	14,359	6,857	21,216	28,373	2,781
1975	27,563	387	27,950	36,768	3,603
1978	10,994	2,630	13,624	13,306 ²	1,304 ²
79	10,111	3,612	13,723	17,580 ³	1,723 ³
80	11,830	3,400	15,230		1,775

¹Source: Appendix I of Northern Anchovy FMP (PFMC 1978)

²Stauffer and Parker 1980

³Stauffer 1980

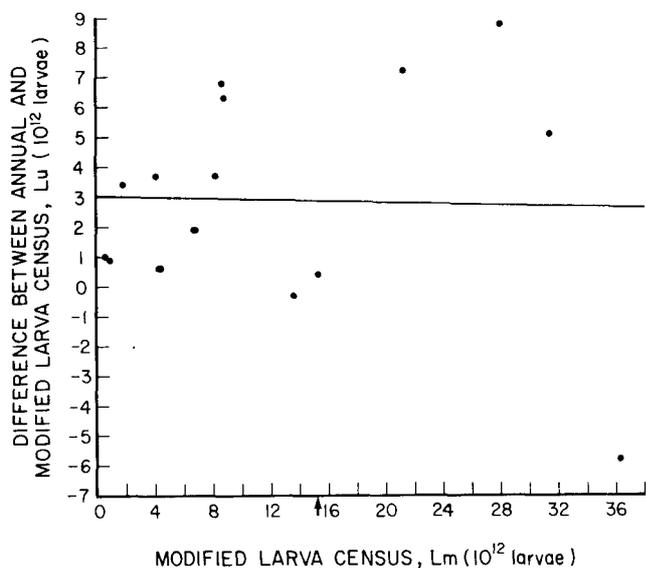


Figure 3. The regression model for expanding the modified larva census, L_m , to the annual larva census, L_a .

and is shown in Figure 3. Although the slope (-0.0107) is not significantly different from zero, equation (1) was used to estimate L_u for 1980. The incomplete winter and spring larva census numbers for 1980 were $11,830 \times 10^9$ and $3,400 \times 10^9$ larvae. These values are quite similar to the recomputed 1978 and 1979 larva census numbers. The sum of 1980 winter and spring numbers gives L_m value of $15,230 \times 10^9$ larvae. From (1) the 1980 value of L_u is $2,880 \times 10^9$ larvae. Approximate 95% confidence limits for $L_u \pm$ are 8.400×10^9 larvae. The equivalent annual larva census value, L_a , for 1980 is $18,110 \times 10^9$ larvae, the sum of L_u and L_m .

The estimate of the 1980 anchovy spawning biomass for the central subpopulation, using the larva census method developed by Smith (1972)

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

is 1,775,000 short tons for L_a equal to $18,100 \times 10^9$ larvae. Stauffer and Picquelle (1980) using the new egg production method (Parker 1980) estimated the 1980 anchovy spawning biomass to be 942,100 short tons. However, the larva census estimate is the appropriate estimate for setting the 1980 harvest quota by the procedure set forth in the anchovy FMP, since the model used in the evaluation of the harvest policy was dependent on the historical larva census estimates of anchovy biomass. Based on the larva census method, the 1980 anchovy spawning biomass is relatively unchanged from the 1979 level of 1,723,000 tons (Stauffer 1980). Optimum yield for the central subpopulation during 1980-81 season as specified in the FMP was 255,750 short tons. Within the U.S.

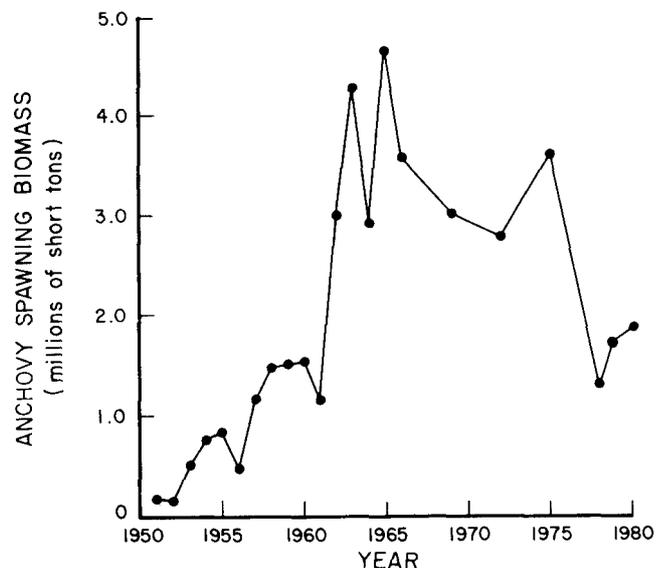


Figure 4. Estimated spawning biomass for the central subpopulation of northern anchovies, 1951-80.

Fisheries Conservation Zone the optimum yield was 179,400 short tons with a U.S. anchovy reduction quota set at 166,400 short tons. Because of the concern for the status of the anchovy resource arising from the egg production estimate of less than 1,000,000 tons, the California Fish and Game Commission in the fall of 1980 established an 80,000 short ton limit on the amount of northern anchovy that could be processed by shore-based reduction plants in California. The Commission's action included a provision for considering future increase if the reduction plants approach the 80,000 ton limit.

ACKNOWLEDGMENTS

The collection and processing of the egg and larva data for this biomass estimate depend on the cooperation of many people on the staff of Southwest Fisheries Service (SWFC), Scripps Institution of Oceanography (SIO), Instituto Nacional de Pesca, NOAA ship R/V *David Starr Jordan* and USSR R/V *Tikhookeanskiy*. Some of the data were collected under the authority of the Secretaria de Relaciones Exteriores and the Departamento de Pesca of Mexico. I especially thank the SIO plankton sorting group and James Thraikill, Richard Charter, Oden Burris, William Flerx, Dimitry Abramenkoff, and Jack Meteyor of SWFC. We also thank Daniel Huppert and Alec MacCall of California Department of Fish and Game for their suggestions and review.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

IDYLLWILD, CALIFORNIA

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**LOW-FREQUENCY EVENTS IN THE CALIFORNIA
CURRENT**

LARGE-SCALE SEA-SURFACE TEMPERATURE ANOMALIES IN THE NORTHEAST PACIFIC OCEAN

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ABSTRACT

Slow-developing, long-lasting perturbations of sea-surface temperature in the eastern North Pacific are revealed by anomaly patterns representing monthly deviations from the mean seasonal cycle. These patterns are typically defined by a central core of anomalously warm (or cold) water located approximately between latitudes 30° – 45° N, and west of longitude 140° W, which is partially surrounded by anomalously cold (or warm) water to the north, east, and south. They can persist up to several years and then, in a relatively short time, undergo a pattern reversal in which warm anomalies are replaced by cold anomalies and vice versa. Some examples are presented that represent selected periods in the 1960s and 1970s. A comparison of mean wind fields for January 1976 and January 1980, which were periods of sharply contrasting sea-temperature anomaly patterns, suggest that air-sea interaction processes have an active role in forming and maintaining these patterns.

RESUMEN

Perturbaciones de lento desarrollo y larga duración de temperaturas de la superficie del mar en el Pacífico nordeste son reveladas por patrones de anomalías que representan desviaciones mensuales del ciclo estacional medio. Estos patrones se identifican típicamente por un núcleo central de agua anómalamente templada (o fría), que se encuentra aproximadamente entre las latitudes 30° y 45° N, y al oeste de la longitud 140° O, y que está parcialmente rodeado por agua anómalamente fría (o templada) al norte, este y sur. Los patrones pueden persistir durante unos cuantos años y de repente, en un período relativamente corto, se puede reversar el patrón, donde se reemplazan las anomalías templadas con anomalías frías y viceversa. Se presentan algunos ejemplos que representan períodos selectos durante los 1960s y los 1970s. Una comparación del promedio de los campos del viento para enero de 1976 y enero de 1980, períodos en que se exhibían patrones anómalos contrastantes de temperatura marina, sugiere que los procesos de interacción aire-mar juegan un papel activo en la formación y el mantenimiento de estos patrones.

INTRODUCTION

Large-scale departures of sea-surface temperature from mean conditions in the North Pacific Ocean can persist over extensive periods of time. Surface temperatures reflect thermal conditions in the entire upper mixed layer, which may reach to depths of 100m or more. Consequently, a variation of 1° or 2° C from normal may reflect a significant gain or loss of heat in this layer.

Monthly charts of sea-surface temperature for the northeast Pacific, along with charts showing deviations from long-term monthly means, have been prepared since 1960 for Fishing Information (Southwest Fisheries Center). These charts are based on data contained in radio reports of ship's synoptic weather observations, collected through the National Weather Service. The sea-surface temperature fields were analyzed from values averaged for areas 1° latitude by 1° longitude. Anomaly charts were constructed by subtracting the corresponding long-term monthly mean field from the analyzed temperature field for a particular month. Prior to 1974, the long-term monthly means were based on charts in H.O. 225 (U.S. Hydrographic Office). After that, a new set of monthly means were prepared from data representing the period 1948–67, obtained through the U.S. Navy's Fleet Numerical Weather Facility. All of the figures presented here were taken directly from, or are based on, charts published in Fishing Information. Temperature units used for these charts were converted from Fahrenheit to Celsius between 1977 and 1978. Consequently, both kinds of units appear in the figures.

The charts are all based on observations from January so that interyear comparison will be unaffected by seasonal variation and because sea-surface temperatures in winter months are less affected by transient fluctuations in thin surface layers.

SEA-TEMPERATURE ANOMALY PATTERNS

The examples selected for presentation here depict anomaly patterns that are typically defined by a central core of anomalously warm (or cold) water located approximately between latitudes 30° – 45° N, and west of longitude 140° W, which may be partially surrounded by anomalously cold (or warm) water to the

north, east, and south. Similar patterns have been found for periods in the 1950s (Eber 1971).

Figure 1 shows the sea-temperature anomalies for January 1965 and represents a regime characterized by positive values in the central core with scattered areas of negative anomalies in the peripheral region. This was a very stable pattern which persisted more than three years, into 1968. Figures 2-4 show the evolution of this regime in successive Januarys. The warm central core remained the dominant feature throughout the period, in terms of both spatial distribution and magnitude of deviations from normal conditions. In January 1967 the negative anomalies had nearly vanished, but by January 1968 the pattern had returned to a state remarkably like that of January 1965.

This general type of regime characterized by a warm central core and cool periphery reappeared again in January 1974 (Figure 5). However, in this case the negative anomalies were the dominant feature, extending well offshore along the entire west coast of North America. At this time, the central core of the positive anomalies was poorly defined. During the ensuing year, however, the evolution of the warm core continued between latitudes 25°-35°N while the negative anomalies spread further into the surrounding areas, as shown in Figure 6. By January 1976 (Figure 7) the warm central core had consolidated in the vicinity of latitude 30°N, longitude 160°W and was almost completely encircled by the peripheral cold region.

In 1976, a transition began to take place which led to a nearly complete pattern reversal in the anomaly field. Figure 8 depicts the new regime as it existed in January 1977, with a central cold core between latitudes 35°-40°N and relatively warm conditions everywhere east of longitude 145°W. During 1977, the negative anomalies spread eastward to about longitude 135°W while positive anomalies spread out along the southern periphery (Figure 9). Midway through 1978, a disruption of the pattern occurred, which led to the occurrence of negative anomalies along the coastal zone and in most of the area between latitudes 25°-35°N (Figure 10). This was relatively short-lived, and by January 1980 the typical pattern characteristics were again evident (Figure 11).

Although it is beyond the scope of this paper to try to explain why these patterns of anomalous sea-

temperature distributions develop, it is reasonable to assume that air-sea interaction processes are involved. In particular, one would expect to find contrasting atmospheric conditions corresponding to contrasting sea-temperature anomaly patterns. The anomaly fields for January 1976 and January 1980 are examples of opposite temperature regimes (Figures 7 and 11). Figure 12 shows the difference in the temperature fields for these two months. These differences portray an enhanced image of the typical anomaly pattern described in this study. Negative differences in the central core area represent lower temperatures in 1980 than in 1976, and positive differences along the North American coast and in the peripheral region represent higher temperatures in 1980 relative to 1976.

For comparison, Figure 13 shows the difference in the surface wind field for January 1976 and January 1980. The arrows represent the vector difference of wind observations averaged by areas 5° latitude by 5° longitude for the respective months. In terms of air circulation, Figure 13 shows that the flow in 1980 was from the south (relative to that in 1976), east of longitude 135°W and south of latitude 40°N, where the maximum positive temperature differences occurred. Conversely, the flow in 1980 was from the north (relative to that in 1976) in the area between latitudes 25°-35°N and longitudes 145°-160°W, where the maximum negative temperature differences occurred.

The magnitude of differences in wind speed between the two years is substantial, and the described relationships between differences in winds and sea temperatures are consistent with the effects that would be expected from wind-induced advection, evaporation, and sensible heat transfer. It appears likely, therefore, that air-sea interaction processes have a tangible role in forming and maintaining persistent patterns of sea-surface temperature anomalies.

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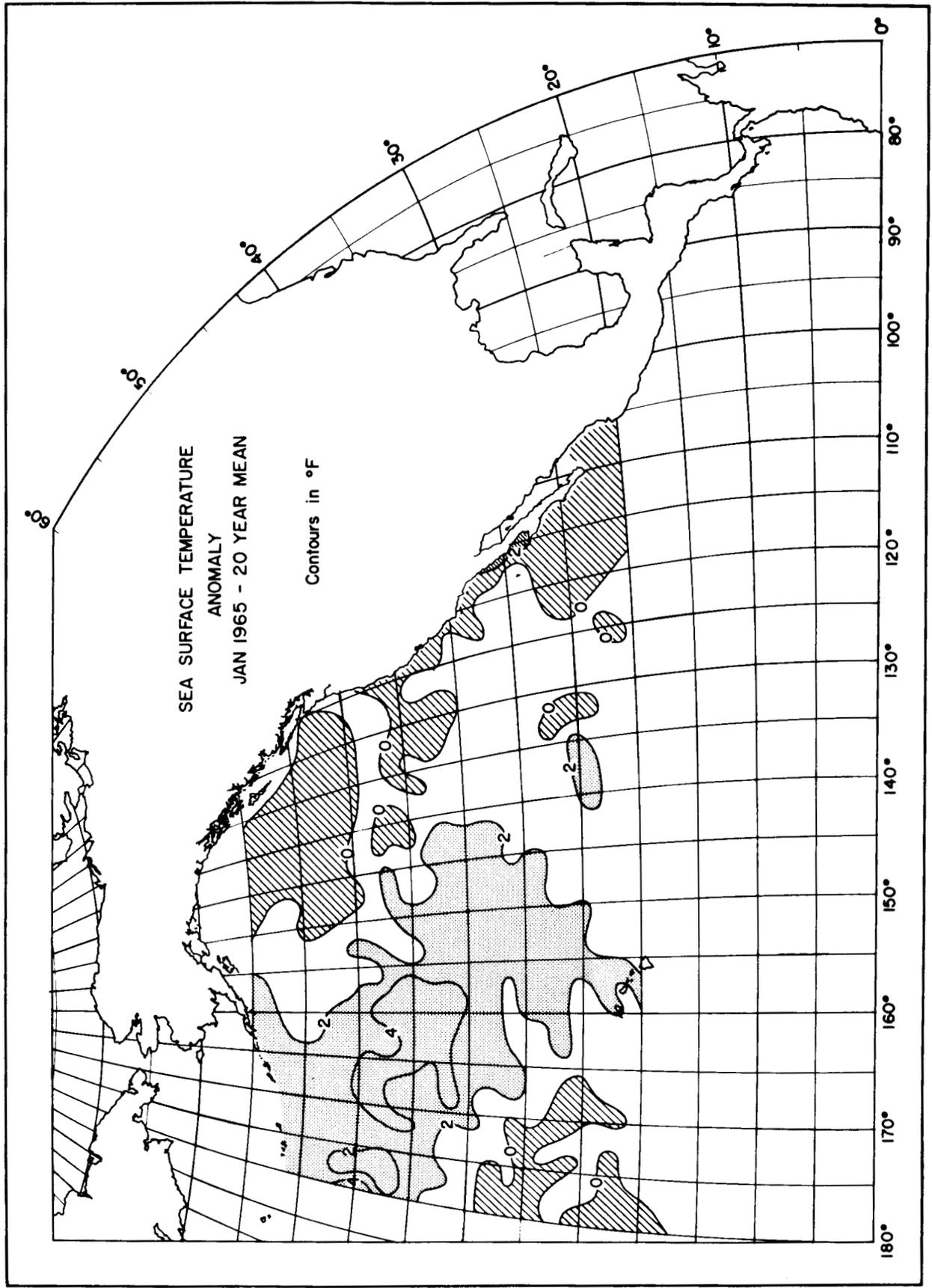


Figure 1. Deviation of sea-surface temperature for January 1-31, 1965, from the long-term mean. Hatched areas colder in 1965, clear and stippled areas warmer in 1965.

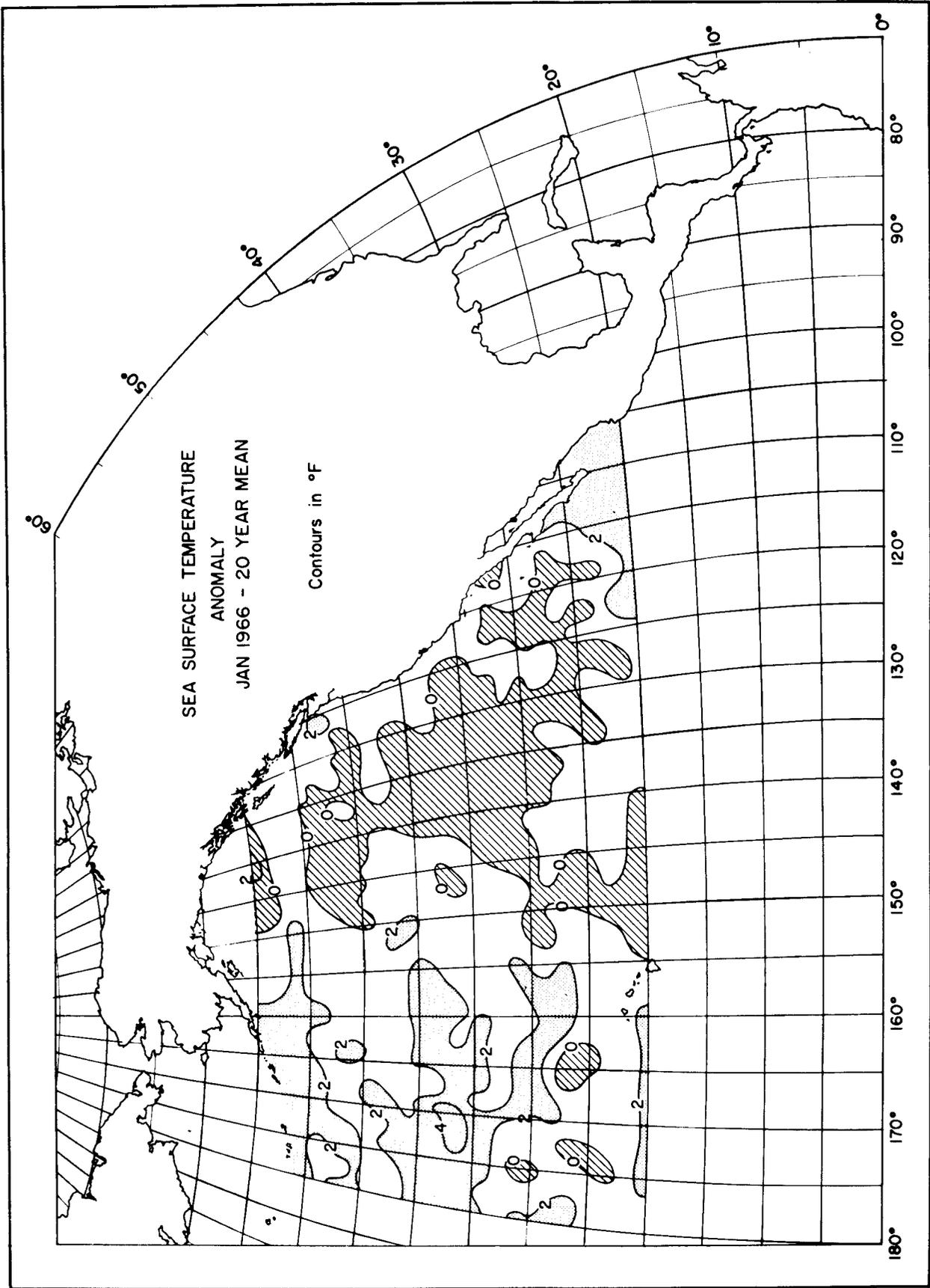


Figure 2. Deviation of sea-surface temperature for January 1-31, 1966, from the long-term mean. Hatched areas colder in 1966, clear and stippled areas warmer in 1966.

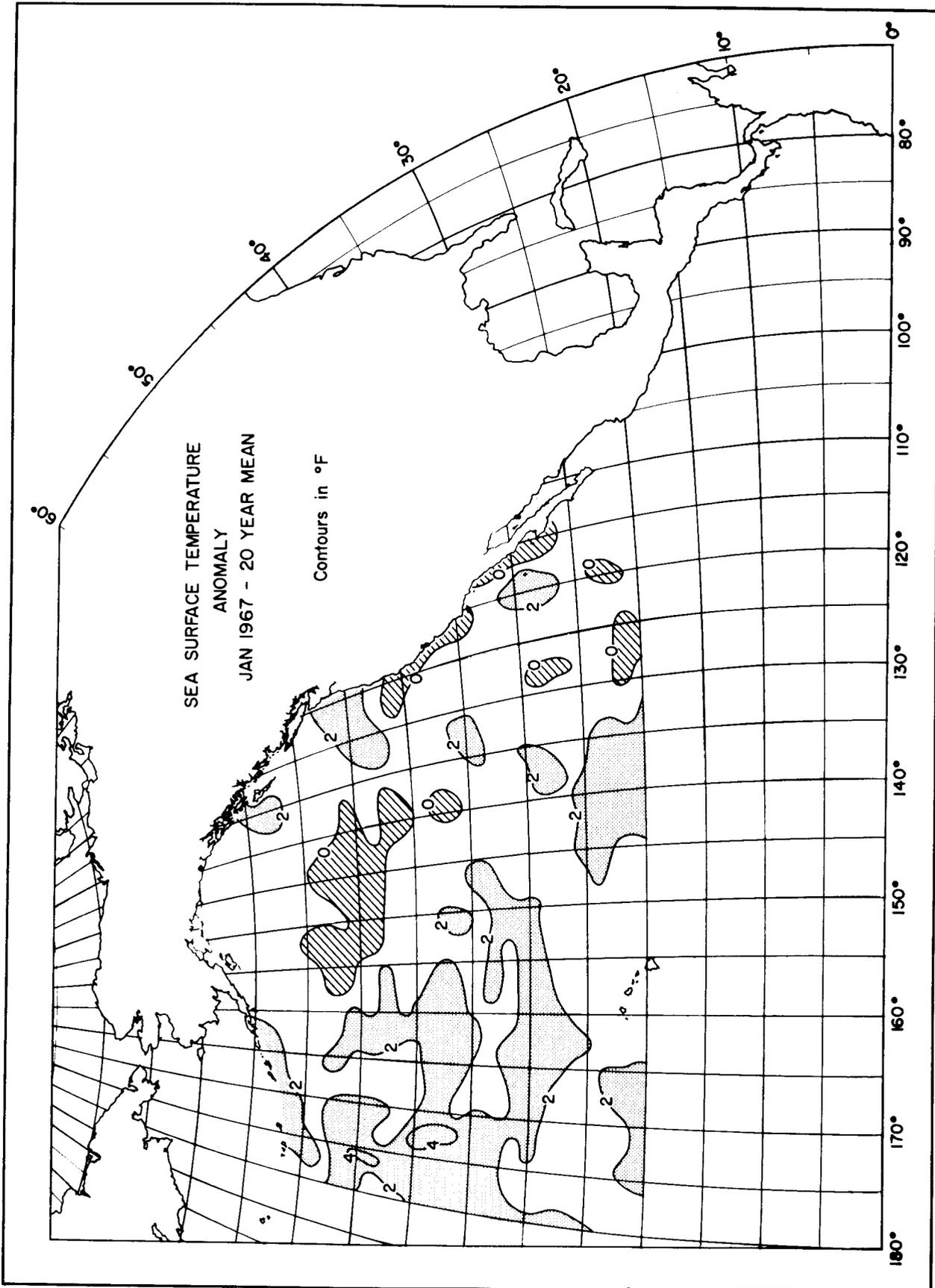


Figure 3. Deviation of sea-surface temperature for January 1-31, 1967, from the long-term mean. Hatched areas colder in 1967, clear and stippled areas warmer in 1967.

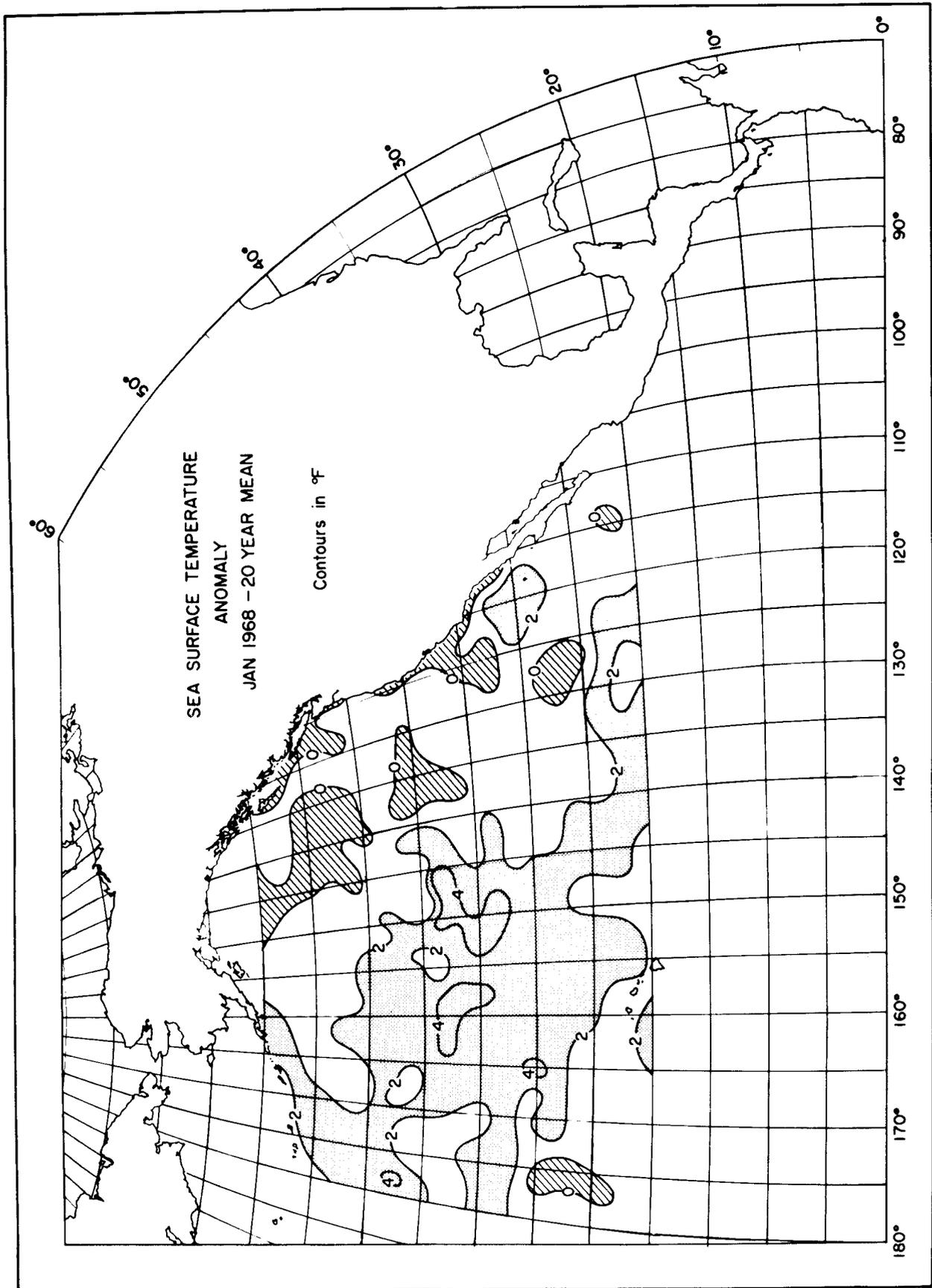


Figure 4. Deviation of sea-surface temperature for January 1-31, 1968, from the long-term mean. Hatched areas colder in 1968, clear and stippled areas warmer in 1968.

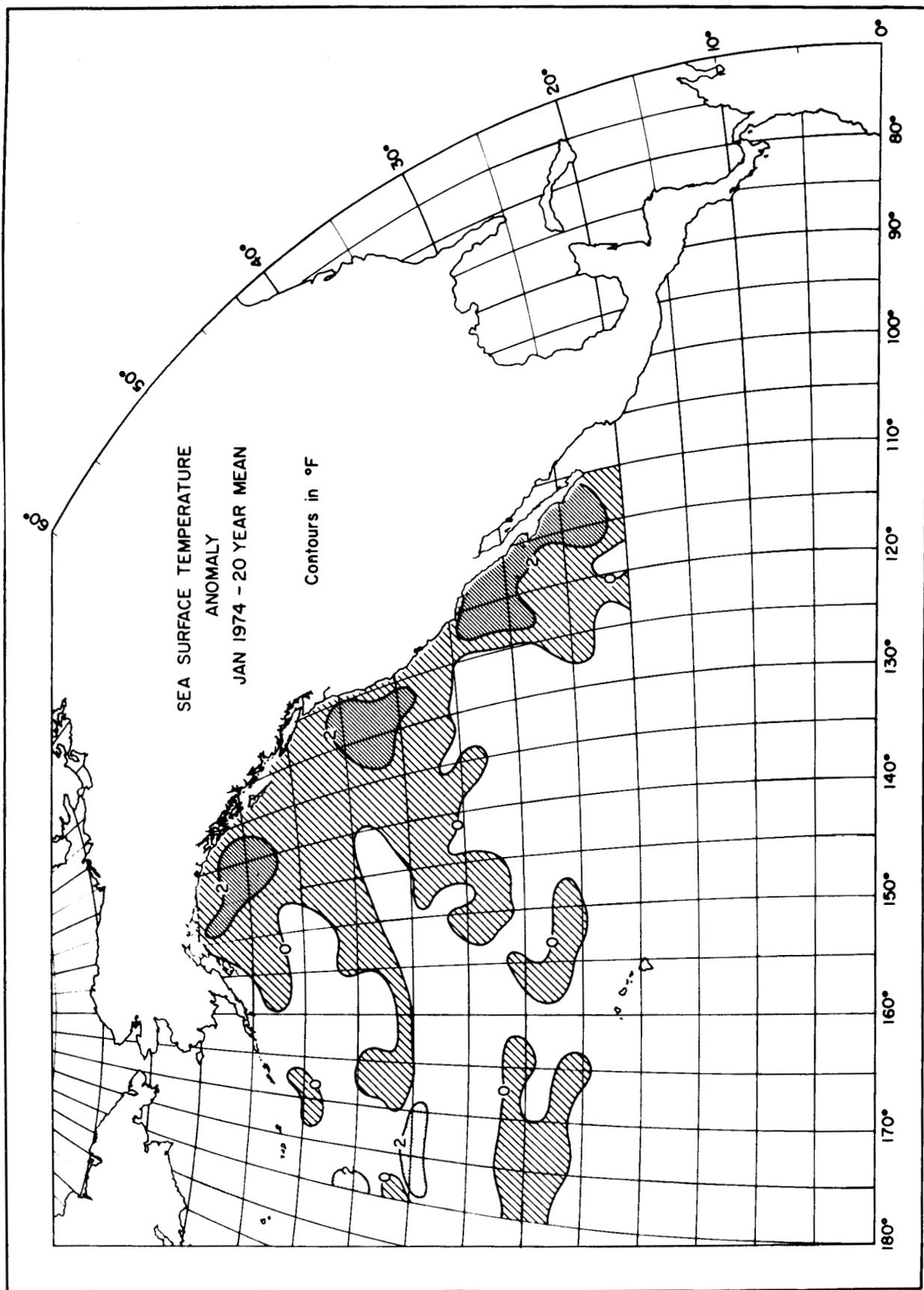


Figure 5. Deviation of sea-surface temperature for January 1-31, 1974, from the long-term mean. Hatched areas colder in 1974, clear and stippled areas warmer in 1974.

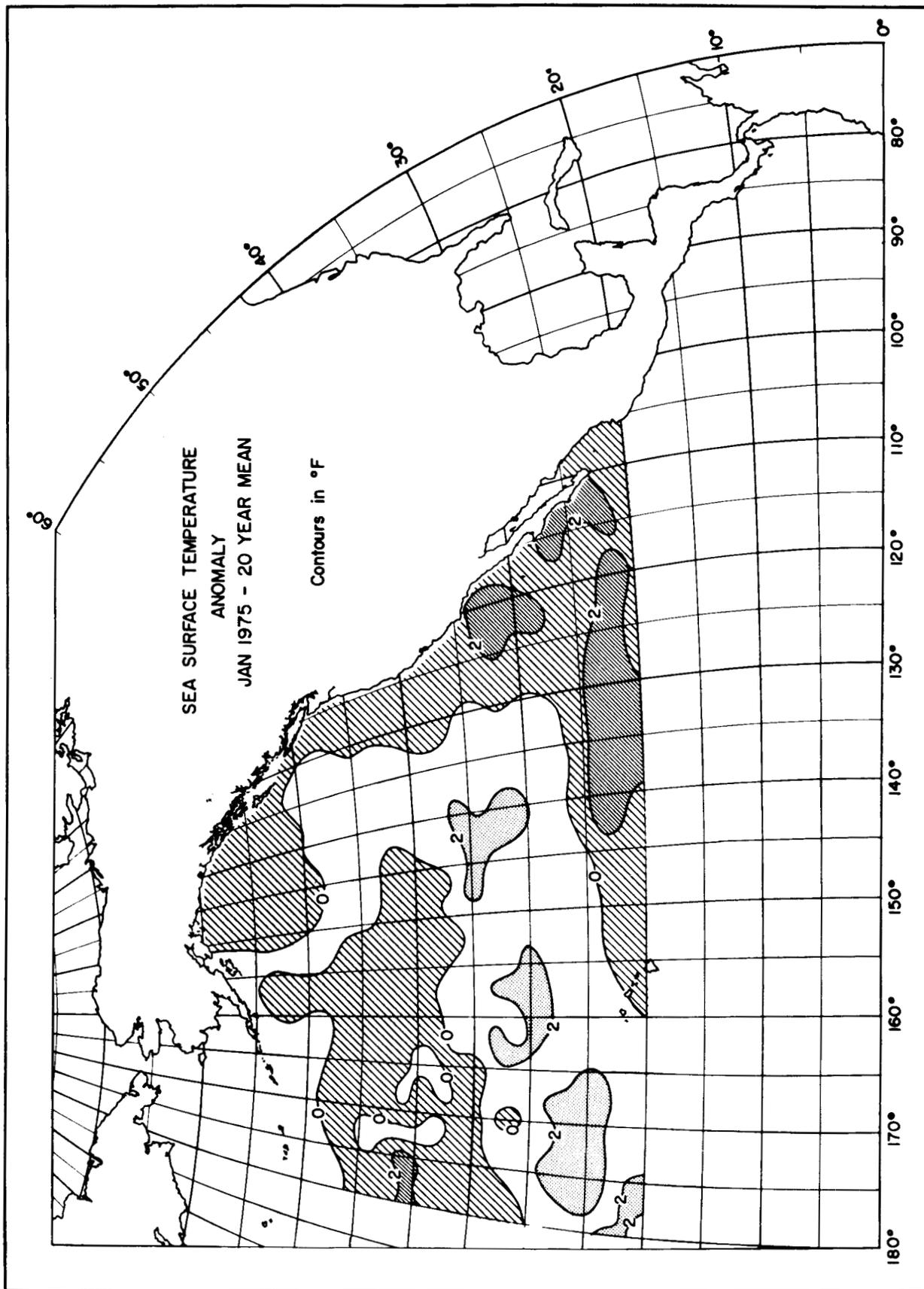


Figure 6. Deviation of sea-surface temperature for January 1-31, 1975, from the long-term mean. Hatched areas colder in 1975, clear and stippled areas warmer in 1975.

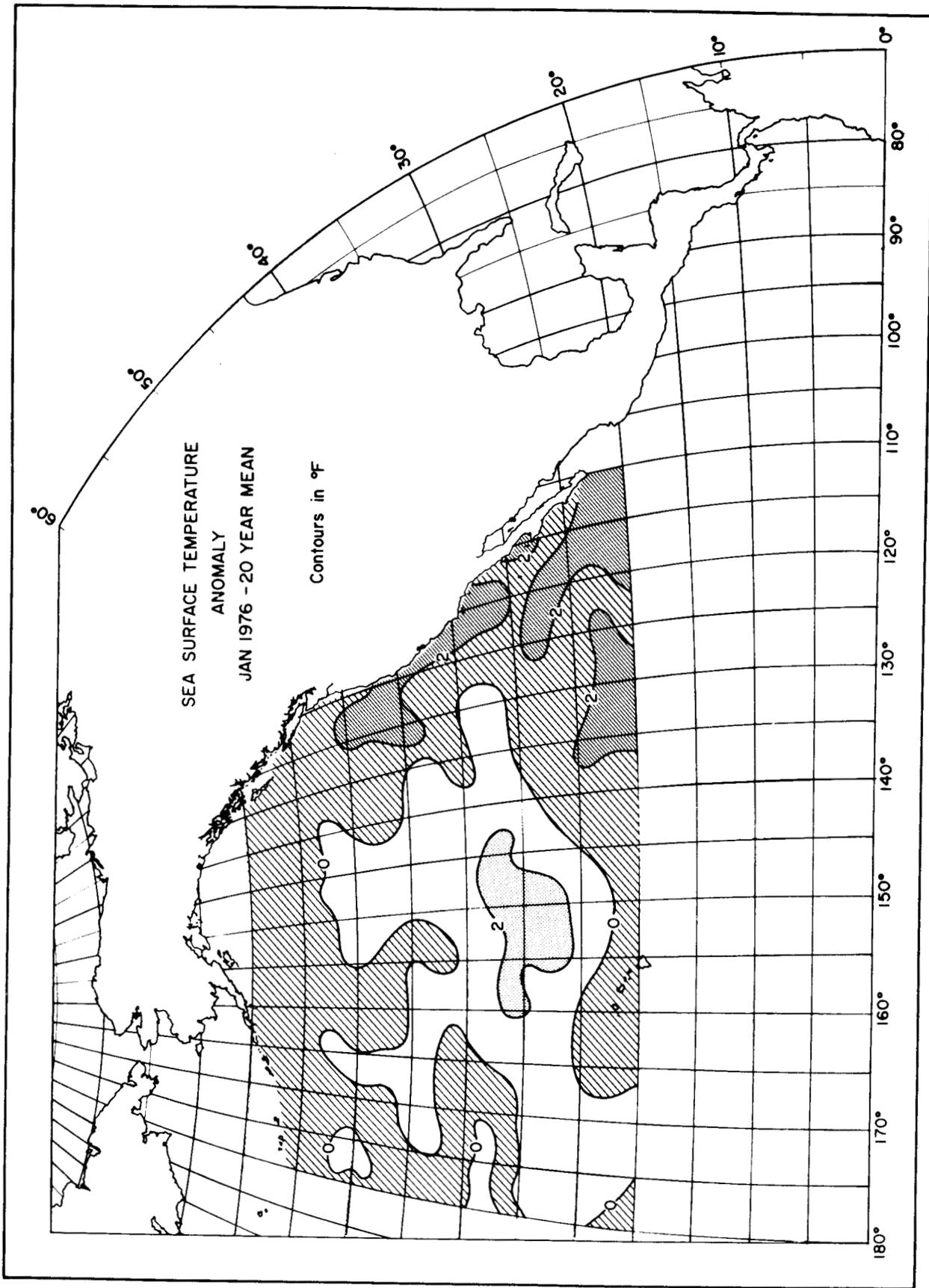


Figure 7. Deviation of sea-surface temperature for January 1-31, 1976, from the long-term mean. Hatched areas colder in 1976, clear and stippled areas warmer in 1976.

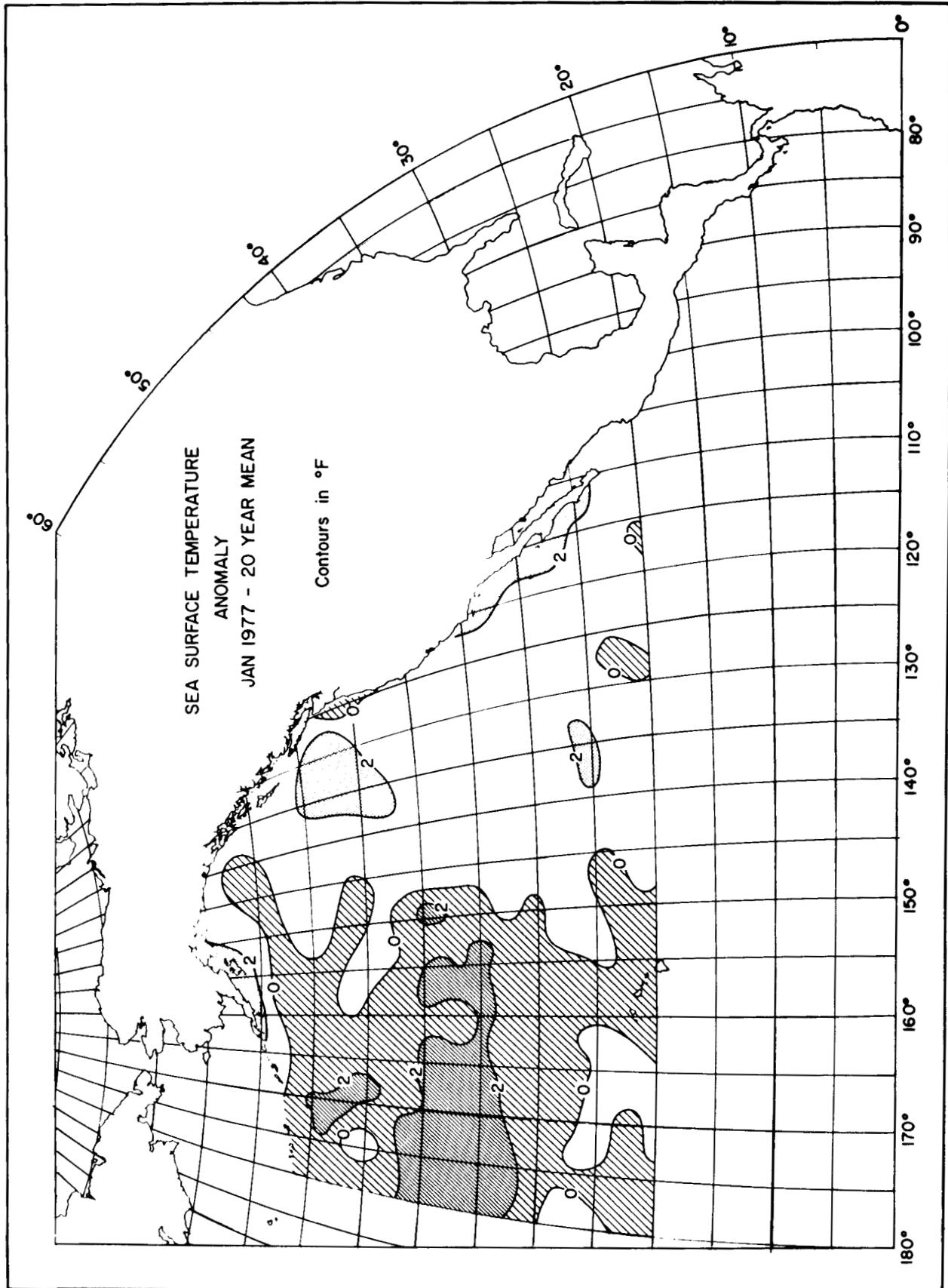


Figure 8. Deviation of sea-surface temperature for January 1-31, 1977, from the long-term mean. Hatched areas colder in 1977, clear and stippled areas warmer in 1977.

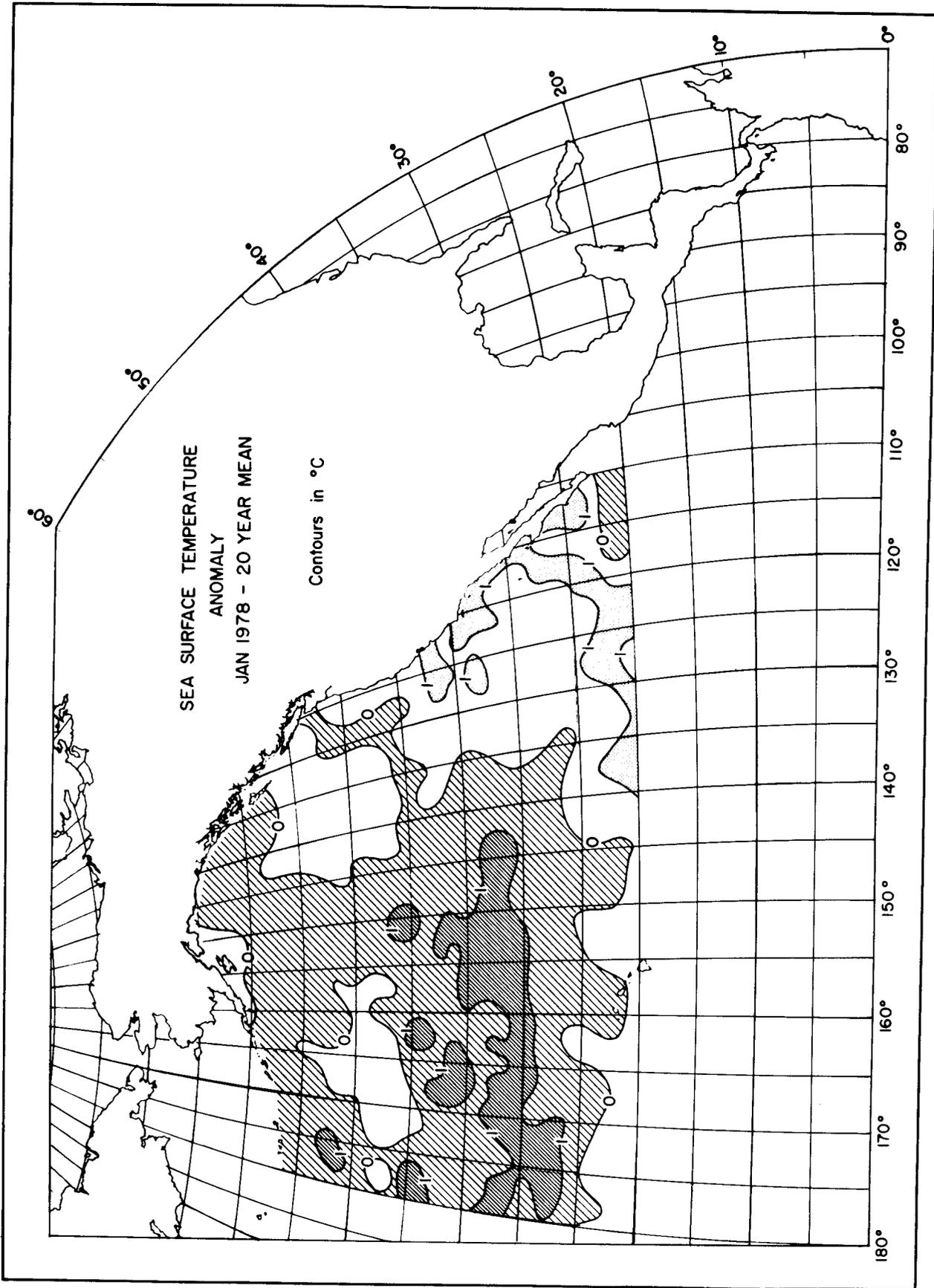


Figure 9. Deviation of sea-surface temperature for January 1-31, 1978, from the long-term mean. Hatched areas colder in 1978, clear and stippled areas warmer in 1978.

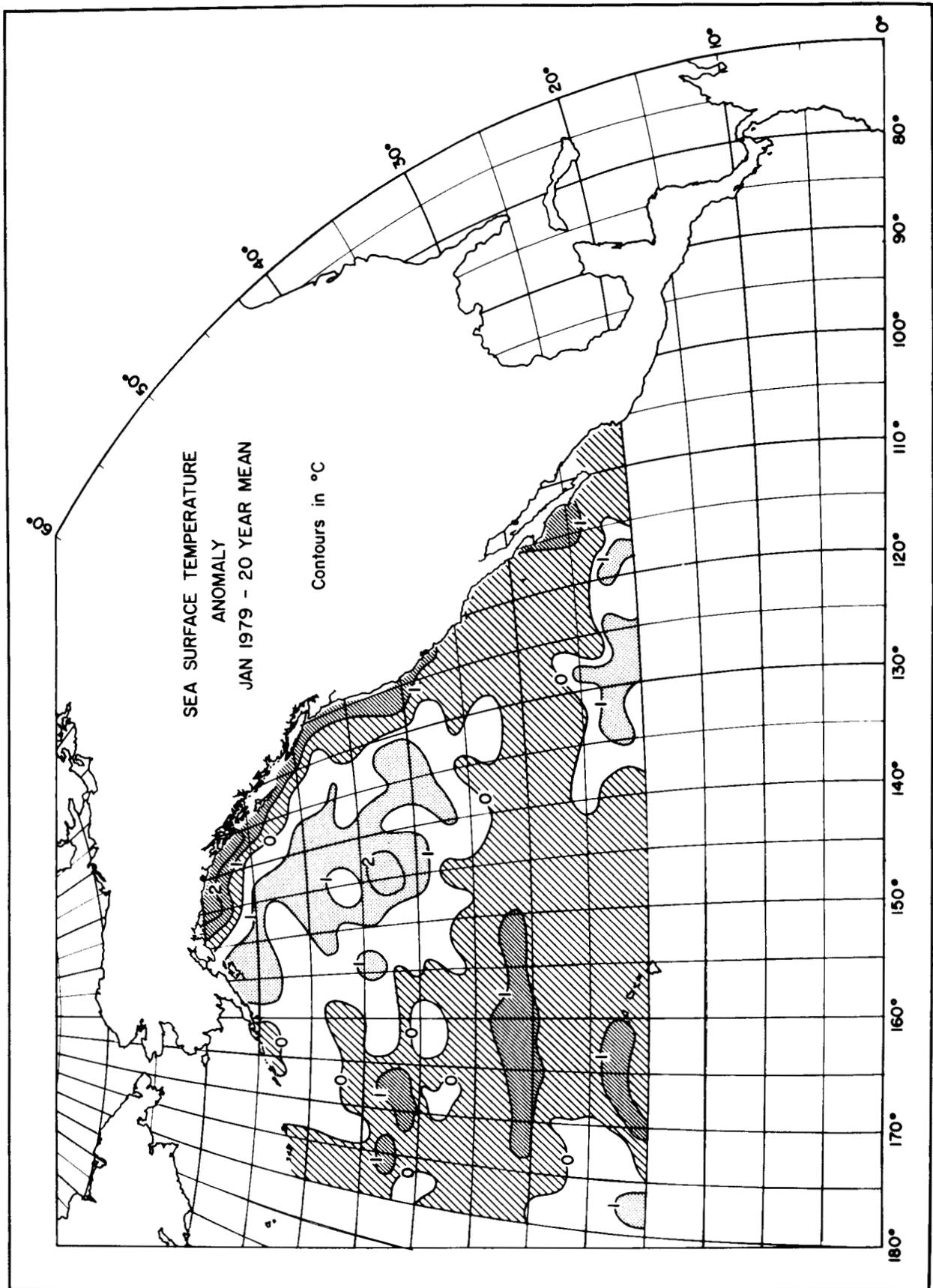


Figure 10. Deviation of sea-surface temperature for January 1-31, 1979, from the long-term mean. Hatched areas colder in 1979, clear and stippled areas warmer in 1979.

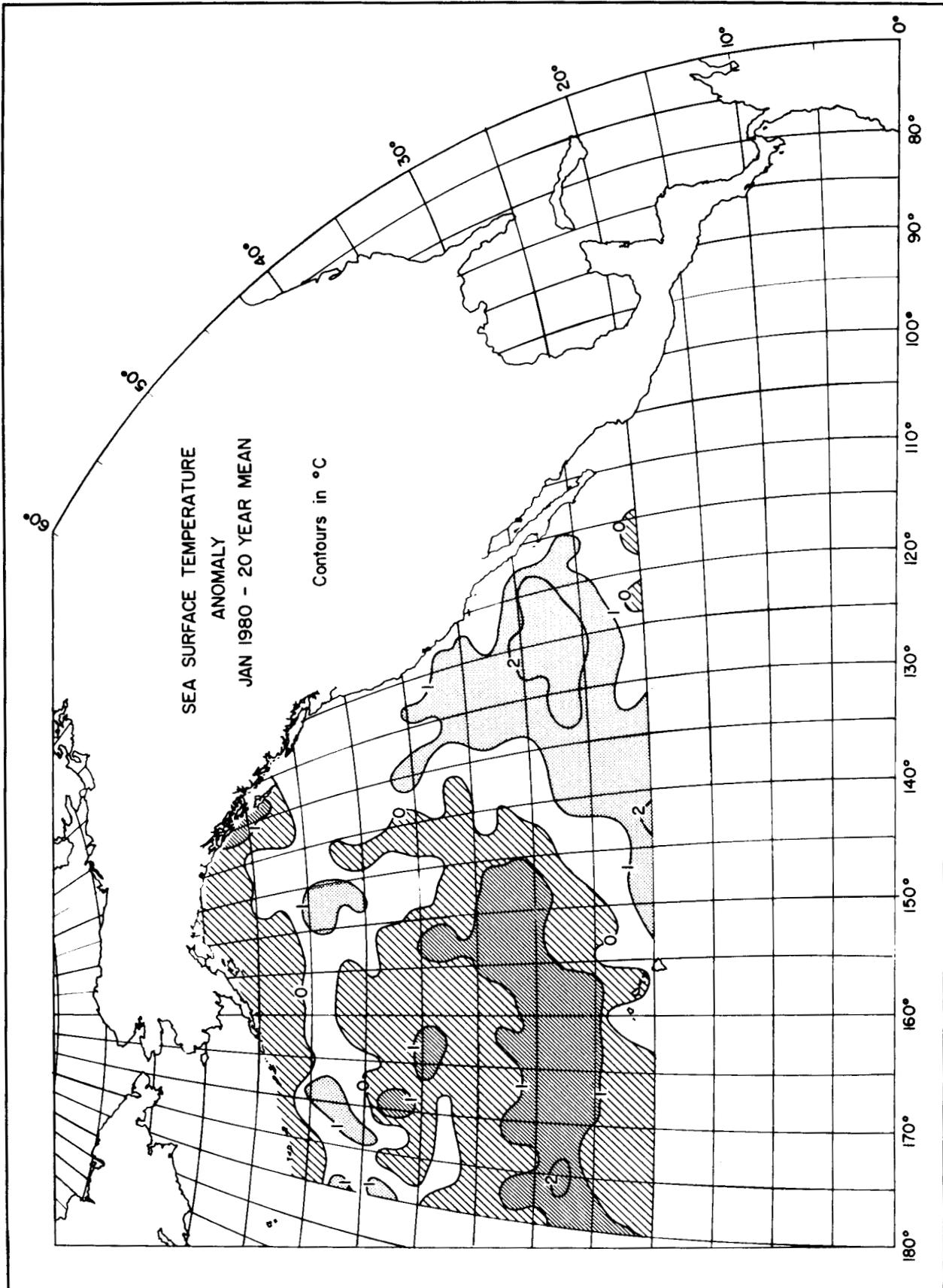


Figure 11. Deviation of sea-surface temperature for January 1-31, 1980, from the long-term mean. Hatched areas colder in 1980, clear and stippled areas warmer in 1980.

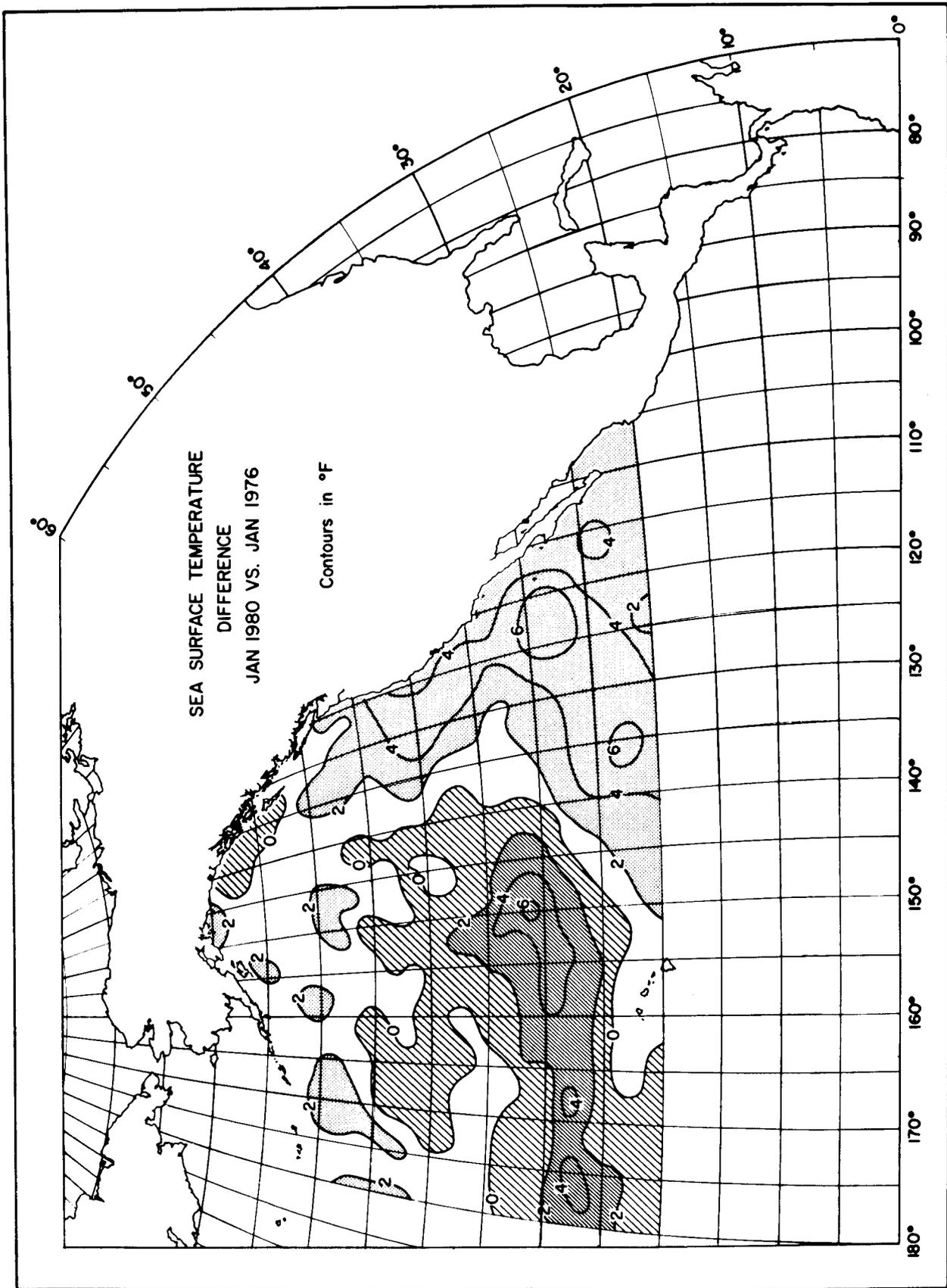


Figure 12. Difference of sea-surface temperature between January 1-31, 1976, and January 1-31, 1980. Hatched areas colder in 1980, clear and stippled areas warmer in 1980.

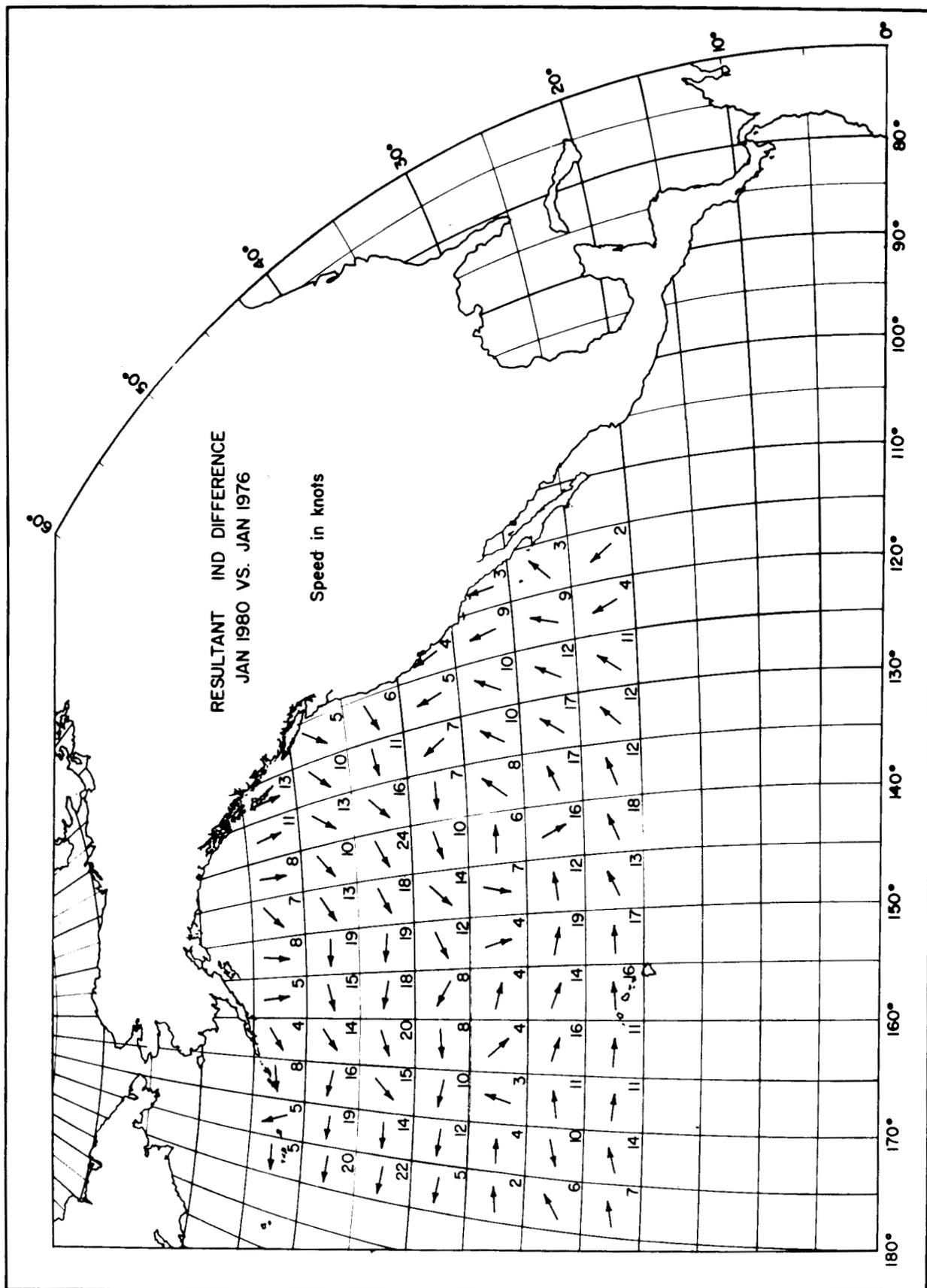


Figure 13. Arrows represent vector differences of winds averaged by areas 5° latitude by 5° longitude for January 1-31, 1976, and January 1-31, 1980. Numbers represent corresponding differences in wind speed. Differences were computed by subtracting 1976 from 1980 values.

INTERANNUAL VARIABILITY OF THE CALIFORNIA CURRENT—PHYSICAL FACTORS

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ABSTRACT

Monthly variations in the physical characteristics of the California Current system from 1950 to 1979 are examined to explore the potential causes of zooplankton variability. It is shown that variations in the large-scale zooplankton biomass cannot be explained solely on the basis of coastal upwelling. However, large-scale advection in the California Current appears to play a major role in controlling the large-scale zooplankton variability over interannual time scales. Coastal tide gauge records provide a simple and convenient means of monitoring this interannual variability, and since these records date back to the early 1900's, they provide a very long record of large-scale, low-frequency changes in the California Current.

An attempt is made to identify the source of these large-scale changes in the flow. It is shown that, in many cases, the variations bear a strong resemblance to El Niño events in the eastern tropical Pacific with a time lag of several months. There are occasionally, however, strong events off the coast of California with no eastern tropical Pacific counterpart. Particular attention is focused here on a strong event during 1978 where anomalous poleward flow of the California Current was associated with an expected increase in water temperature but an unexplainable decrease in salinity.

RESUMEN

Se examinan las variaciones mensuales en las características físicas del sistema de la Corriente de California de 1950 a 1979, para explorar las causas potenciales de la variabilidad del zooplancton. Se muestra que las variaciones en la biomasa del zooplancton de gran escala no se pueden explicar solamente a base de la surgencia costera. Sin embargo, la advección de gran escala en la Corriente de California parece jugar un papel importante en el control de la variabilidad del zooplancton de gran escala a través de escalas de tiempo interanuales. Los registros de mareógrafos en la costa permiten un método fácil y conveniente de seguir esta variabilidad interanual, y ya que estos registros datan del comienzo de los años 1900, proveen una documentación que cubre un largo período de cambios de gran escala y de baja frecuencia en la Corriente de California.

Se intenta identificar el origen de estos cambios de gran escala en el flujo. Se ha mostrado que, en muchos casos, las variaciones son muy parecidas a los acontecimientos de El Niño en el Pacífico oriental tropical, con un retraso de varios meses. Sin embargo, se encuentran en ocasión unos fuertes acontecimientos frente a la costa de California, sin la ocurrencia de su contraparte en el Pacífico oriental tropical. En este trabajo se enfoca en un acontecimiento fuerte durante 1978, donde el flujo anómalo de la Corriente de California hacia el polo estuvo asociado con el aumento que se esperaba en la temperatura del agua, pero con un descenso inexplicable en la salinidad.

INTRODUCTION

The California Cooperative Oceanic Fisheries Investigation (CalCOFI), as it was initiated by Sverdrup and others in the late 1940's, was primarily intended as an ecological study of the fisheries off California. Numerous studies have noted that high biomass in the California Current is associated with low water temperature (Reid et al. 1958; Colebrook 1977). It is generally believed that the source of the cold water is coastal upwelling driven by the longshore component of local wind stress. The wind-driven offshore Ekman transport results in a divergence of water at the coast which must be replaced by the cold, nutrient-rich water at depth. Analyzing 21 years of CalCOFI zooplankton data (1949-69), Bernal (1980) and Bernal and McGowan (1981) have suggested an alternative mechanism for large-scale biological changes. They have presented evidence that advection of nutrient-rich water from high latitudes plays a major role in controlling the biomass of the eastern Pacific Ocean. This importance of advection to zooplankton variability in the California Current was first suggested by Wickett (1967).

In addition to zooplankton measurements, vertical profiles of temperature and salinity have been routinely made by CalCOFI. These hydrographic surveys have continued through 1979 on a fixed grid system providing a 30-year record of the physical characteristics of the California Current. The purpose of this study is to examine these time series of temperature and salinity and their relation to the large-scale biological changes described by Bernal (1979; 1980). The vertical hydrographic profiles can be used to

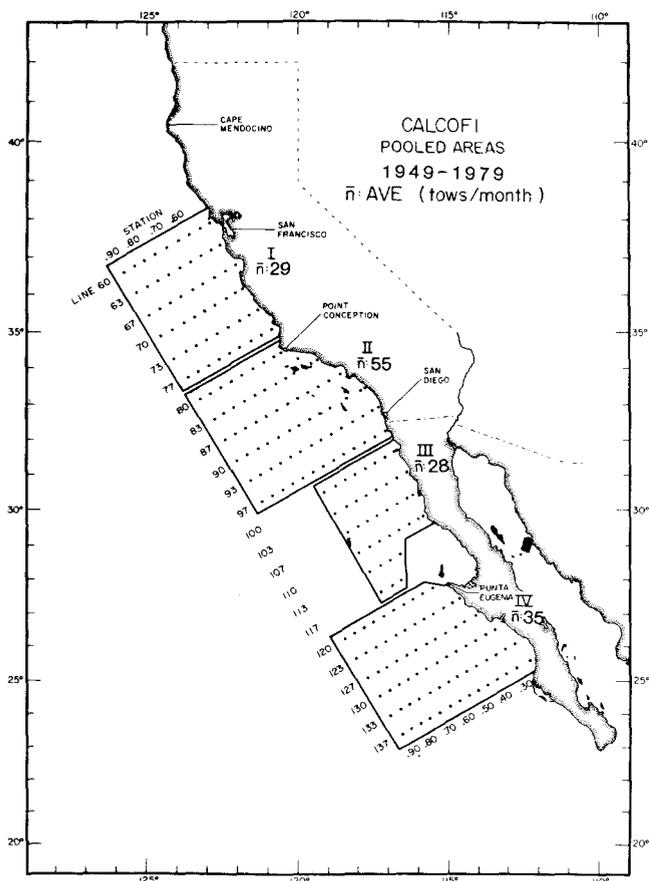


Figure 1. The four regions in the California Current over which spatial averages of zooplankton volume were computed; \bar{n} refers to the average number of individual samples pooled into a typical monthly estimate.

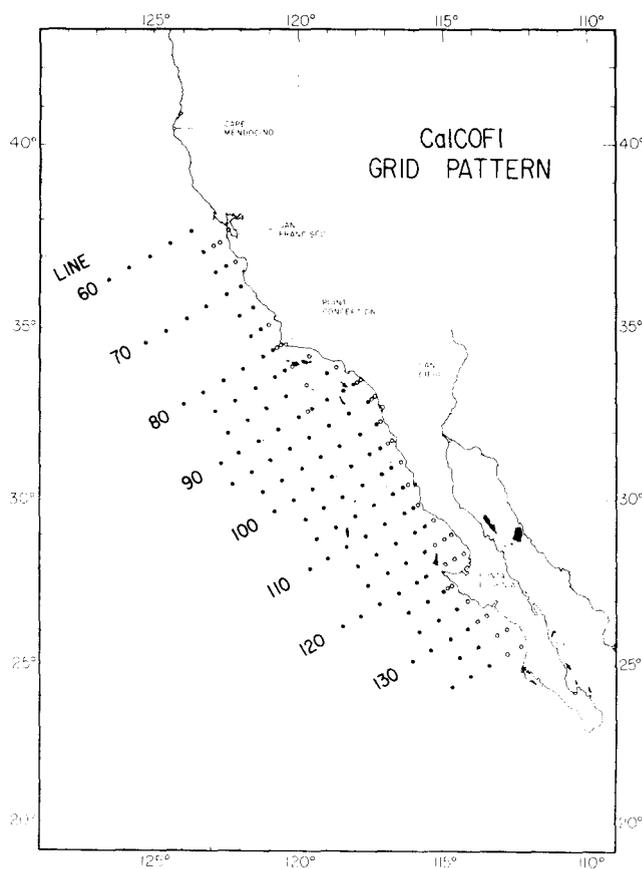


Figure 2. Grid of CalCOFI hydrographic stations occupied 40 or more times over the 30-year time period from 1950 to 1979. CalCOFI cardinal lines are labeled.

compute the steric height of the sea surface from which relative geostrophic flow can be inferred. This allows a quantitative assessment of the relation between advection and zooplankton biomass in the California Current.

DATA DESCRIPTION

Time series of log-transformed zooplankton volume from 1949 to 1979 were obtained from P. Bernal for the four regions of the California Current shown in Figure 1. Monthly means were constructed by averaging all observations at stations within each geographical area for each calendar month. The details of this procedure can be found in Bernal (1979; 1980).

The CalCOFI hydrographic (temperature and salinity) data were obtained from Larry Eber at the National Marine Fisheries Service in La Jolla, California. Monthly mean values from 1950 to 1979 were interpolated to 16 standard depths down to 1000 m. The data were then sorted by spatial grid location, and those with fewer than 40 observations over the 30-year time period were rejected from the analysis that fol-

lows. The number of spatial grid points remaining amounted to a total of 150 of which 114 extend to a depth of 500 m or more (Figure 2). The typical number of observations at any given grid point over the 30-year period was around 90.

SEASONAL VARIABILITY

The first analysis step was to describe the seasonal variability of zooplankton biomass. The method used consists of computing the 30-year algebraic mean value for each month of the year. The resulting mean annual cycles for each of the four areas are shown in Figure 3. The zooplankton biomass is largest at high latitudes and decreases equatorward. A seasonal signal is clearly present in each of the areas with a maximum generally occurring in late spring or early summer and a minimum in early winter. The maximum and minimum in Area IV occur about two months later than in those areas further north.

The annual cycles of the equatorward longshore component of wind stress for each of the four areas are also shown in Figure 3. These winds may be consid-

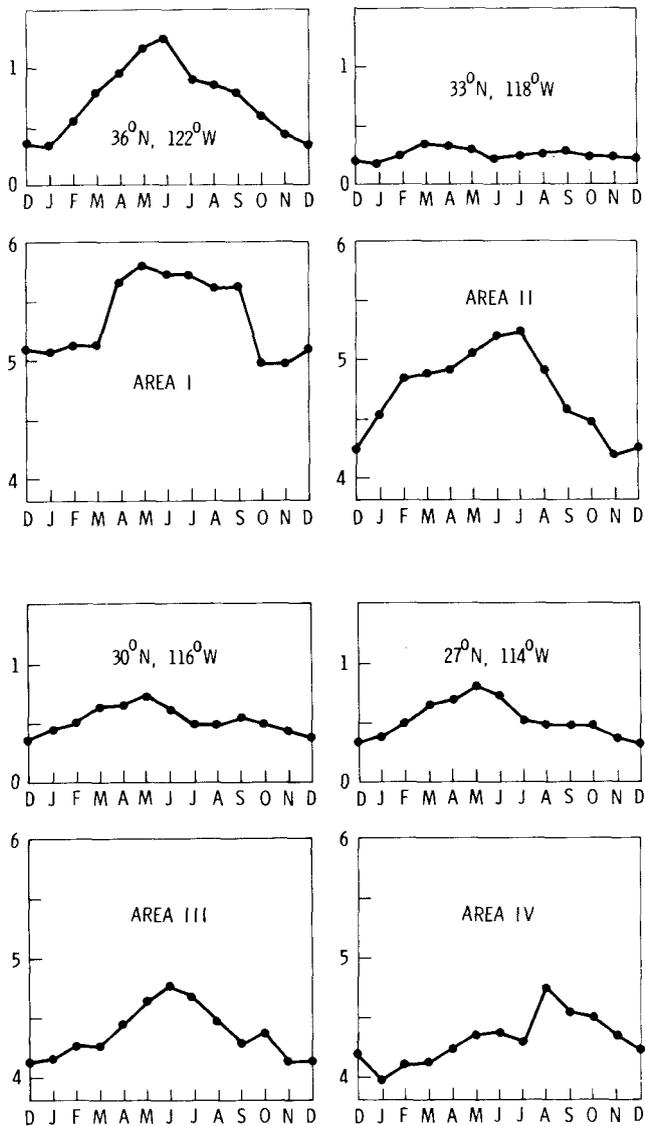


Figure 3. Annual cycles of the longshore (equatorward) component of wind stress in dynes/cm² (upper panels) and the zooplankton volume in log_e (ml/1000 m³) (lower panels) for each of the four geographical regions shown in Figure 1.

ered an index of coastal upwelling intensity: an increase in equatorward longshore winds corresponds to an increase in coastal upwelling. The seasonal mean wind stress values were taken from Nelson (1977) who compiled direct ship observations by 1-degree square areas from records dating back to the mid-19th century. These are probably the best available long-term measure of winds over the California Current. The figure shows that the winds are favorable for coastal upwelling year-round in each of the four areas with a maximum intensity in late spring or early summer.

A comparison of winds and zooplankton variability in Area III reveals what appears to be a strong relation between the two. There are two peak upwelling

periods. The strongest occurs in May, and it is followed one month later by a maximum in zooplankton volume. There is a secondary peak upwelling period in September, again followed one month later by a peak in zooplankton volume. From this simple relation, it is tempting to conclude that coastal upwelling is the primary source of nutrients controlling zooplankton biomass in the California Current. However, this appealing picture breaks down in the other three areas where there appears to be little or no relation between coastal upwelling (as indexed by the longshore wind stress) and zooplankton biomass.

It might be argued that the mean seasonal cycle has not been properly resolved here. This seems unlikely in the case of the wind data but could possibly be true in the case of the somewhat more limited zooplankton data set. There are other methods for defining the seasonal cycle, but considering the large number of zooplankton observations involved, it is doubtful that the resulting time series would differ significantly from those shown in Figure 3. An alternative explanation for the poor agreement with coastal upwelling is that some other process is at least partially responsible for controlling the zooplankton variability.

Wickett (1967) found a significant relation between zooplankton volume off California and wind forcing in the Alaskan Gyre one year earlier. He has suggested that the zooplankton off southern California respond to the upwelled nutrients in the Alaskan Gyre that are advected downstream by the southward flowing California Current. Bernal (1980) and Bernal and McGowan (1981) have also presented evidence from 21 years of data that advection plays a major role in controlling the zooplankton biomass. They found a significant correlation between zooplankton variability and the transport of low-salinity water across CalCOFI line 80 (running directly offshore from Point Conception). The objective of this study is to examine the importance of large-scale advection to zooplankton biomass in greater detail using the complete 30-year CalCOFI zooplankton and hydrographic data sets (1950-79).

The problem with looking at cause and effect relationships in the seasonal cycle is that nearly all geophysical and biological time series show a seasonal variation and any two seasonal cycles are highly correlated if one allows for a phase lag. However, since there are only 12 (nonindependent) data values, the statistical significance of any relation is based on a very small number of degrees of freedom. It is therefore better to remove the annual cycle from the data and look for causality in the residuals. The remainder of this study deals only with nonseasonal aspects of variability.

NONSEASONAL VARIABILITY

Anomalous zooplankton volume for a given month is defined to be the departure of the observed value from the seasonal mean value as shown in Figure 3 for that particular month. After removing the seasonal cycle, the log-transformed zooplankton anomalies for each of the four regions were normalized to have unit standard deviation. The resulting time series for 1949 to 1969 are shown in Bernal (1979). It is apparent from these figures that, underlying the seasonal signal, there are large year-to-year variations in the zooplankton biomass which tend to persist for 1-3 years. This anomalous behavior is in many respects more interesting than the seasonal variability discussed in the last section. In this study, Bernal's time series of nonseasonal zooplankton volume have been extended through 1979.

The wind-stress data were seasonally corrected in the same manner. The temporal and spatial sampling distribution of the direct ship observations compiled by Nelson (1977) is adequate for describing the seasonal variability discussed in the last section but not sufficient to resolve the detailed anomalous year-to-year variability of interest here. Instead, geostrophically computed winds produced by Fleet Numerical Oceanography Center (FNOC) were used to derive time series of wind-stress anomalies from each of the four areas. A detailed explanation of the method used by FNOC in computing these winds can be found in Caton et al. (1978).

The time-lagged correlation between nonseasonal zooplankton volume and the local equatorward longshore component of wind stress is shown in Figure 4 for each of the four areas. The results clearly indicate that locally forced coastal upwelling is not the dominant process controlling the zooplankton biomass. Zooplankton volume does tend to be positively correlated with upwelling, but the relationship is at best very weak.

From the individual time-series plots of zooplankton volume shown in Bernal (1979), it is evident that the nonseasonal variations in all four areas are very closely related. This study focuses attention on only the very large-scale variability which can be extracted by averaging the four individual time series. The resulting index of large-scale secondary productivity in the California Current is shown in Figure 5a. The figure reveals a strong interannual signal.

The cause of these significant variations in zooplankton biomass can be investigated by examining the nonseasonal variability of temperature and salinity in the California Current. The sampling distribution of the hydrographic data at each of the individual stations shown in Figure 2 is not adequate to accurately resolve

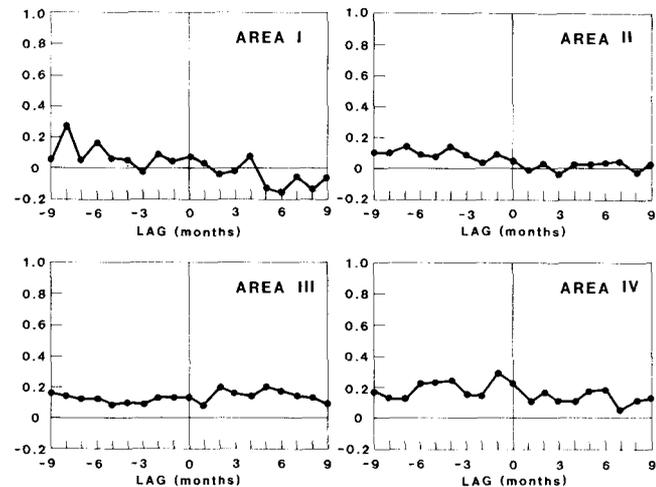


Figure 4. Correlation between nonseasonal zooplankton volume in month t and the local longshore (equatorward) component of wind stress in month $(t + \text{lag})$ for each of the four geographical regions in Figure 1.

the seasonal cycle by the long-term averaging method used on the zooplankton data. In particular, the sampling is biased toward summertime cruises. The statistical reliability of seasonal mean values estimated using the averaging technique varies from month to month and from location to location, depending on the number of samples used to estimate the mean.

An alternative and preferred method is to represent the temperature and salinity seasonal cycles by two harmonics, one with an annual and the other with a semiannual period. These two sinusoids were fit to the full 30 years of CalCOFI hydrographic data using least squares regression analysis. It should be noted that when the number of samples is large and evenly distributed throughout the year, the annual cycle computed using the harmonic method very closely resembles that computed by the averaging technique. The resulting seasonal cycles (described in Chelton, 1980) were used to compute monthly anomalies of temperature and salinity as with the zooplankton data.

Of particular interest here are the very large-scale nonseasonal variations of temperature and salinity. There are a number of methods for extracting the large-scale aspects of a parameter. The simplest is to form spatial averages as was done with the zooplankton data. This technique is obviously of limited value in cases where there are large horizontal variations in the parameter or when the horizontal gradients of the parameter are of primary interest (as in the case of the steric height data to be examined later in this section). All the important information can easily be lost using such a procedure. An alternative method that proves to be extremely useful is a technique called Empirical Orthogonal Function (EOF) or principal component analysis. The method essentially consists

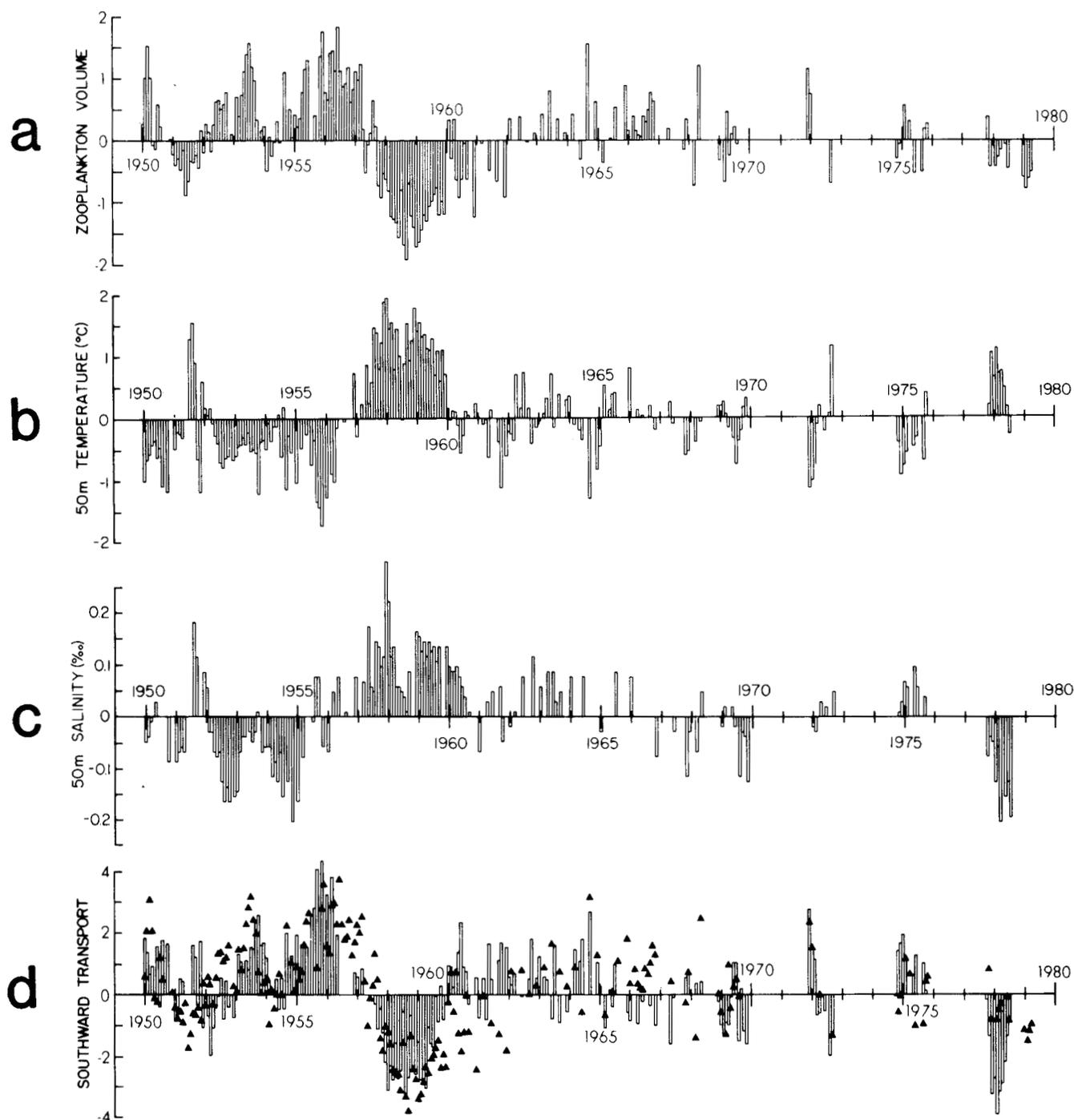


Figure 5. Time series of nonseasonal values of four parameters in the California Current: a) The average of the individual zooplankton time series in the four regions shown in Figure 1; b) The amplitude time series of the principal EOF of 50 m temperature shown in Figure 6; c) The amplitude time series of the principal EOF of 50 m salinity shown in Figure 9; d) The amplitude time series of the principal EOF of 0/500 db steric height shown in Figure 10. The zooplankton time series in a) has been reproduced as the triangles in d).

of separating the time and space dependence of a parameter in a manner that optimally describes the variance in a least squares sense. A time series of maps of some scalar variable $\phi(x,t)$ at N locations x can be expressed in terms of a set of N orthogonal functions $F_n(x)$ by

$$\phi(x,t) = \sum_{n=1}^N a_n(t) F_n(x).$$

The EOFs are uniquely defined among all possible sets of orthogonal functions by the constraint that their

time amplitudes $a_n(t)$ be uncorrelated over the data set. A detailed explanation of the method used to compute $F_n(x)$ and $a_n(t)$ can be found in Davis (1976). Methods of filtering to extract the large-scale aspects of variability in gappy data sets such as the CalCOFI hydrographic data are described in Chelton (1980).

The dominant spatial EOF of anomalous water temperature at 50 m depth is shown in Figure 6. Shallower temperature measurements were found to be very noisy. This pattern accounts for nearly half of the variability at 50 m over all 150 stations. It indicates that the temperature generally rises or falls (depending on the sign of the amplitude time series) everywhere over the California Current. The magnitude of temperature changes are largest close to the coast and tend to decay to a value of zero offshore. The time series associated with this pattern of 50 m temperature is shown in Figure 5b. The results are perhaps not surprising: The water temperature bears a very strong inverse relationship to the zooplankton variability. High zooplankton biomass is associated with cold water. Conversely, anomalously warm periods tend to be associated with low zooplankton volume.

There are two processes by which the water in the

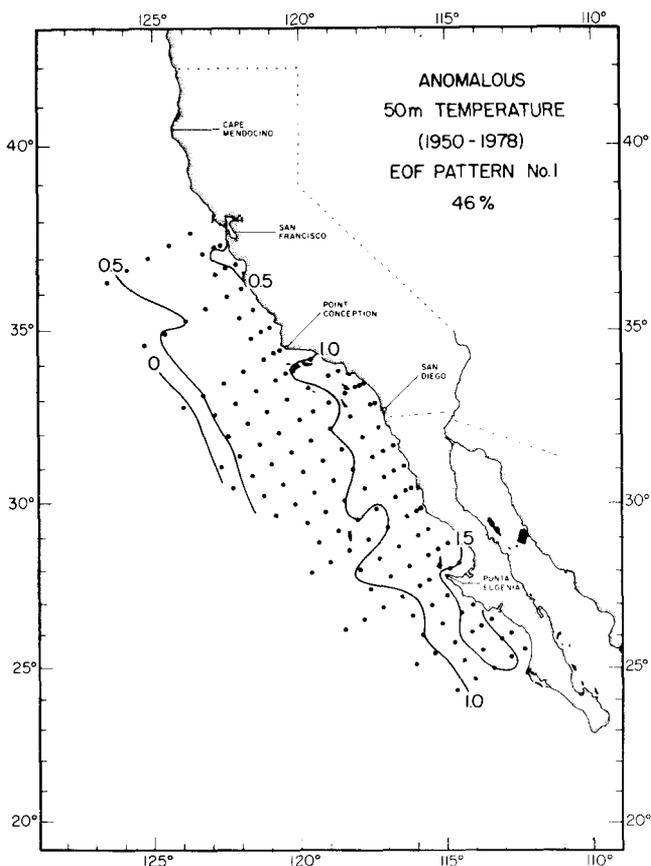


Figure 6. The principal spatial EOF of nonseasonal temperature at 50 m depth. The function values have been normalized to have mean square value of 1.

California Current can cool: either by upwelling of cold water from depth or by advection of cold water from higher latitudes. Either process provides the nutrients necessary for increased zooplankton productivity. Separating these two effects is a difficult task because the two are closely related. An increase in the flow of the California Current, either nonlocally forced or driven by the local wind stress (upwelling), results in an increased southward advection of cold water. It also results in a geostrophic adjustment of the density field with isotherms tilting in a manner that cools the nearshore waters.

Although both processes produce a similar signature in the temperature field, they differ in their effect on salinity. The mean cross-shore salinity distribution along CalCOFI line 93 is shown in Figure 7. The important features are the same throughout the

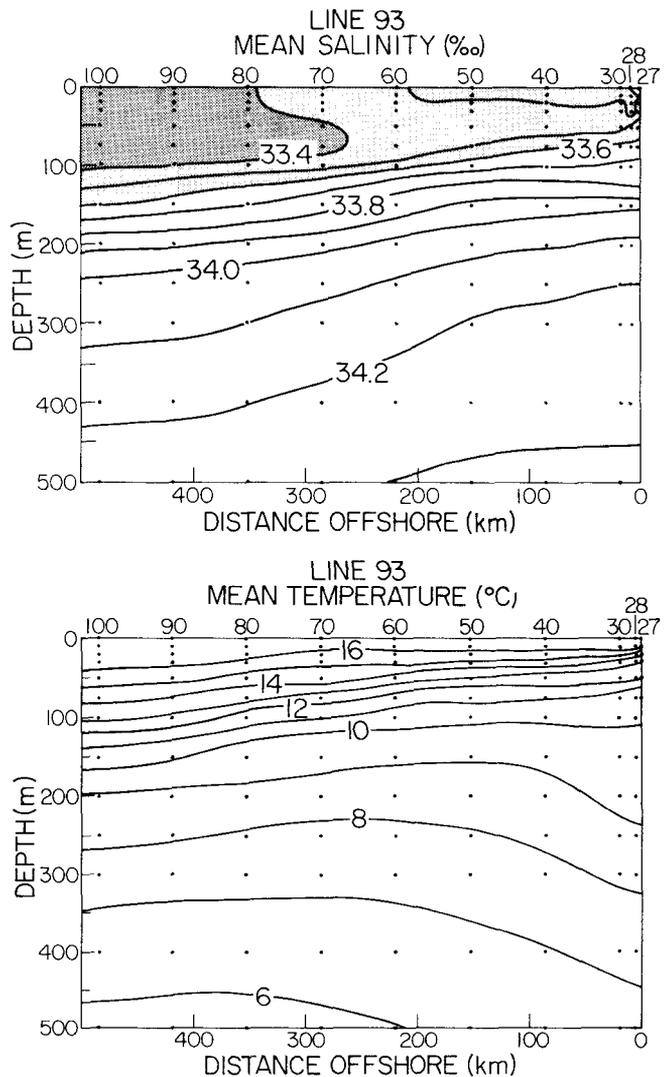


Figure 7. The mean cross-shore salinity and temperature distribution along CalCOFI line 93. Station numbers are shown along the upper axis.

California Current. The salinity increases with depth and decreases offshore. (Farther offshore beyond station 100, the salinity near the surface begins to increase again.) Thus, upwelling would lead to an increase in the nearshore salinity, and conversely, downwelling would tend to decrease the nearshore salinity. Then, if upwelling of deeper water (and nutrients) were solely responsible for fluctuations in secondary productivity, high zooplankton biomass would be associated with high salinity.

Advection produces quite a different signature in the salinity field. A section showing the mean longshore salinity distribution in the California Current is shown in Figure 8. The increase in salinity with depth previously noted in Figure 7 is clearly present throughout the California Current. The important feature here is the tongue of low-salinity water extending from high to low latitudes. Increased southward transport would cause the salinity to decrease and, correspondingly, decreased transport would result in an increase in the salinity. If advection of high-latitude water (and nutrients) were responsible for variations in secondary productivity, high zooplankton biomass would be expected to be associated with low salinity.

Because upwelling and advection produce opposite effects on the salinity distribution, the salinity can be used as a tracer for differentiating between the two processes. As with temperature, salinity observations

close to the surface were found to be quite noisy. The dominant EOF of salinity at 50 m is shown in Figure 9. This pattern accounts for 40% of the variability over all 150 stations. It indicates that the salinity tends to increase or decrease simultaneously everywhere over the California Current. The time series associated with this pattern of salinity variability is shown in Figure 5c. It is somewhat noisier than temperature or zooplankton volume (perhaps to some extent reflecting the complex interrelation between upwelling and advection), but high zooplankton biomass generally tends to be associated with low salinity and conversely. The correlation between the two is -0.53 . This relation statistically favors advection as the predominant source of nutrients controlling zooplankton biomass.

It should be pointed out that there are some instances when the advective model does not appear to hold. Although temperature and salinity do generally fluctuate in phase, they are out of phase during 1975 and 1978. The extreme 1978 event where low zooplankton volume was associated with low salinity is an indication that not all low-salinity water is high in nutrients. Although advection appears to be the dominant mechanism, it is apparently not the only source of nutrients controlling zooplankton productivity. This will be discussed in greater detail in the next section.

Up until this point, the suggested biological impor-

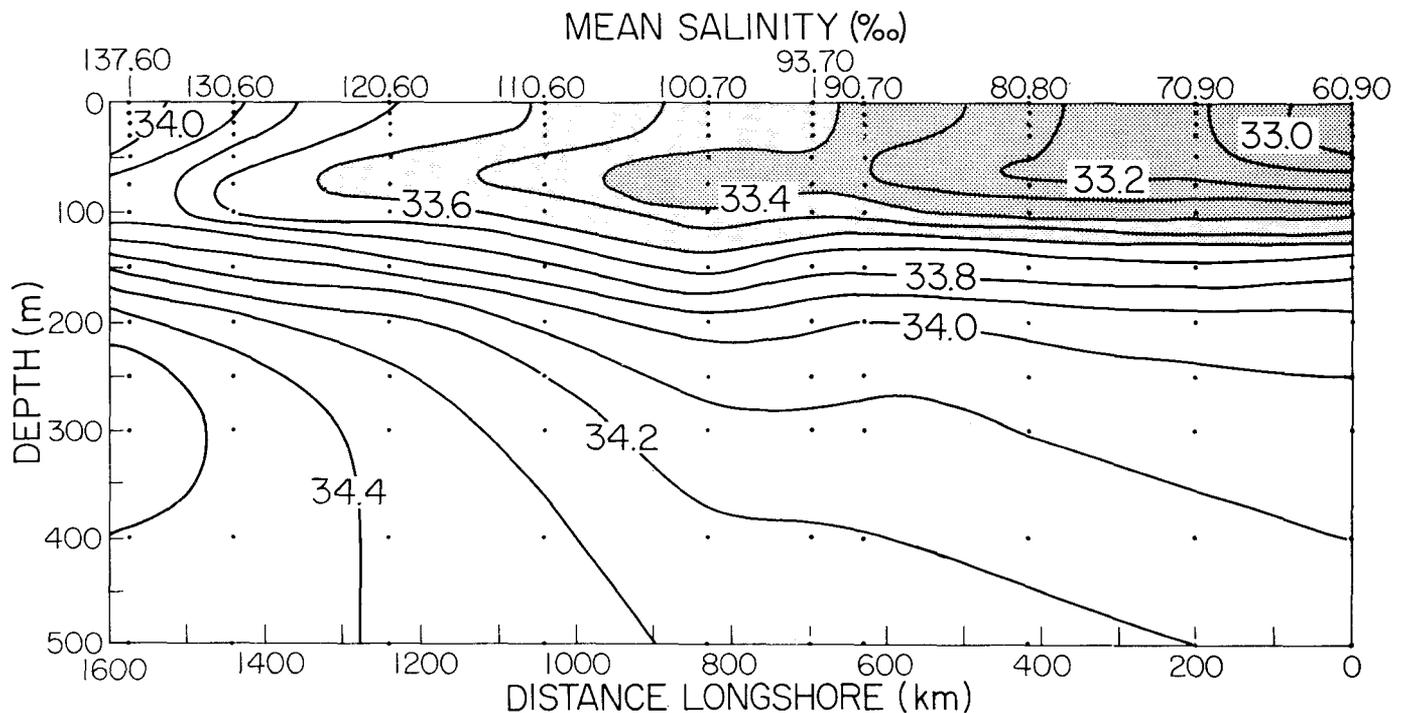


Figure 8. The mean longshore salinity distribution. The CalCOFI line and station numbers used in the figure are shown along the upper axis. (e.g. 100.70 refers to line 100 station 70).

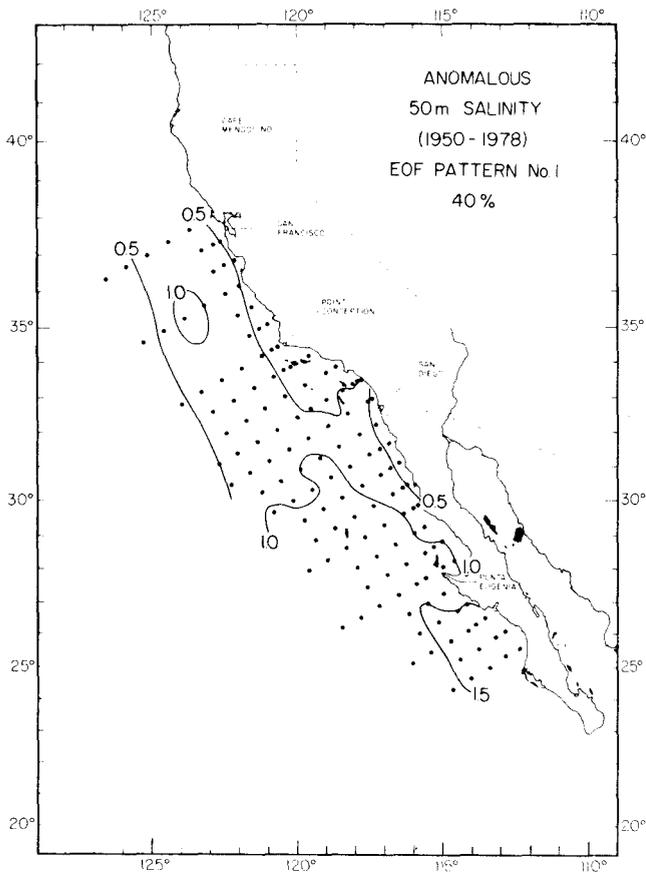


Figure 9. The principal spatial EOF of nonseasonal salinity at 50 m depth. As in Figure 6, the function values have been normalized to have mean square value of 1.

tance of advection has been indirect and purely qualitative. The large-scale anomalous variations in the flow of the California Current can be quantified by looking at the steric height, which gives an integrated measure of the effects of temperature and salinity. The steric height of the sea surface relative to a reference pressure surface p_o is computed by

$$h = -\frac{1}{g} \int_{p_o}^0 \delta dp$$

where δ is the specific volume anomaly defined to be departures of the reciprocal value of density from a standard ocean of temperature 0°C and salinity 35‰. The specific volume anomaly is a function of temperature, salinity, and to a lesser extent pressure. Warm or low-salinity water displaces a larger volume and causes the sea surface to stand higher than cold or high-salinity water. Horizontal gradients of steric height give a measure of the geostrophic flow at the sea surface relative to the reference pressure surface p_o .

The steric height relative to 500 db was computed at

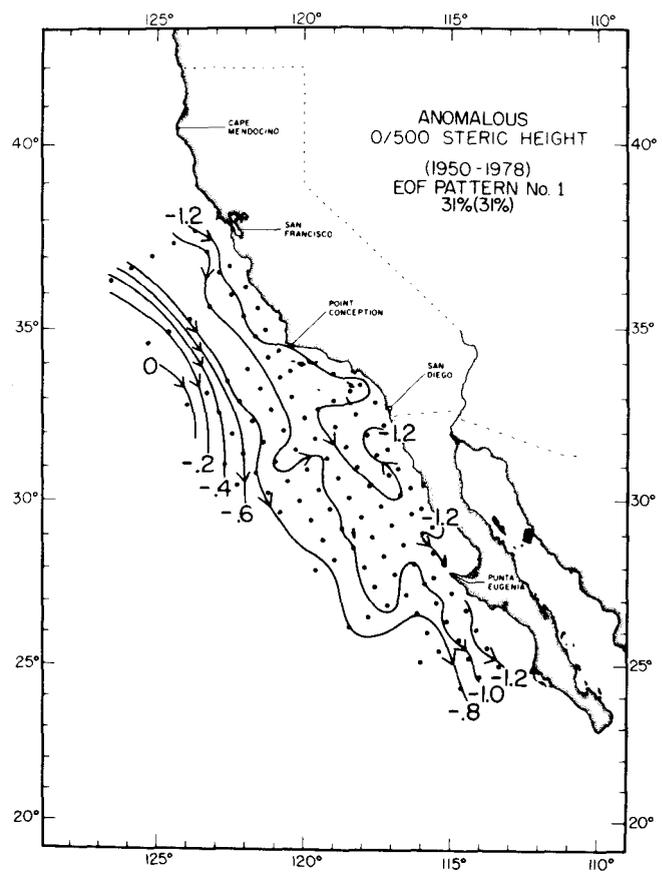


Figure 10. The principal spatial EOF of nonseasonal 0/500 db steric height. As in Figures 6 and 9, the function values have been normalized to have mean square value of 1. Arrows indicate direction of flow when the amplitude time series shown in Figure 5d is positive. Negative values of the time series correspond to a reversal in the anomalous flow (i.e. poleward transport).

each of the stations shown in Figure 2. The seasonal cycle at each station was then computed and removed in the same manner as for temperature and salinity. The dominant EOF of 0/500 steric height anomalies accounting for one-third of the variability is shown in Figure 10. When the time amplitude of this pattern is positive, the southward flow of the background California Current is intensified. Conversely, when the time amplitude is negative, the southward flow is weakened. A strong enough weakening could actually result in a reversal of the flow.

The time series associated with this pattern of anomalous large-scale advection is shown in Figure 5d where, for easy comparison, the zooplankton time series shown previously in Figure 5a have been reproduced as the triangles. The figure supports the hypothesis that increased southward advection leads to an increase in zooplankton biomass. Correspondingly, when the southward flow is below normal, so is the zooplankton biomass. The time-lagged correlation between the two time series is shown in Figure 11. The plot is distinctly asymmetric and indicates that

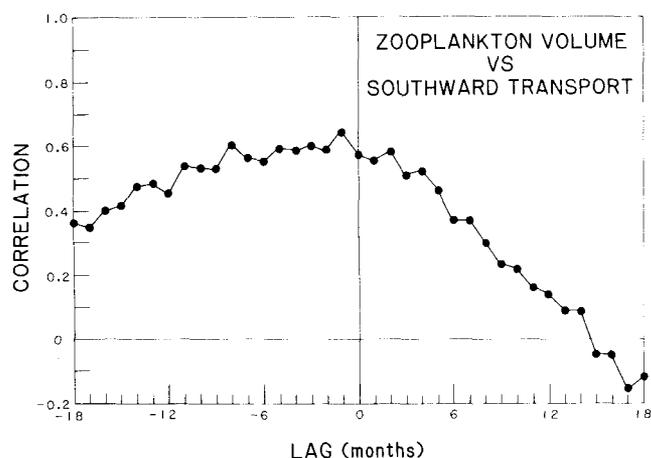


Figure 11. Correlation between large-scale zooplankton biomass in month t as shown in Figure 5a and anomalous southward transport of the California Current in month $(t+\text{lag})$. The index of southward transport is the EOF amplitude time series of 0/500 db steric height shown in Figure 5d.

zooplankton volume is more highly correlated with preceding than with subsequent anomalous flow. That is, the effects of advection on secondary productivity tend to persist for many months. A maximum correlation of 0.65 occurs when advection leads zooplankton biomass by one month. This correlation is rather impressive considering the serious sampling problems associated with both data sets.

It would clearly be advantageous to find a simple means of monitoring these large-scale changes in the flow without taking time-consuming and expensive hydrographic observations from ships. Two potentially useful land-based oceanographic measurements are coastal tide gauge-measured sea level and coastal sea-surface temperature. Figure 12a shows the correlations between sea level and sea-surface temperature at La Jolla and the index of large-scale advection shown in Figure 5d. Both the sea level and sea-surface temperature records have been low pass filtered with a one-year running mean, and the sea level data have been corrected for the inverse barometric effects of atmospheric pressure (1 cm/mb). The results yield further insight into the importance of advection. Both sea level and sea-surface temperature are significantly correlated with anomalous flow; low sea level and cold water are associated with increased southward transport. The interesting feature from Figure 12a is that changes in the flow follow changes in sea level by about one month but *precede* changes in sea-surface temperature by about two months. The lag between changes in flow and changes in sea-surface temperature supports the notion that the source of cold water anomalies in the California Current is advection rather than upwelling.

The correlations between sea level and sea-surface

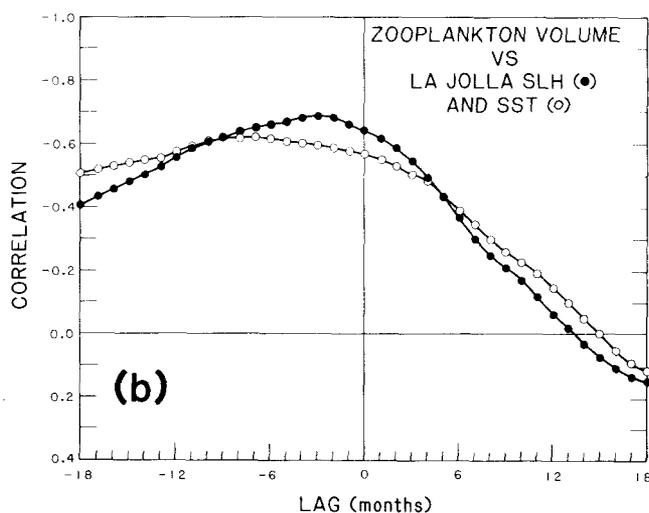
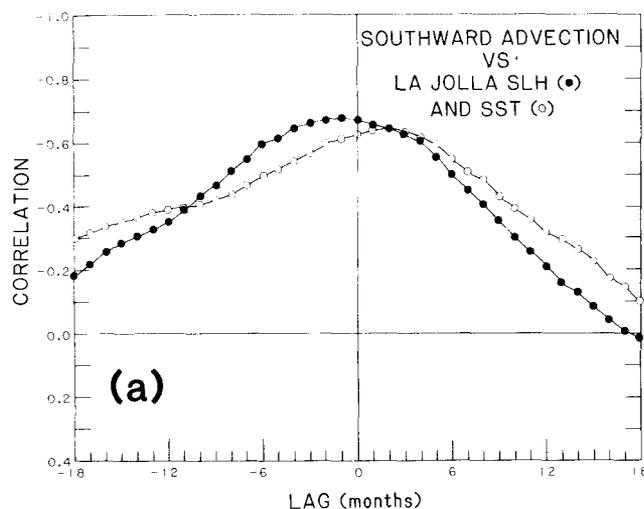


Figure 12. Correlations between sea level height (SLH) and sea-surface temperature (SST) in month $(t+\text{lag})$ at La Jolla, California, and a) the index of southward advection in month t shown in Figure 5d; b) large-scale zooplankton biomass in month t as shown in Figure 5a. The sea level data has been corrected for the inverse barometric effects of atmospheric pressure (1 cm/mb).

temperature at La Jolla and the large-scale variability of zooplankton biomass (Figure 5a) are shown in Figure 12b. The sea-surface temperature observations are somewhat noisy, and the zooplankton volume is more closely related to sea level which gives an integrated measure of upper ocean density variations. Sea level anomalies tend to precede changes in zooplankton volume by about three months. Note, however, that the frequencies involved are too low for this to be useful as a predictive tool.

The strong relation between sea level and anomalous flow of the California Current is further demonstrated in Figure 13. The vertical bars represent the index of southward advection shown previously in Figure 5d. The continuous curve represents a one-year running mean of the average of sea level (corrected for

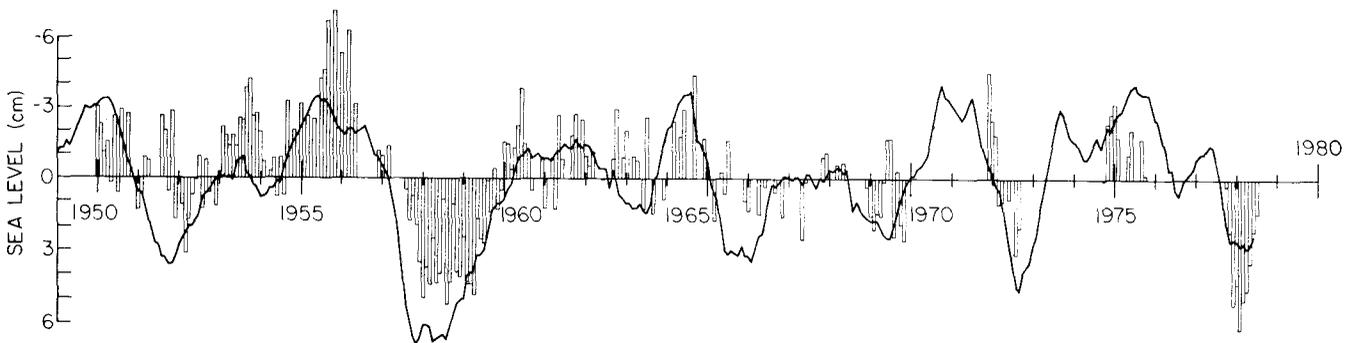


Figure 13. Time series of low-frequency (one-year running mean) sea level (corrected for inverse barometer effects) averaged over San Francisco, Los Angeles, and San Diego. The vertical bars represent the index of southward transport shown previously in Figure 5d. Note that the ordinate for sea level has been inverted; low sea level corresponds to above normal southward flow.

inverse barometric effects) at San Francisco, Los Angeles, and San Diego. Note that the ordinate of sea level has been inverted; low sea level corresponds to above normal southward flow and high sea level signals anomalous poleward flow.

Since tide records date back to the early 1900's, they can give some indication of large-scale changes in the flow of the California Current over the last 80 years. Figure 14 shows the average of sea level at San Francisco, Los Angeles, and San Diego from 1900 to 1979 (again smoothed by a one-year running mean). If these sea level variations can be interpreted as an index of secondary productivity, the figure indicates that very large biological changes occur on a regular basis and tend to persist for time scales of 1-3 years. It would be interesting to compare this time series with the anaerobic sediment records of biological debris described by Soutar (1971).

DISCUSSION

The preceding section has documented a significant interannual variability in both the physical and biological oceanography of the California Current. The results suggest that large-scale variations in zooplankton volume primarily reflect a response to nutrients advected downstream from high latitudes. When the flow weakens, the nutrient input decreases and so does the zooplankton biomass. This zooplankton response to nutrients is presumably indirect, reflecting a response of phytoplankton (the food source of zooplankton) to nutrient availability. The causes of these low-frequency changes in the flow have yet to be identified. Figure 4 indicates that they are apparently not forced by the local wind field.

However, using the sea level records as an index of flow, Figure 15 shows that the strength of the California Current is rather closely related to El Niño occur-

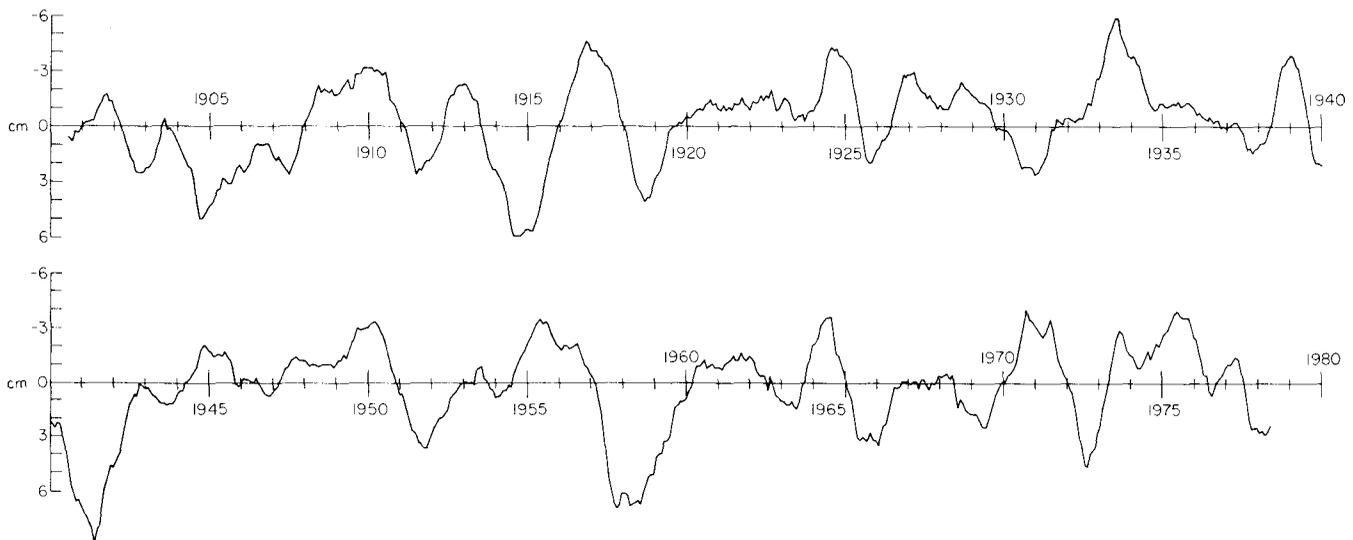


Figure 14. Low-frequency (one-year running mean) sea level averaged over San Francisco, Los Angeles, and San Diego from 1900 to 1979. With some caution, this time series can be taken as an index of large-scale biological changes in the California Current over the last 80 years. Note that the ordinate has been inverted; low sea level corresponds to above normal zooplankton biomass.

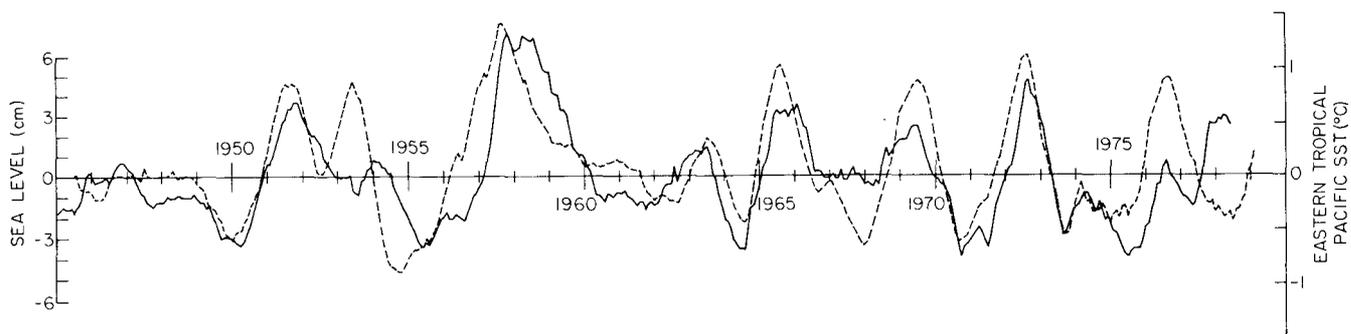


Figure 15. The time series of low-frequency sea level previously shown in Figure 13 (solid line) and low frequency (one-year running mean) sea-surface temperature in the eastern tropical Pacific (dashed line). Note that the sea level ordinate is no longer inverted as in Figures 13 and 14.

rences in the eastern tropical Pacific. The index of El Niño used here (the dashed line) is a one-year running mean of sea-surface temperature averaged over a region in the eastern tropical Pacific from the equator to 10°S and from 80° to 100°W. The major El Niño events of 1957-58, 1965, 1969, and 1972, as well as a number of more minor events are clearly evident in both time series. The correlation between these two time series is 0.72. Note that the ordinate for sea level is no longer inverted as it was in Figures 13 and 14. El Niño is associated with positive California sea level anomalies which (from Figure 13) correspond to anomalous poleward flow.

Figure 15 suggests a tendency for El Niño in the eastern tropical Pacific to lead California sea level by 2-3 months. This lagged relationship can be demonstrated more quantitatively through correlation analysis. Figure 16 is a contour plot of the time-lagged correlation between the El Niño index and low-frequency (one-year running mean) sea level at each of 20 stations from southern Mexico to the tip of the Aleutian Islands. The amount by which sea-surface temperature in the tropics leads sea level along the west coast of North America increases in a fairly systematic manner with increasing distance from the tropics. The El Niño signal in the tropics occurs nearly simultaneously with sea level anomalies at Acapulco but precedes sea level at San Francisco by about three months. The dashed line locates the approximate maximum lagged correlation and corresponds to northward propagation at a phase speed of about 50 cm/sec. This is the character of response expected from simple theoretical considerations which indicate that El Niño originates in that tropics from anomalous forcing by the trade winds. Sea-surface temperature and sea level rise in the eastern tropics, and these sea level anomalies propagate poleward as coastally trapped waves which lead to anomalous poleward geostrophic flow (McCreary, 1976).

Although this relation between El Niño and the strength of the flow off California is simple and ap-

pealing, there are several incidences where the relationship breaks down. Most notable are 1953, 1967-68, 1976 and 1978. Special attention will be focused here on the 1978 event when there was anomalous poleward flow (see Figure 13) which would be expected to occur during an El Niño. However, Figure 15 indicates that the water in the tropics was colder than normal indicating, if anything, the presence of an "anti-El Niño." A plausible explana-

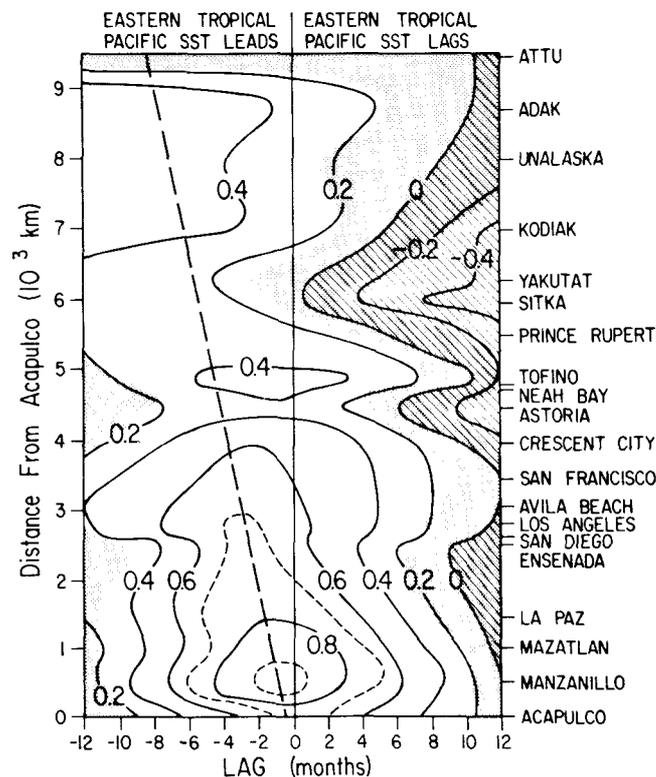


Figure 16. Contour plot of the correlation between low-frequency (13-month running mean) SLH in month t at each of the 20 tide gauge stations and low-frequency eastern tropical Pacific SST in month $(t + \text{lag})$. Shaded region corresponds to artificial correlation expected purely by chance from sampling errors, and cross hatching indicates negative correlations. Dashed straight line is meant to aid the eye in locating the approximate region of maximum correlation and corresponds to approximately 50 cm/sec northward propagation.

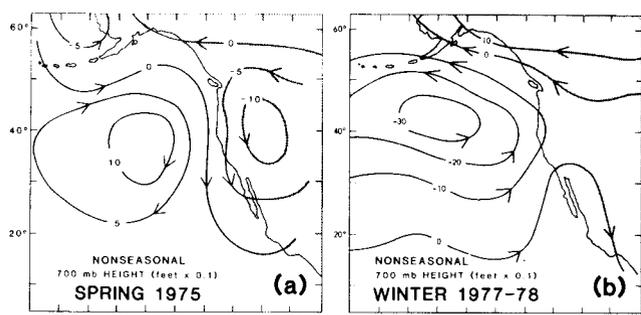


Figure 17. Contour plots of nonseasonal 700 mb height for a) spring of 1975 and, b) winter of 1977-78. Arrows indicate direction of nonseasonal upper air flow.

tion for the discrepancy can be found from an examination of meteorological records over the eastern Pacific. The anomalous 700 mb height taken from Namias (1979) for winter 1977-78 is shown in Figure 17b. The arrows indicate the direction of anomalous air flow in the upper atmosphere. There was a very large-scale air flow from the south which was responsible for the 1978 heavy rainfall in southern California (more than twice the normal value). These basin-wide winds would be expected to drive an anomalous poleward flow as observed during 1978. Recall from Figure 5 that the salinity behaved differently during 1978 than was anticipated from the advective model. The anomalous poleward flow would produce the observed increase in temperature at 50-m depth shown in Figure 5b by advection. However, an increase in salinity would also be anticipated but Figure 5c shows that in fact the salinity at 50 m decreased during 1978.

Figure 18 shows the time development of the vertical structure of temperature and salinity along CalCOFI line 93 during the winter of 1977-78. The temperature field for December of 1977 shows an increase nearshore and a decrease farther offshore. A maximum temperature anomaly of about 1°C occurred at a depth of about 100m which, as can be seen from Figure 7, corresponds to the depth of the permanent thermocline. This suggests that tilting of the isotherms was responsible for the temperature anomalies. During January and February of 1978 this anomalous temperature signal became better developed with warm water nearshore throughout the water column and anomalously cold water farther offshore throughout the water column. Again, the region of maximum anomaly is located at about the depth of the permanent thermocline reflecting the tilting of isotherms associated with geostrophic adjustment of the pycnocline to anomalous poleward flow. That is, with poleward flow, the isotherms nearshore tilt downward while those farther offshore rise toward the surface.

The salinity field cannot be explained in the same manner. In December of 1977 the salinity was near

normal. There is the hint of a tongue of low salinity water offshore at station 80 (unfortunately stations 90 and 100 were not occupied during December of 1977). By January and February of 1978 the low salinity anomaly was fully developed. A maximum of -0.4‰ occurred near the surface at the farthest offshore stations.

The combination of warm, low-salinity water near the surface cannot be explained by a local rearrangement of any of the water masses typically present in this region. It must be concluded that some new water was somehow introduced to the region. The heavy rainfall during winter 1977-78 would reduce the salinity of the surface waters but would not be expected to have much of an effect below the thermocline. However, Figure 18 shows that, although most of the decrease is concentrated near the surface, the anomalously low salinity extended throughout the water column. The magnitude of the anomaly at 500 m was around 0.02-0.04‰ during February of 1978. An estimate of the amount of excess freshwater from precipitation required to produce the observed anomalous salinity can be made by ignoring effects of advection and assuming that all mixing occurred locally. Then, the total amount of salt in the water column remains fixed so that

$$\iiint_{\text{Volume}} S dV = \text{Constant}$$

and the excess freshwater that must be added to an initial column of water of depth D_M and salinity S_M to produce an anomalous salinity S_A is given by

$$\Delta D = D_M \left(\frac{S_M}{S_A} - 1 \right).$$

The integrated effects of the observed anomalous salinity for February of 1978 from the mean February salinity distribution for the upper 500 m along line 93 are shown in Figure 19. Although the distribution of rainfall over the ocean is not well understood, the values shown in Figure 19 seem too high when compared with the precipitation values recorded at the coast. The excess rainfall in southern California amounted to about 0.5 m for the entire rainy season (late November through May). Figure 19 indicates that about 0.5 m of excess rainfall would be required prior to February to account for the observed salinity anomaly nearshore and about 1-2 m of excess rainfall would be required at the offshore stations. It is also difficult to explain how this freshwater could be mixed to depths of 500 m. So, although the high precipitation off southern California certainly contributed to the winter 1977-78 salinity anomaly near the surface, it cannot account for all of the necessary excess fresh-

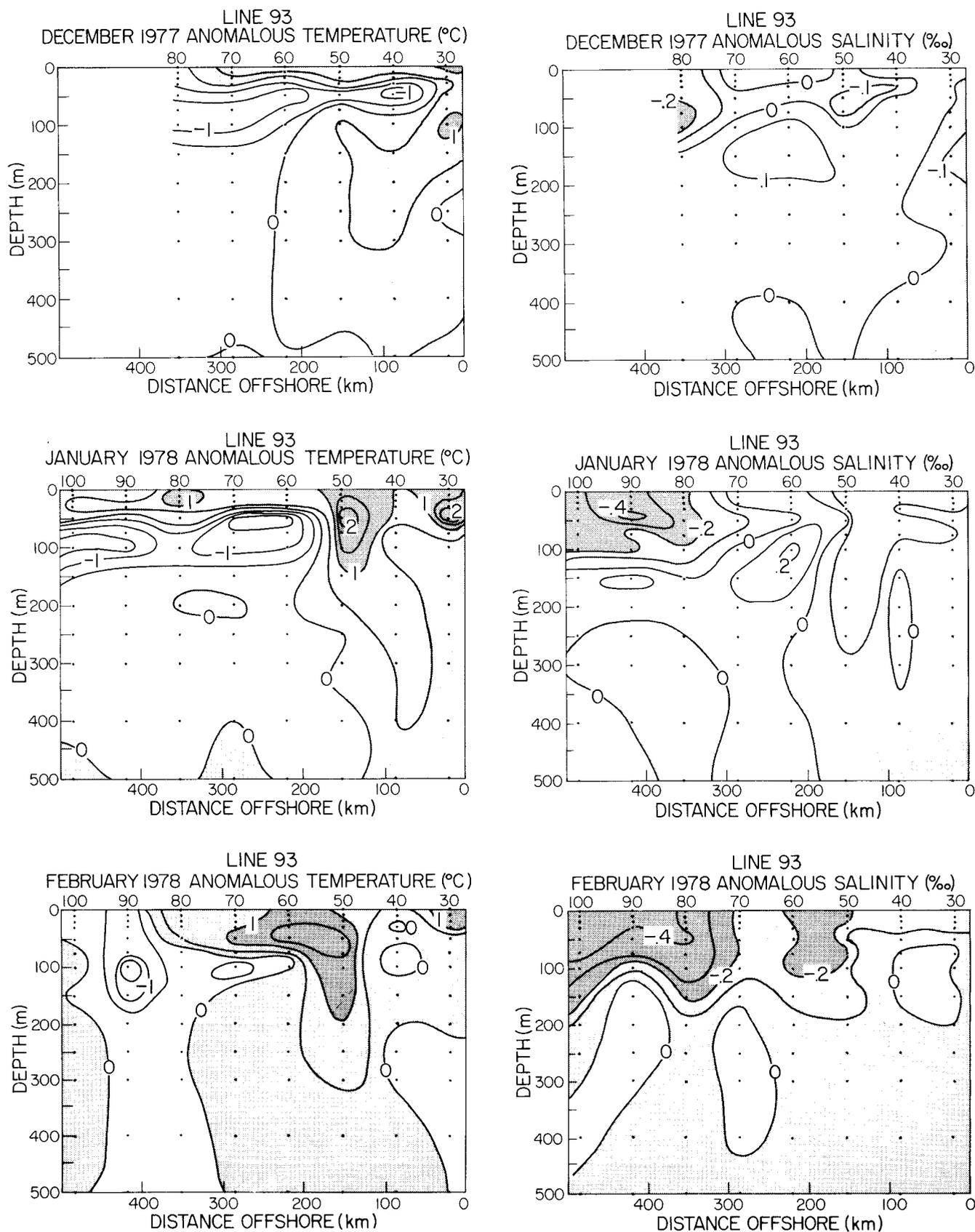


Figure 18. Anomalous temperature and salinity along CalCOFI line 93 for the months of December of 1977 and January and February of 1978. The CalCOFI station number is shown along the top of each plot. Positive temperature anomalies and negative salinity anomalies are shaded in the figures.

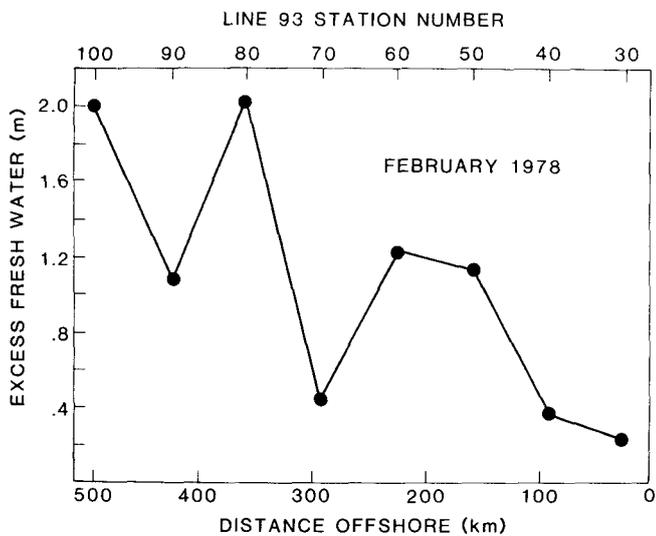


Figure 19. Excess freshwater required to explain the anomalous salinity of a column of water at each station along CalCOFI line 93 for the month of February 1978.

water. There must have been horizontal movement of freshwater into the region off southern California from some other region.

The source of this freshwater remains a mystery at the present time. Two plausible explanations can be proposed. The first is that the freshwater may have originated off the northwest coast of the United States from excess rainfall during the preceding summer. With a southward velocity of 20 cm/sec, water off the coast of Washington would reach San Diego 4-5 months later.

A second possible explanation is suggested by the large-scale wind pattern shown in Figure 17b. The southerly winds would drive an onshore Ekman transport, resulting in broad-scale downwelling conditions. This could produce the thin layer of warm water present near the surface everywhere during December of 1977 and January of 1978. And if the salinity was below normal in the offshore waters, it could also produce the observed salinity anomalies.

Unfortunately, the three-year sampling pattern subsequent to 1969 and the limited geographical extent of the CalCOFI program preclude the possibility of testing either of these hypotheses. Data from 1977 and data farther offshore are needed to look at the time evolution of the temperature and salinity fields leading up to the winter of 1977-78. The expendable bathythermograph (XBT) and surface salinity data collected from merchant ships by the National Marine Fisheries Service between San Francisco and Honolulu may shed some light on the processes leading to the 1977-78 winter conditions in the California Current.

It is worth pointing out that the temperature and salinity conditions in the California Current during 1975 are the reverse of those found in 1978. Figure 5d shows that the southward transport was higher than normal, so anomalously low temperatures and salinities would be anticipated. Figures 5b and 5c show that the 50-m temperature was about 0.5 degree below normal as expected but the salinity was about 0.1‰ higher than normal. Figure 17a shows that anomalous atmospheric conditions during spring 1975 were also the reverse of those found in winter 1977-78, with large-scale northerly air flow off the coast of California. This suggests that there might be a connection between the atmospheric and oceanic conditions and the physical processes responsible for both anomalies. This discussion has been purely qualitative based on case studies from only two events and is certainly worthy of more detailed study. But it does point out the lack of a complete understanding of all of the large-scale processes in the California Current. A quantitative index of the large-scale aspects of atmospheric forcing in a time series sense would allow a statistical comparison between this broad-scale wind forcing and the biological and physical oceanography of the California Current.

SUMMARY

In summary, it has been demonstrated here that increased zooplankton volume is associated with a decrease in water temperature. The two potential sources of this cold water (upwelling and advection) produce opposing effects on the salinity distribution; advection of high-nutrient water from high latitudes would decrease the salinity, whereas upwelling of deeper high-nutrient water would result in an increase in salinity. Local coastal upwelling appears to be poorly related statistically to the zooplankton variability. It is concluded that large-scale advection plays the dominant role in controlling zooplankton biomass in the California Current. These large-scale variations are significantly related to El Niño occurrences in the eastern tropical Pacific and can be conveniently monitored from coastal tide gauge records along the California Coast.

A great deal of attention was drawn to the anomalous conditions in the California Current during 1978. Temperature and salinity anomalies generally tend to be of the same sign. That is, anomalously cold water generally tends to be low in salinity, reflecting higher latitude origin. Similarly, anomalously warm water generally tends to be high in salinity, reflecting low-latitude origin. However, during 1978 the water in the California Current was unusually warm but low in salinity. It was shown that anomalous rainfall during

the same time period cannot account for all of the salinity anomaly. It was suggested that the excess freshwater required to produce the observed salinity anomaly must have been transported horizontally into the region either by downstream advection or by on-shore Ekman transport driven by anomalous wind forcing. Similar but opposite conditions existed during 1975: anomalously cool water was high in salinity.

An important result of this study is that it points out some limitations in the present three-year CalCOFI sampling pattern. In particular, the three-year spacing is not adequate to determine the physical processes responsible for the anomalous events of 1975 and 1978. It also points out that, although the dominant patterns of physical and biological variability have been drawn out in this analysis, there are still other important large-scale processes occurring that are not yet understood.

ACKNOWLEDGMENTS

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A REVIEW OF THE LOW-FREQUENCY RESPONSE OF THE PELAGIC ECOSYSTEM IN THE CALIFORNIA CURRENT

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ABSTRACT

Recent analyses of CalCOFI data collected during the last three decades have revealed the existence of long-period fluctuations occurring in the California Current. This paper reviews the biological response of the ecosystem to these fluctuations in terms of zooplankton biomass, which is shown to have large-scale, low-frequency trends.

This low-frequency response is found to be coherent with interannual changes in flow pattern occurring in the Eastern Boundary Current. The ecological implications are that the California Current ecosystem might be permanently under nonequilibrium conditions, which in turn would suggest that the classical biologically interactive processes of competition and predation are only secondary mechanisms in regulating plankton abundance and species proportions.

RESUMEN

Recientes análisis de los datos colectados durante las tres últimas décadas por CalCOFI han revelado la existencia de fluctuaciones de período largo en la Corriente de California. En este trabajo se reexamina la respuesta biológica del ecosistema a estas fluctuaciones en términos de la biomasa del zooplancton, datos que muestran modos de variación de gran escala y baja frecuencia.

La respuesta de baja frecuencia es coherente con cambios interanuales en el patrón de circulación que tienen lugar en toda la Corriente de Margen Oriental. Las implicaciones ecológicas son que el ecosistema de la Corriente de California estaría en forma permanente bajo condiciones de desequilibrio, lo que a su vez sugiere que los procesos biológicos interactivos clásicos, competencia y depredación, serían solamente mecanismos secundarios en la regulación tanto de la abundancia como de las proporciones de especies en el plancton.

REVIEW

Introduction

After the disappearance of the Pacific sardine fishery from the coast of California, The California

Cooperative Oceanic Fisheries Investigations (CalCOFI) were started with the intention of monitoring the reproductive success of the pelagic stocks inhabiting the region. Since 1949 CalCOFI has accumulated a huge amount of information on a series of physical and biological variables of the California Current System. The long time series resulting from this effort and the information contained are unique compared to the usual temporal scale of oceanographic observations.

From the point of view of fisheries research, it is of primary importance to predict with relatively high precision the changes of the stocks under exploitation. Fisheries models based on stock-recruitment relationships show adequate predictive abilities for some types of stocks, in particular demersal fish. However pelagic stocks seem to be more variable, and standard techniques do not provide consistently reliable answers for management purposes. From the theoretical side of the problem, a review of classical theory is long overdue in order to remove these models from the relative "ecological vacuum" where they were designed to function. From the empirical side, therefore, consideration of other aspects of the problem, such as density independence and other ecological factors, are still needed and useful. Analysis of the long time series of zooplankton biomass collected by CalCOFI provides some insights into the kind of variability observed at the ecosystem level in the interannual and interdecadal time scales. These have been shown to be important time scales for the fluctuation of some fish stocks (Parrish and MacCall 1978; Cushing 1976).

My work, together with that of Dudley Chelton, has coalesced into a single characterization of an important low-frequency mode of variability observed in this region that is coherent for the physical and biological components of the system. In this presentation I will discuss first the spatial and temporal scales relevant to the problem, then review the work done to characterize the low-frequency response of the ecosystem, and finally present evidence of the causal connections that this mode of variability seems to have and discuss its implications.

The work presented in this review has had several antecedents. Among them are the studies by Reid et

al. (1958), Wickett (1967), and Colebrook (1977), all of which indicated that some large-scale, low-frequency events were occurring in the biota (see also the papers presented at the Symposium on The Changing Pacific Ocean in 1957-58, held at Rancho Santa Fe, June of 1958, in *CalCOFI Reports*, Volume VII, 1960). More recently, longer time series of data have been analyzed (Bernal 1979, 1980; Bernal and McGowan in press; Chelton 1980, 1981), and that work is reviewed here.

Spatial Boundaries of the California Current Pelagic Ecosystem

At subtropical latitudes in the eastern half of the North Pacific there are at least two well defined

oceanic plankton communities: the assemblage of the Central Water mass and the assemblage of the California Current System. These assemblages inhabit two drastically different environments, the former in oligotrophic waters showing a well developed halocline underlying high salinity and warm waters at the surface. The latter lies within waters of low salinity, cold, and with high nutrients and dissolved oxygen concentrations. Figure 1 shows a section extending from 74 km offshore the California coast to a point well out into the North Pacific Central Gyre. Shoreward of 126° W there is a well developed surface low-salinity minimum (upper panel), a feature typical of the California Current, and beginning at 138° W, 1,570 km offshore, the well developed halocline typi-

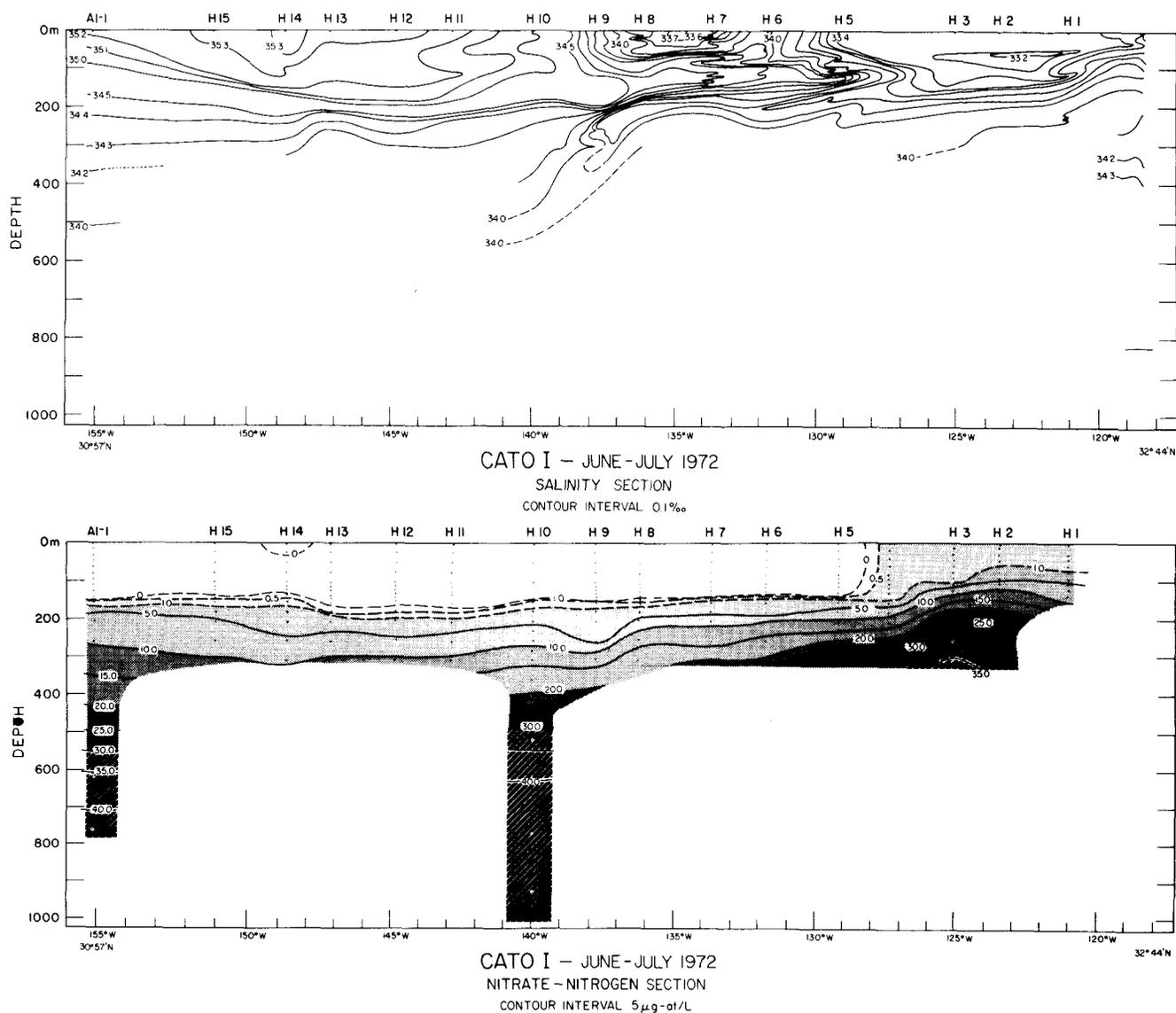


Figure 1. Sections of salinity and nitrate-nitrogen between San Diego and the Central Gyre of the North Pacific (155°W 30°57'N). Upper panel: distribution of salinity; between the most inshore station (right) and station H5, located 800 km offshore, waters of subarctic origin are present. Lower panel: distribution of nitrate-nitrogen expressed in µg-atoms/liter. Data collected during expedition CATO-I from Scripps Institution of Oceanography. (From Bernal and McGowan, in press.)

cal of the North Pacific Central Water mass appears. The nitrate concentration (lower panel) in the low-salinity area clearly differs from the oligotrophic Central Gyre, where the concentration of nitrate in the surface layer is uniformly below the level of detection of analytical techniques. Two interesting points are well illustrated here: first, that there is good agreement in the offshore extension of the surface low-salinity minimum and the area of enrichment in the California Current (nitrate above $0.5 \mu\text{g-atom/liter}$) and second, that both boundaries lie about 820 km offshore (station H5).

To illustrate the typical cross-shore dimensions of the region of high production in the California Current ecosystem, two sets of replicate monthly samples of zooplankton collected along CalCOFI lines 60 and 90 during spring-summer are shown in Figures 2 and 3. These cross sections begin a few kilometers from the coast and extend more than 1,000 km offshore, thus sampling the western boundary of the ecosystem. These sections of zooplankton biomass are accompanied with information describing the cross-shore patterns of transport during July. The average integrated transport from 0 to 200 m was calculated from CalCOFI's dynamic heights data files (1950-78) assuming the existence of a level of no motion at 500 db. The units of transport are Sverdrups (Svd) per 100 km of cross section, positive values indicating

southward flow.

In Figure 2 the maximum of biomass occurs well offshore from the coast at about 180 km, and the region of high biomass (greater than $200 \text{ ml}/1,000 \text{ m}^3$) extends up to 500 km. Seaward than 800 km, the biomass reaches values typical of the Central Water mass of the North Pacific. Inshore of 180 km the dominant flow is northward, and its mass transport is about $0.45 \text{ Svd}/100 \text{ km}$. Offshore of 180 km the flow is southward at about $1 \text{ Svd}/100 \text{ km}$. In a comparison of upper and lower panels, it is noteworthy that the first maximum of biomass at 180 km (A in the figure) and a secondary maximum at 400 km offshore (B) coincide with areas where the cross-shore gradient of average transports is also maximum. In A the gradient is associated with the edge between the Davidson Current and the California Current itself; in B with the westward boundary of a region of intensified southward flow located between 350 and 400 km offshore. These maximum gradients of average flow, although not strictly comparable with maximum shear, point to regions where turbulent mixing might become a three-dimensional process and the vertical introduction of nutrients from below could be enhanced. In Figure 3 the patterns along CalCOFI line 90 are shown. These somewhat parallel those described for line 60, the high biomass zone (greater than $150 \text{ ml}/1,000 \text{ m}^3$) extends from 100 to 350 km offshore with two maxima. The maximum inshore (A in the figure) here again coincides with the edge of the northward flow, but the second, in contrast with line 60, coincides with the maximum of southward flow at 270 km (B).

An important feature common to both lines is the

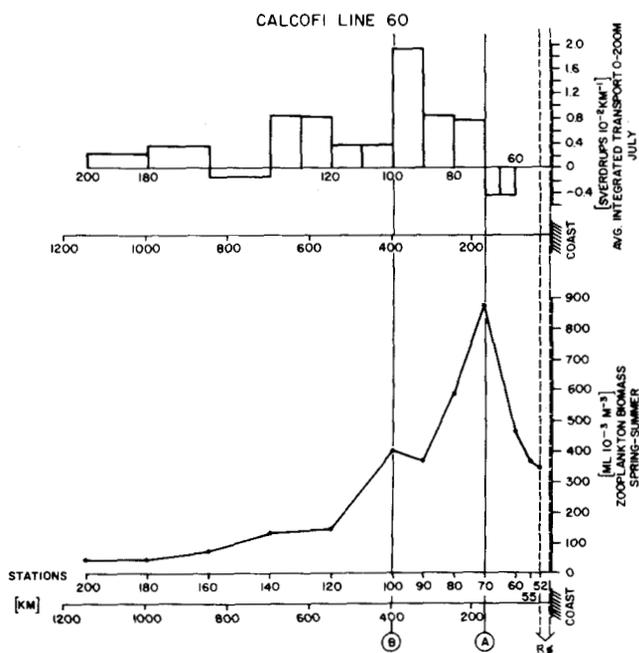


Figure 2. Average longshore transport and zooplankton biomass across CalCOFI line 60 during spring and summer. Positive values of transport indicate southward flow. R_ϕ is the distance equivalent to one local baroclinic Rossby radius of deformation. A and B label regions discussed in text. (From Bernal 1980.)

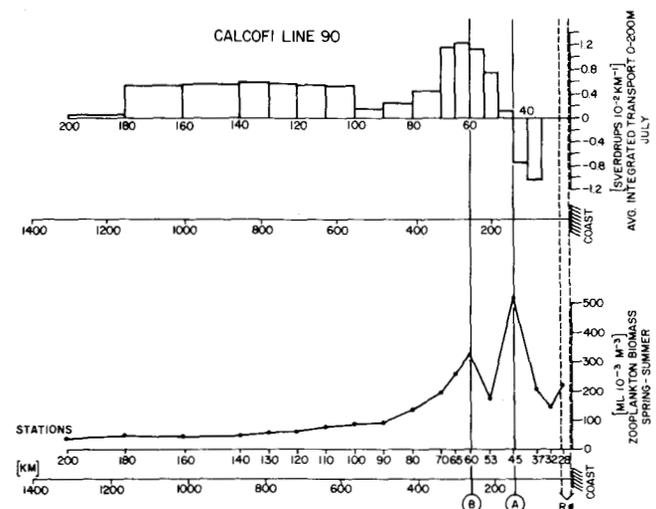


Figure 3. Average longshore transport and zooplankton biomass across CalCOFI line 90 during spring and summer. (From Bernal 1980.)

relative scale of the zone influenced by coastal upwelling when compared with the width of the zone of high biomass, since for eastern boundary currents like the California Current, coastal upwelling is the process usually associated with the introduction of non-regenerative nutrients into the euphotic zone. Coastal upwelling occurs in a narrow boundary region with typical cross-shore horizontal scale of the same order of magnitude as the local baroclinic Rossby radius of deformation R_ϕ (Yoshida 1955; Allen 1973; O'Brien et al. 1977). Estimates of this length scale parameter are illustrated in Figures 2 and 3 by a band adjacent to the coastline. The width of this band is one order of magnitude smaller than the zone of high biomass. In Figure 3 there is a small maximum of zooplankton biomass, within one R_ϕ -distance from the coast, which is separated from the bulk of the biomass and the two larger offshore maxima by a biomass minimum located at 70 km offshore. This feature does not appear in line 60.

Figure 4 shows the distribution patterns of phytoplankton and zooplankton biomass in the horizontal and the extension of the low-salinity water in the region during April of 1963. Despite significant meso-scale structure in the zooplankton distribution, these maps reflect the major trends and patterns described above for the sections. For example, in the northern region between San Francisco (line 60) and Point Conception (line 80) the contour of 0.10 mg/m^3 of chlorophyll-*a* is found up to 460 km offshore. Similarly, the region of high zooplankton biomass extends farther offshore than 350 km. The cross-shore dimension of the large extension of the low-salinity water of subarctic origin is quite apparent, extending at least 500 km offshore. There is another feature yet illustrated in this figure: the north-south trend of decreasing zooplankton biomass that can be seen (insert, zooplankton biomass map) where the average biomass per each 10 latitudinal lines are summarized in a bar graph. Between San Francisco and Point Conception the average values are over 600 ml/1,000 m^3 whereas in the Southern California Bight and off Baja California values less than 200 ml/1,000 m^3 are the norm. This trend is certainly one of the dominant features of the ecosystem since it persists when regional averages for the whole 1949-78 period are considered.

As the main conclusions of this section we can extract the following: First, the width of the region of high biomass characteristic of the California Current pelagic ecosystem extends a distance offshore at least eight and, depending on the latitude and season, ten times the local baroclinic Rossby radius of deformation, R_ϕ , (500 km and 50 km respectively). Second, the locus of highest biomass in the cross-shore direc-

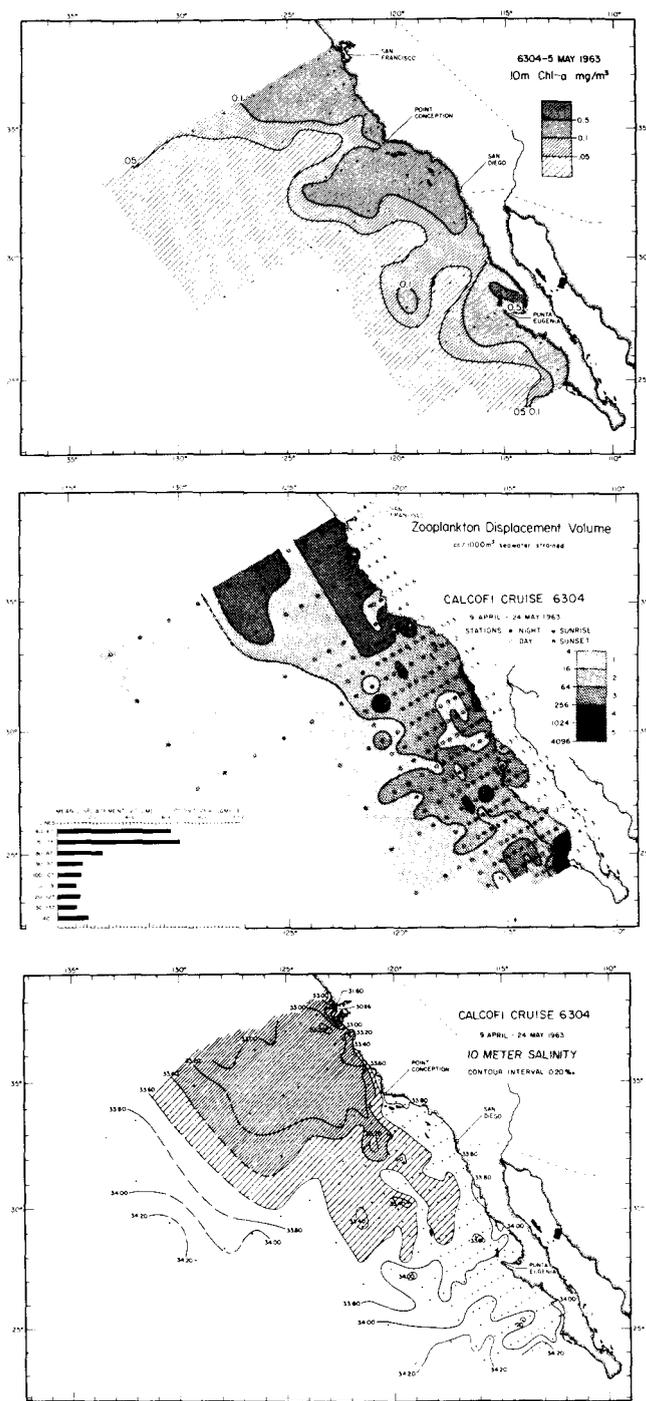


Figure 4. Horizontal distribution of phyto- and zooplankton biomass and 10-m salinity in the California Current region, April-May 1963 (CalCOFI cruise 6304). *Top*: phytoplankton biomass estimated as chlorophyll-*a*: units are mg/m^3 . *Middle*: zooplankton biomass in ml/1,000 m^3 . *Bottom*: salinity at 10-m contour intervals each 0.20 ‰ ; dark shading indicates salinities less than 33.40 ‰ ; light shading between 33.40 and 33.60 ‰ . (From Bernal and McGowan, in press.)

tion is consistently located offshore at a distance equivalent to at least 3 to $4 R_\phi$. Third, the dimensions of the region with detectable nutrient concentrations and high phyto- and zooplankton biomass corresponds

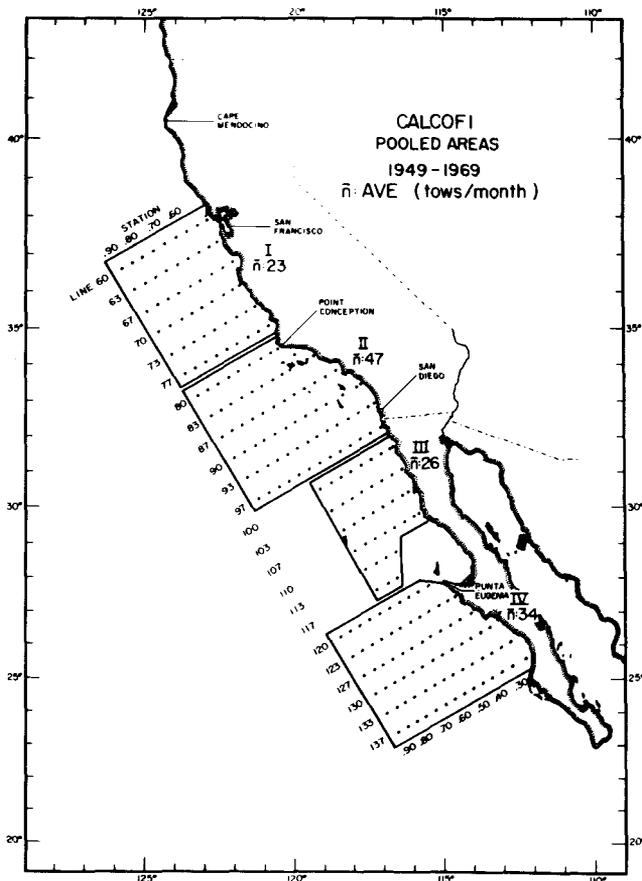


Figure 5. CalCOFI pooled areas. Dots mark positions of CalCOFI stations defined by line number on the left margin and by station number on top and bottom. Since not all stations within an area were occupied each cruise, average number of occupancies per month is given as *n*. (From Bernal 1980.)

with the areal extension of a water mass that has a northern origin. Fourth, there is a north-south trend of biomass with higher values in the north.

The Low-Frequency Response of the Pelagic Ecosystem

In a previous paper (Bernal 1979), using the offshore boundaries defined in the preceding paragraph and biogeographical information from the literature, I divided the CalCOFI sampling grid into four geographical areas and generated for each one of them time series of zooplankton biomass extending from 1949 to 1969. Figure 5 shows these areas. Each element of these time series is the average over space of the log-transformed zooplankton biomass of all the stations occupied within each area on a given month. This treatment filters out the short-term and small-scale spatial variability.

Since in the California Current ecosystem there is a well defined seasonal response, an evaluation of its importance was made. In Table I, the total and seasonal variability of the series are compared. The pro-

TABLE 1
 Total and Seasonal Variability Per CalCOFI Area

	Uncorrected series sum squares	Seasonally corrected sum squares	Seasonality sum squares	% total
Area I	43.9	30.7	13.2	30.0
Area II	79.9	61.7	18.2	22.7
Area III	84.6	77.5	7.1	8.4
Area IV	44.8	38.7	6.1	13.6

cedure used consisted of calculating the total variance, subtracting the seasonal component from the series, and recomputing the variance of the new seasonally corrected series. By difference an estimate of the magnitude of the seasonal component for each area is obtained. The seasonal component is more important in the northern part of the region (Area I, 30%) and is less important to the south (about 10%). On the average for the whole California Current ecosystem, seasonality represents less than 20% of the total variability, and given the pattern of distribution of biomass in the cross-shore direction and the very large extent of the areas upon which the series were constructed (between 100,000 to 200,000 km² each), it can be concluded that the nonseasonal variability is the dominant and most important component of the total response of the ecosystem.

Figure 6, illustrating the four seasonally corrected time series for Areas I through IV, shows that there are large-scale, low-frequency (i.e. long periods) trends. Particular years, 1950, 1953, and 1956, have simultaneous maxima in at least two of the areas; years 1958 and 1959 show coherent sets of minima in all four areas. A more systematic and objective inspection was performed using spectral analysis, the results of which are reproduced in Table 2. The main feature of the spectra is that a large fraction of the total variance lies within the low-frequency band, i.e. less than 1.6×10^{-3} cycles/day, or with characteristic periods larger than 608 days. The north-south trend of biomass is paralleled by an increasing proportion of the total variance clustered in the low-frequency band. We have discussed elsewhere (Bernal and McGowan, in press) the reasons why we think this phenomenon represents the response of the ecosystem to external driving. If

TABLE 2
 Percentage of Total Variance in Low-Frequency Bands of the Spectra

	Frequency (cycles/day)		
	<0.0008	0.0008-0.0016	<0.0016
Area I	16.75	18.17	34.93
Area II	44.72	11.72	56.43
Area III	46.10	8.18	54.28
Area IV	53.97	3.27	57.24
Characteristic periods (days)	>1217	1217-608	>608

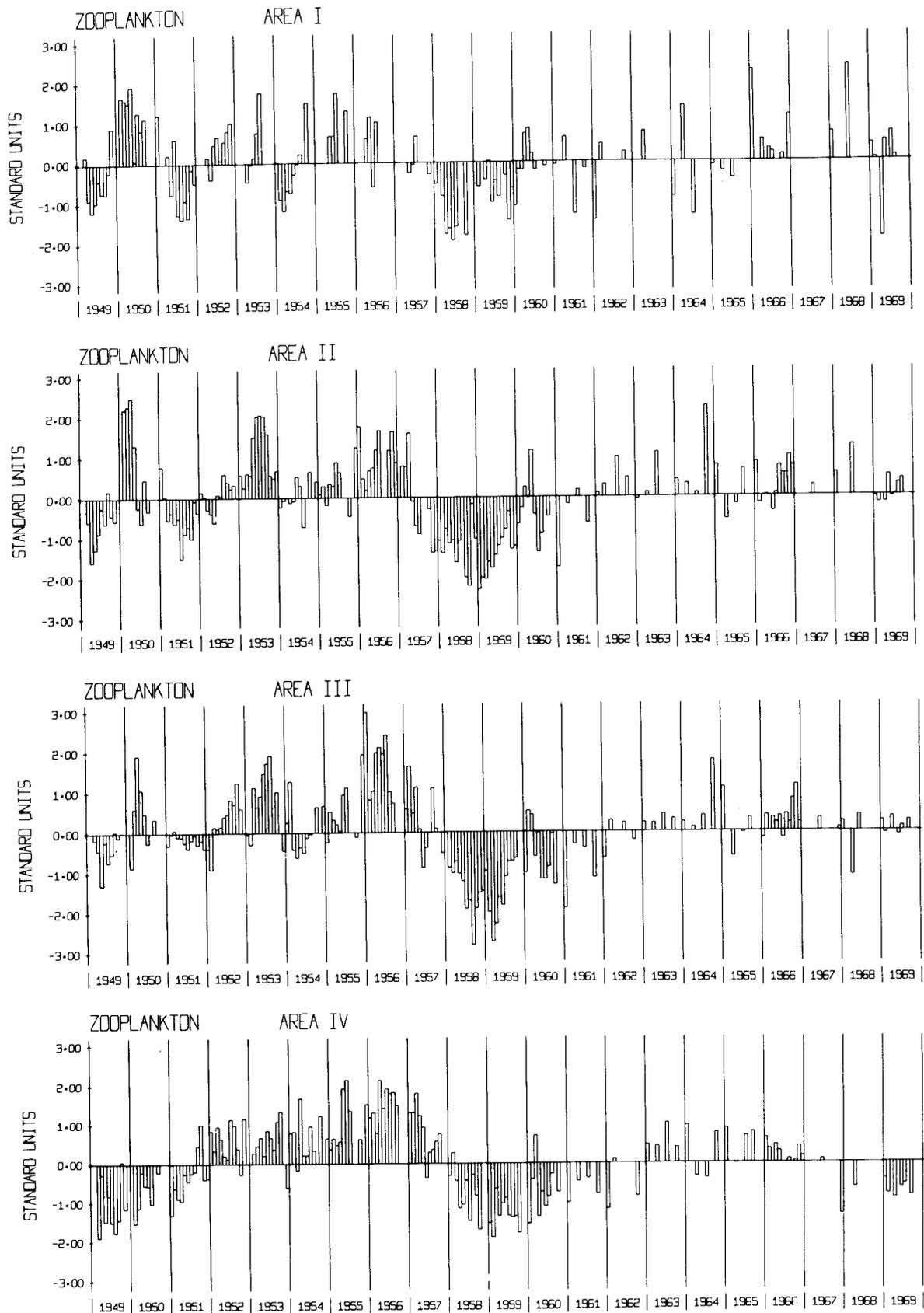


Figure 6. Seasonally corrected time series of zooplankton biomass. These are anomalies calculated as difference with respect to corresponding long-term monthly average. Magnitude of this variable given in standard units; hence, value of 1.00 is equivalent to one standard deviation from the mean. (From Bernal 1980.)

this assumption is correct, the results of the spectral analysis say that a significant proportion of the total variability of planktonic biomass should be driven by a low-frequency physical process dominant on an inter-annual time scale, in any case with characteristic periodicity greater than 608 days.

Walsh and Howe (1976) and Walsh (1977) have proposed a hypothetical spectrum of physical forcing functions, presumably connected to the major biotic compartments of the pelagic ecosystem in Eastern Boundary Currents. The spectrum proposed by these authors predicts a broad spectral peak between 0.016 and 0.060 cycles/day, associated with the zooplankton response. Our results strongly contradict this hypothesis, since Table 2 show that close to 50% of the nonseasonal variability is clustered below 0.0016 cycles/day, an entire order of magnitude below the prediction. Furthermore, the low-frequency component cannot be an artifact of the elimination of seasonality, since this component only accounted for 20% of the total variance, meaning that at least 40% of the total variance, seasonality included, is clustered in the low-frequency band.

Coastal Upwelling and Horizontal Advection as Forcing Functions of the Low-Frequency Response of the Ecosystem

The presence of a dominant low-frequency response of the pelagic ecosystem of the California Current poses the question: what is the forcing mechanism driving the system in this frequency domain? The first step to answer this question is provided by the existence of a significant negative correlation between sea-surface temperatures and zooplankton biomass (Reid et al. 1958; Reid 1962). However this correlation by itself, interesting as it is, does not allow us to differentiate between the two causal mechanisms potentially involved with the input of nonregenerative nutrients; namely coastal upwelling and large-scale horizontal advection from the north, since both processes by lowering the sea-surface temperature, could have forced the statistical association. I have attempted to resolve this dichotomy by assuming, first, that variations in coastal upwelling intensity are the dominant process and, second, by assuming that large-scale advection (and eventual mixing) of cold, low-salinity, high-nutrient water from the north is the dominant process. The method used was, first, to perform time-lagged correlations with the time series of zooplankton biomass as the dependent variable and the index of coastal upwelling derived from the Ekman layer model (Bakun 1973, 1975) and second, to perform the same correlations with indices of horizontal advection as independent variables. Two separate in-

dices of advection were used.

Figure 7 shows the time series of coastal upwelling indices computed at locations within each of the four areas described above. These series were treated in the same way as zooplankton data; i.e. seasonality was subtracted by the same methods and they were standardized to mean zero and unit standard deviation. Figure 8 shows the cross-correlation functions of zooplankton and upwelling, with time lags from 0 to 18 months. Almost none of the values were significantly different from zero at the 95% level. This result represents a strong rejection of the hypothesis that coastal upwelling is the principal physical mechanism responsible for the input of nonregenerative nutrients into the ecosystem. For the sake of completeness and brevity, I will only mention that a measure of offshore or average upwelling, a type of vertical motion driven by the local curl of the wind offshore (Yoshida 1955), is also uncorrelated with the biomass series (Bernal 1980).

Since there is abundant circumstantial evidence that large amounts of cold, low-salinity, high-nutrient water enters the system from the north and northwest, it is reasonable to attempt the same kind of analysis with measures of horizontal transport from the north. I have used the 33.40 o/oo isohaline as an index of the degree of penetration of these northern waters. Figure 9, modified from Wyllie and Lynn (1971), shows the sections of average salinity across four CalCOFI lines, where the extension and depth of the surface low-salinity minimum and its gradual disappearance to the south are evident. Using this marker, its variability, and the CalCOFI data files of steric heights, an index of transport of northern waters was calculated. First, for each month the geostrophic transport across a section off Point Conception (line 80) was computed, then with the information from the observed salinity field along the same section, the transport associated with waters less than 33.40 o/oo in the upper 200 m was obtained by numerical integration. These transport estimates, expressed in Sverdrups per 100 km of cross-shore distance, were also seasonally corrected and standardized to zero mean and unit standard deviation. Figure 10 shows the time series of this index, and Figure 11 the cross-correlation functions with zooplankton biomass as dependent variable. The results for northern Area I, although having some significant but very low correlations at lags 2 and 5 months, indicate that here the zooplankton is not predicted very well by the index: this might be due to the fact that line 80 lies downstream from the area. However, in Areas II and III the cross-correlation function attains highly significant values of $r(t)$ [$r(t) \neq 0$; $P \leq 0.05$] uniformly in lags from 0 to 7 months in

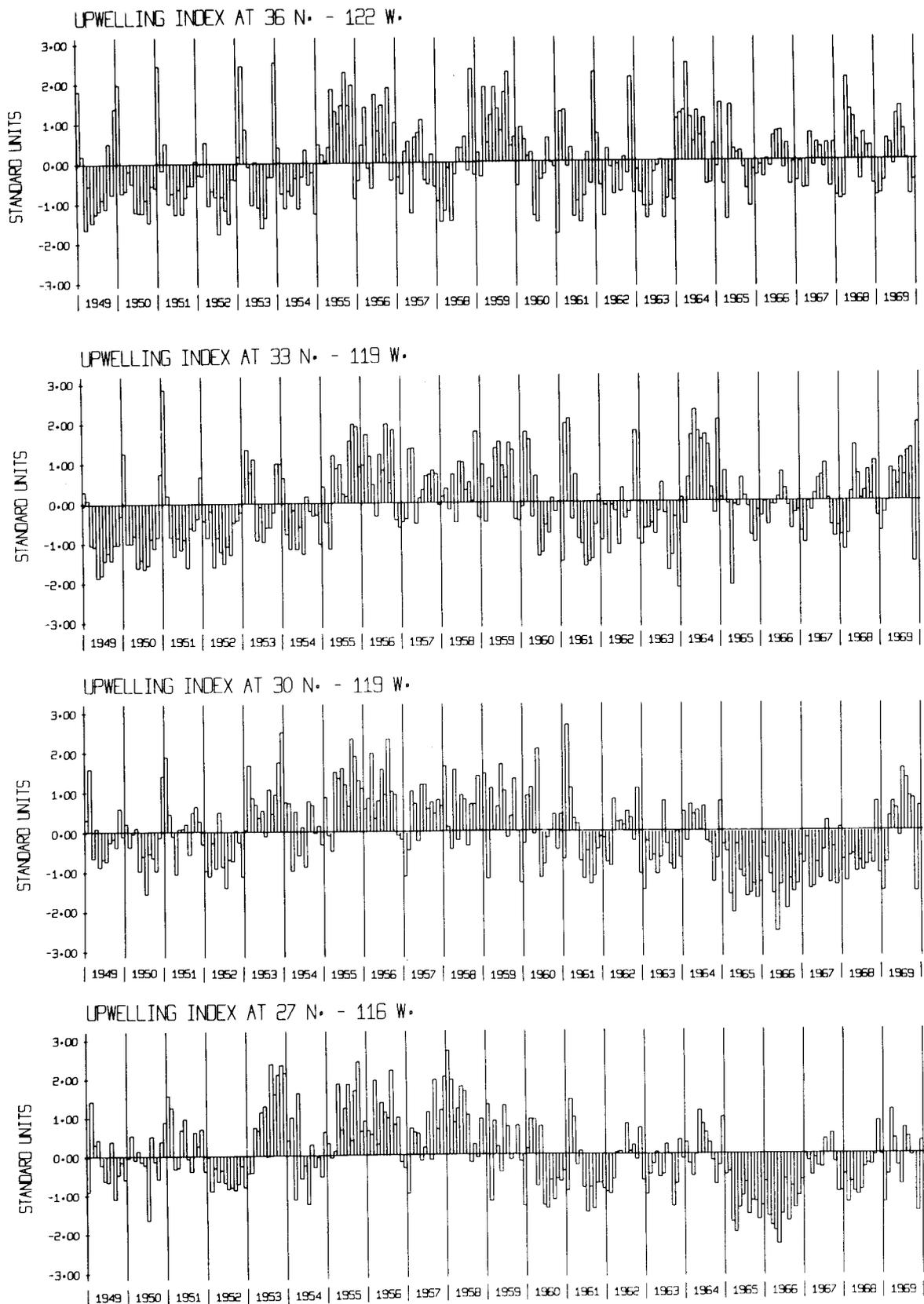
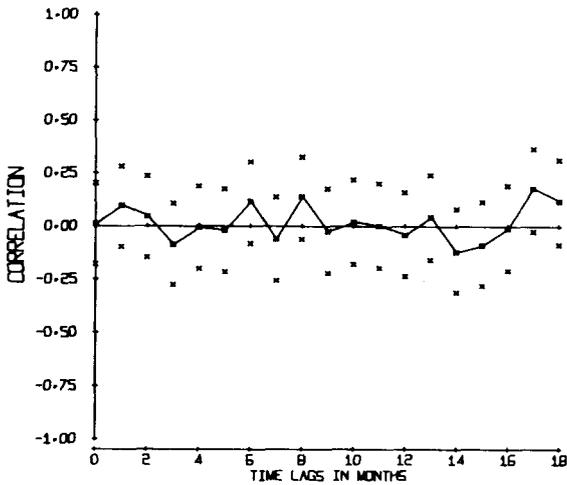


Figure 7. Seasonally corrected time series of upwelling indices. These indices derived by Bakun (1973, 1975), using a wind-driven coastal Ekman layer model. The series have been standardized and therefore have zero mean and unit standard deviation. (From Bernal 1980.)

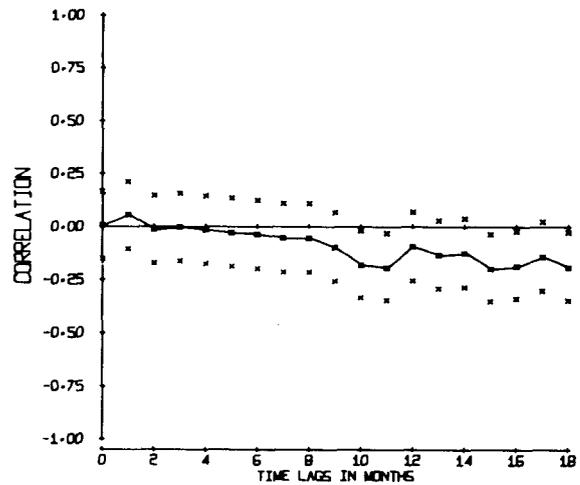
CROSS-CORRELATION FUNCTION

UPWELLING INDEX AT 36 N - 122 W
 LEADS ZOOPLANKTON AREA I



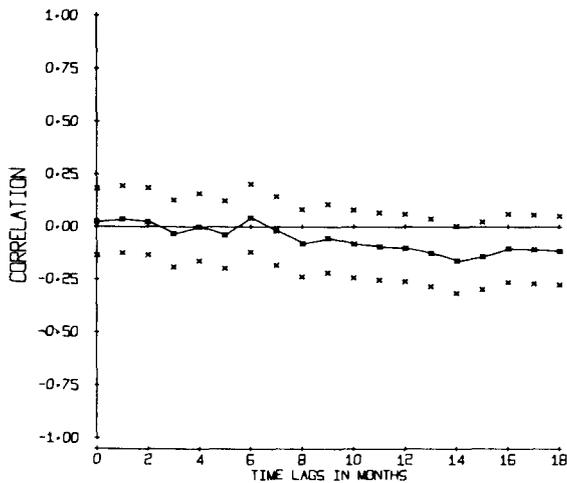
CROSS-CORRELATION FUNCTION

UPWELLING INDEX AT 33 N - 119 W
 LEADS ZOOPLANKTON AREA II



CROSS-CORRELATION FUNCTION

UPWELLING INDEX AT 30 N - 119 W
 LEADS ZOOPLANKTON AREA III



CROSS-CORRELATION FUNCTION

UPWELLING INDEX AT 27 N - 116 W
 LEADS ZOOPLANKTON AREA IV

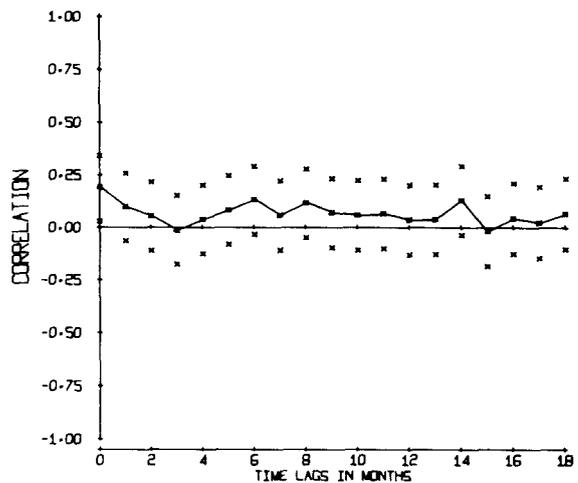


Figure 8. Cross-correlation functions between upwelling indices and zooplankton biomass. Time lags in months; 95% confidence limits [$r(t) \neq 0; P \leq 0.05$] represented by crosses above and below continuous line. (From Bernal 1980.)

Area II and in lags from 0 to 5 months in Area III. In Area IV the correlation values become smaller again but are still significantly different from zero in 0 to 5 months lag. These correlations, although significant, are small since they account for only 25 to 30% of the variance. Nevertheless, the main point to stress here is that this index of advection is a much better predictor than the indices of nearshore vertical motion and its predictive performance with respect to biomass is close to or better than that of sea-surface temperatures (Bernal 1980).

The second index of horizontal advection was derived by Chelton (1981) by means of an objective analysis of the steric-heights information collected by CalCOFI from 1950 to 1978. Using an orthogonal

decomposition of the time-space mean-products matrix, Chelton defined a restricted set of time-invariant spatial patterns of steric heights, patterns that account for a large proportion of the total variance present in the record. Hence, each time-invariant pattern or spatial Empirical Orthogonal Function (EOF) represents dominant modes of variability of the steric height field and therefore dominant patterns of flow in the California Current that are uncorrelated to each other. Figure 12 shows, on the left, the spatial averages of steric heights in the region and, on the right, the first mode of variation or EOF number one, which in this case accounts for 35% of the total variance of the field. For each month for which there are observations, each EOF has a time amplitude coefficient associated with

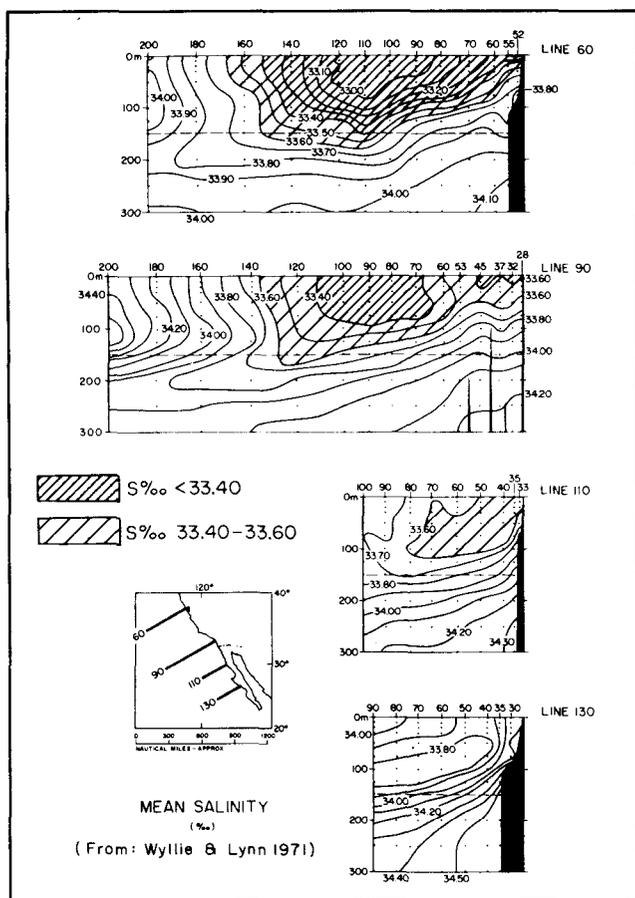


Figure 9. Average vertical sections (1949-69) of salinity across CalCOFI lines 60, 90, 110, and 130. Contour interval, 0.20 ‰. (Modified from Wyllie and Lynn, 1971.)

it that tell us how important or dominant was that particular spatial pattern during that month. Figure 13 shows the time series of the amplitude coefficients for EOF number one. The sign convention with respect to the average patterns is such that a positive value represents an intensification of the flow in the direction of the arrows in Figure 12 and a negative value of the coefficient a reversal of the direction of the flow along the level lines. For example, during years 1958 and 1959 the flow pattern was reversed with respect to the map in the figure. A zero or close to zero value of the coefficient means that flow along this pattern did not exist or contributed very little to the total observed flow pattern during a given month. The results of the cross-correlation analysis with this index of horizontal advection predicting the changes in zooplankton biomass are shown in Figure 14. In all four areas the positive correlation values are uniformly significant from 0 to 11 months lag, and the proportion of the variance accounted for by the highest correlations

TABLE 3
 Maximum Values of Correlation and Coefficients of Determination between Zooplankton Biomass and Anomalous Steric Height (EOF Number 1)

	$r(t)^1$	N	$t = \text{lag}$	$r^2(t)$
Area I	0.57	70	1	0.33
Area II	0.65	97	1	0.42
Area III	0.68	95	1	0.46
Area IV	0.60	84	7	0.36

¹maximum values in the range 0 to 18 months lag.

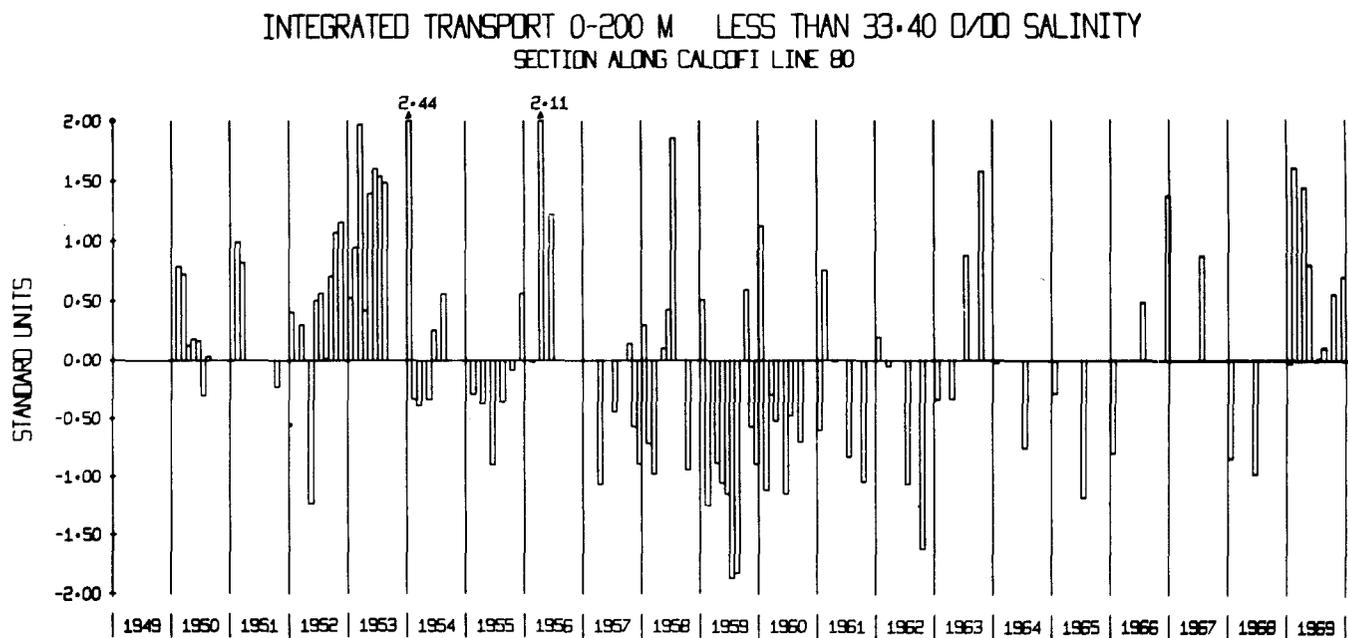
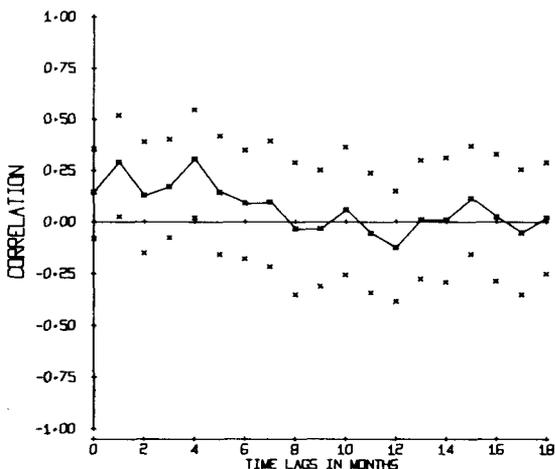


Figure 10. Seasonally corrected time series of index of advection from the north. These indices are estimates of the geostrophic transport across CalCOFI line 80, associated with waters of salinity less than 33.40 ‰. Series have been standardized and therefore have zero mean and unit standard deviation. (From Bernal 1980.)

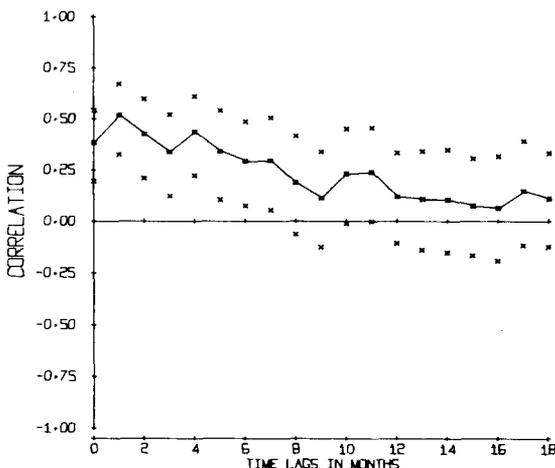
CROSS-CORRELATION FUNCTION

NORTHERN TRANSPORT LESS THAN 33-40 0/00 LINE 80
 LEADS ZOOPLANKTON AREA I



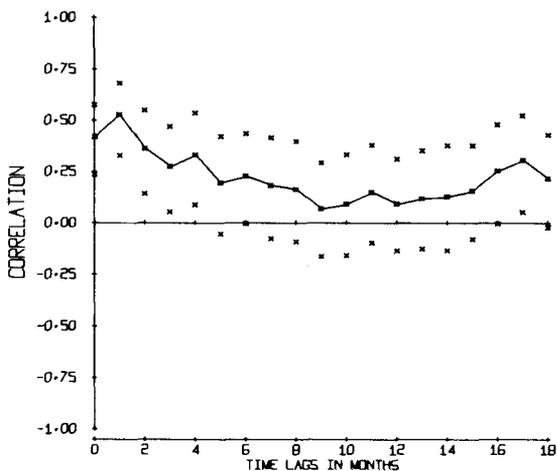
CROSS-CORRELATION FUNCTION

NORTHERN TRANSPORT LESS THAN 33-40 0/00 LINE 80
 LEADS ZOOPLANKTON AREA II



CROSS-CORRELATION FUNCTION

NORTHERN TRANSPORT LESS THAN 33-40 0/00 LINE 80
 LEADS ZOOPLANKTON AREA III



CROSS-CORRELATION FUNCTION

NORTHERN TRANSPORT LESS THAN 33-40 0/00 LINE 80
 LEADS ZOOPLANKTON AREA IV

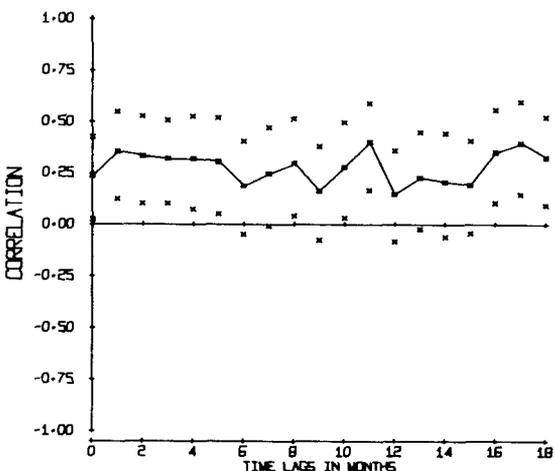


Figure 11. Cross-correlation functions between index of advection from the north and zooplankton biomass. Time lags in months; 95% confidence limits [$r(t) \neq 0$; $P \leq 0.05$] represented by crosses above and below continuous line. (From Bernal 1980.)

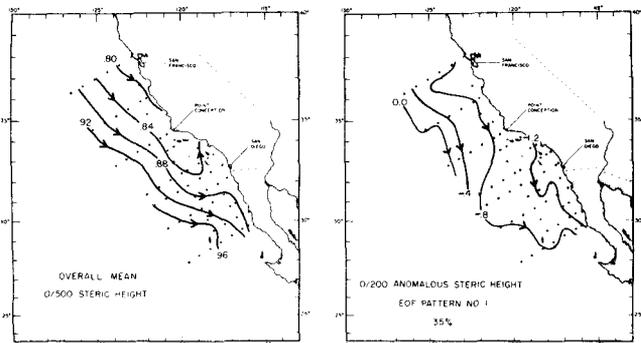


Figure 12. Spatial patterns of dynamic heights (flow) in the California Current. Left: long-term (1950-78) average dynamic height integrated from 500 db to surface; units are dynamic meters. Right: First spatial empirical orthogonal function of dynamic height. This spatial pattern is the first (35% of variance) mode of variation of dynamic height field. Negative values labeling contours indicate slanting of surface from offshore high to inshore low. (Modified from Chelton 1980.)

ranges from 33 to 46% as summarized in Table 3. These results mean that the low-frequency response of the ecosystem is coherent, with changes of the flow pattern occurring in the whole Eastern Boundary Current. Haury et al. (1978) presented a conceptual model of the time-space scales of zooplankton variability in the world oceans. In their description the spectral region in the neighborhood of the response described here is not very active and includes only El Niño-type of events. It is very likely that fluctuations in this spectral region are more important than previously thought and that interannual fluctuations in the strength of eastern boundary currents and concomitant changes in the flow patterns determine to a large degree the behavior of the resident ecosystems. From an ecological point of view, this conclusion also has

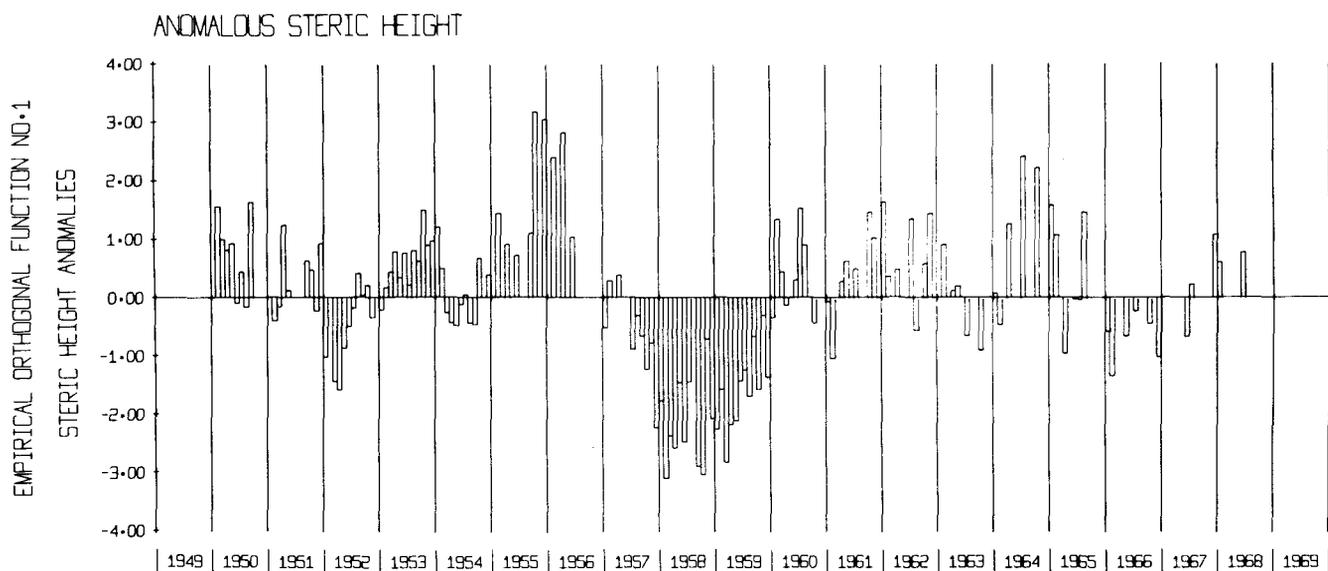


Figure 13. Time series of the monthly amplitude of the first Empirical Orthogonal Function. Coefficients, according to the sign convention used in Figure 12, are positive when flow is southward along EOF contour lines, negative when flow is reversed. (From Bernal 1980.)

important implications, since these ecosystems might be permanently under nonequilibrium conditions. For ecosystems like this, it has been proposed (McGowan 1974) that classical biological interactive processes, such as competition and predation, will be secondary as regulatory mechanisms, since they might not have much of an opportunity to play a dominant role in modulating the changes in abundance of the species, due to the disruptive effect of physical conditions. This contention is not unreasonable, because a strict planktonic population drifting with the average current would have a residence time within the system of only 100 days and its demographic response to environmental and biological factors influencing its reproductive success while inside it would be lost out of the system. Strict planktonic populations might not really exist in nature, and certainly it may be fair to assume that the species assemblage of the California Current pelagic ecosystem has evolved complex adaptations to make full use of this highly variable environment. However this last comment has uncomfortable tautological overtones that need to be removed by formulating testable hypotheses and perhaps developing a new theory. Little is known about the causal mechanism that might drive the low-frequency component of the flow. The fact that the first EOF of dynamic heights displays a flow pattern with a dominant north-south directional component is consistent with both the presence of perturbations originating in the equatorial region (McCreary 1976; Smith 1978) and with basin-wide fluctuations influencing the general pattern of circulation around the North Pacific Ocean. There is some evidence indicating that winter

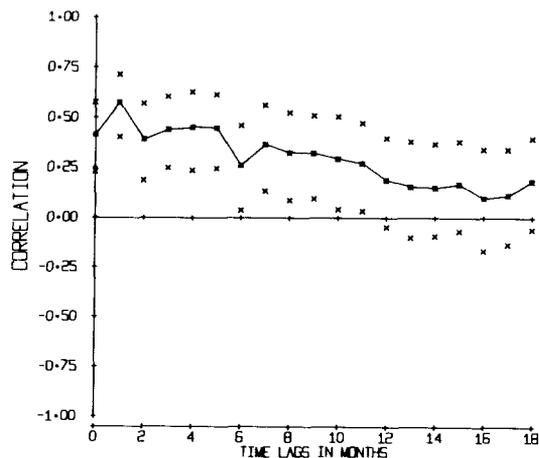
temperature anomalies are conserved in their transit around the subtropical Central Gyre of the North Pacific (Namias 1970) and that extreme years in a time series of very large-scale wind anomalies (expressed as the wind torque over the Gyre) coincide with extreme years in the sea-surface temperature-anomalies record. This suggests that coherent large-scale advection of heat and perhaps momentum are also taking place on basin-wide and interannual scales.

ACKNOWLEDGMENTS

I would like to give thanks to the convenor of this symposium, Joseph L. Reid, for extending me the invitation and for making possible presentation of this review in person, despite the equatorial crossing involved. George Hemingway and Maria Cook were very helpful with travel and other arrangements. Thomas L. Hayward offered his warm hospitality in La Jolla. The results reviewed here are the outcome of research done as a graduate student at Scripps Institution of Oceanography (SIO). To the Chairman of my Doctoral Committee, John A. McGowan, and to all the members who served on it, M.M. Mullin, J.L. Reid, D. Goodman, C. Blanco, and E.L. Venrick, I am very grateful for encouragement and support. To Dudley Chelton I express my gratitude for allowing me to use part of his data and for the many hours of stimulating and fruitful discussions. I take this opportunity to thank the members of the Carl Eckart Prize Committee for honoring me by selecting my work as the "most outstanding dissertation submitted at Scripps Institution of Oceanography during the 1979-80 Academic Year." While at SIO I received

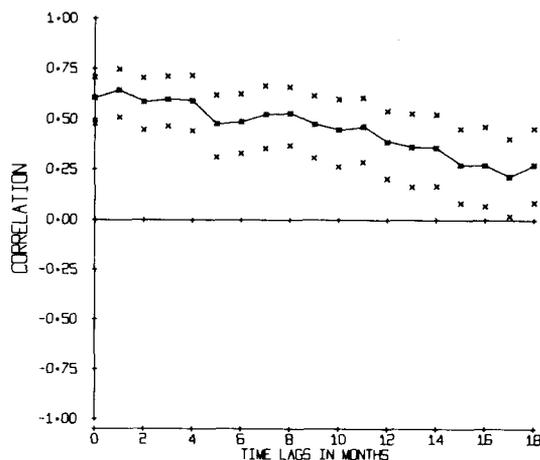
CROSS-CORRELATION FUNCTION

ANOMALOUS STERIC HEIGHT E-O-F. NO. 1
 LEADS ZOOPLANKTON AREA I



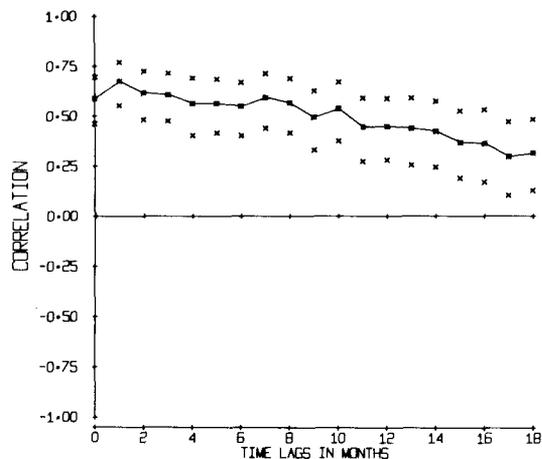
CROSS-CORRELATION FUNCTION

ANOMALOUS STERIC HEIGHT E-O-F. NO. 1
 LEADS ZOOPLANKTON AREA II



CROSS-CORRELATION FUNCTION

ANOMALOUS STERIC HEIGHT E-O-F. NO. 1
 LEADS ZOOPLANKTON AREA III



CROSS-CORRELATION FUNCTION

ANOMALOUS STERIC HEIGHT E-O-F. NO. 1
 LEADS ZOOPLANKTON AREA IV

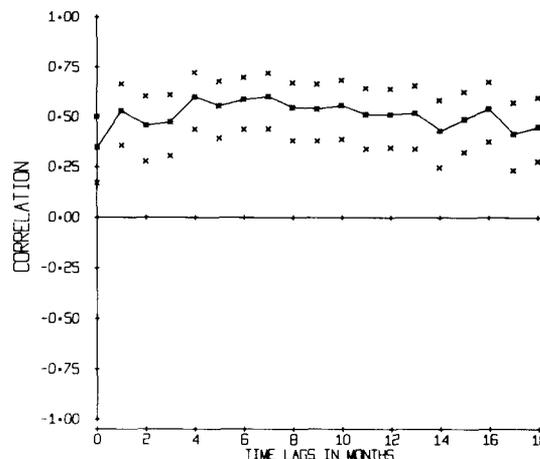


Figure 14. Cross-correlation functions between amplitude of the first EOF of dynamic height and zooplankton biomass. Time lags in months; 95% confidence limits [$r(t) \neq 0$; $P \leq 0.05$] represented by crosses above and below continuous line. (From Bernal 1980.)

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Part III

SCIENTIFIC CONTRIBUTIONS

THE BROWN PELICAN AS A SAMPLING INSTRUMENT OF AGE GROUP STRUCTURE IN THE NORTHERN ANCHOVY POPULATION

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ABSTRACT

Marine birds are known to be sensitive indicators of a variety of factors in the marine environment including pesticide pollution, oil pollution, and abundance of prey. In the Southern California Bight the California brown pelican (*Pelecanus occidentalis californicus*) is a near obligate predator on the northern anchovy (*Engraulis mordax*), and the reproductive success of this bird is related to the availability and abundance of its prey. During investigations of this relationship, sufficient numbers of anchovies were obtained from pelican foods to permit a comparison of the age group composition of these fish with those obtained from commercial fishery samples.

During the two-year study, 244 food samples were obtained from pelicans at three breeding colony locations, and from these samples 3,889 anchovy otoliths were examined and aged. In addition length measurements were obtained from 373 fish.

Anchovies in pelican food from some locales exhibited age and length-frequency characteristics nearly identical to those reported in commercial fishery data. This technique has potential as an alternate means of sampling the northern anchovy population for age and length composition.

RESUMEN

Se conoce que las aves marinas son indicadores sensibles de una variedad de factores en el medio ambiente marino, tales como contaminación por pesticidas, contaminación por petróleo y abundancia de presas. En la Bahía del Sur de California, el pelicano (*Pelecanus occidentalis californicus*) es un depredador casi obligado de la anchoveta del norte (*Engraulis mordax*), y el éxito reproductivo de esta ave se relaciona con la disponibilidad y abundancia de sus presas. Durante la investigación de esta relación, se obtuvo una cantidad suficiente de anchovetas en los alimentos de los pelicanos como para permitir una comparación de la composición de los grupos de edad

de estos peces con la que se obtuvo de las muestras de la pesquería comercial.

Durante los dos años de este estudio, se obtuvieron unas 244 muestras de los alimentos de los pelicanos en tres colonias criaderas. De estas muestras se examinaron y se determinaron las edades de 3,889 otolitos de anchoveta. Adicionalmente, se obtuvieron medidas de longitud de 373 peces.

Las anchovetas del alimento de pelicanos en algunos locales exhibieron características de frecuencia de edad y longitud casi idénticas a éstas reportadas en los datos de la pesquería comercial. Esta técnica puede ser potencialmente una manera alternativa de muestrear la población de anchoveta del norte para determinar su composición por edad y longitud.

INTRODUCTION

Seabirds are recognized as sensitive indicators of various environmental parameters in the marine environment including pesticide pollution (e.g. Anderson et al. 1975), oil pollution (e.g. Vermeer 1976), oceanographic conditions (e.g. Boersma 1978), and primary productivity (e.g. Ashmole 1971). The condition of some seabird populations is so closely associated with their food sources that Crawford and Shelton (1978) used the size of bird colonies as an index of the status of commercial fish stocks.

In the Southern California Bight (SCB), breeding California brown pelicans, *Pelecanus occidentalis californicus*, feed almost exclusively on the northern anchovy, *Engraulis mordax* (Gress et al. 1980; P.R.K., unpublished data), and pelican reproductive success is related to the availability and/or abundance of this fish (Anderson et al. 1980; Anderson et al. in preparation). In the course of studies of this predator-prey relationship, sufficient numbers of anchovies consumed by pelicans were obtained to permit a comparison with anchovies in samples taken from commercial landings. Age and length composition of anchovies from pelican food samples obtained at two breeding colonies in the SCB (Anacapa Island, 1979-1980, and Santa Barbara Island, 1980) were compared

with samples taken from commercial landings at Port Hueneme and the Port of Los Angeles to evaluate the potential for using the pelican as a sampling instrument (Figure 1). The pelican breeding season coincides with anchovy spawning (late winter and spring) and partially overlaps the commercial anchovy fishing season. Anchovies are widely dispersed in the SCB and presumed to be in scattered schools distributed about the pelican breeding colonies during this period. This paper represents a preliminary report of our findings.

METHODS

During the 1979 and 1980 pelican breeding season (approximately January-August), 244 regurgitation samples were collected from pre-fledged young during banding operations, preserved in alcohol, and transported to the laboratory. Intact fish were removed from samples, measured to the nearest millimeter standard length (SL), and otoliths were removed. Lengths from 373 fish and 3,889 otoliths were obtained from the pelican food samples. Otoliths were stored in gelatin capsules and later examined in water under a 20-power binocular microscope to determine the number of annuli present. Criteria for determining age were based on methods described by Fitch (1951).

RESULTS

Age Composition

During the 1979 breeding season, 1,204 anchovy otoliths, of which 197 were unreadable, were obtained from the pelican regurgitations. Our inability to control the time, location, or size of the collections made on the pelican colony, because of the phenology of the pelican breeding season, resulted in only one collec-

tion useful for direct comparison with the commercial fishery. This collection was made on Anacapa Island in May of 1979 and was deemed suitable for comparison with commercial fishery samples from Port Hueneme for the same month. The pelican colony on west Anacapa Island lies about 13 miles southwest of Port Hueneme. We assumed that commercial fishing vessels originating from this port would likely catch fish also available to the Anacapa Island pelicans (based on catch location data extracted from vessel logs and on knowledge of the pelican foraging range; Gress et al. 1980). The 1978 anchovy year class comprised nearly 97% of pelican food samples in 1979. The 1977 year class, the next most numerous cohort, comprised about 2% of the pelican samples. The composition of the commercial samples yielded about 90% 1978 cohort, 8% 1977, and 2% 1976 cohort (Figure 2). The 1979 year class was too small to be recruited into the commercial fishery.

During 1980, 2,685 otoliths representing 1,342 fish from pelican food samples were aged; of these, 47 otoliths were unreadable. Regurgitations were collected from the pelican colony on Santa Barbara Island on April 23 and on Anacapa Island on June 30. The data from these samples coincided temporally with those from the commercial fishery. The Santa Barbara Island collection consisted of about 41% 1979 year class as compared to about 35% for the fishery, whereas the 1978 year class was nearly identical in both with 55% (Figure 3).

The Anacapa Island pelican data were similar to those for the commercial fishery (Figure 3). Each was composed primarily of the 1979 cohort (79% pelican, 70% commercial) and to a lesser extent the 1978 cohort (19% pelican, 26% commercial). Pelicans preyed on small quantities of newly hatched fish unavailable to the commercial fishery in both years.

Length Frequency

Measurements of anchovy lengths (SL) from pelican foods were compared with those of commercial

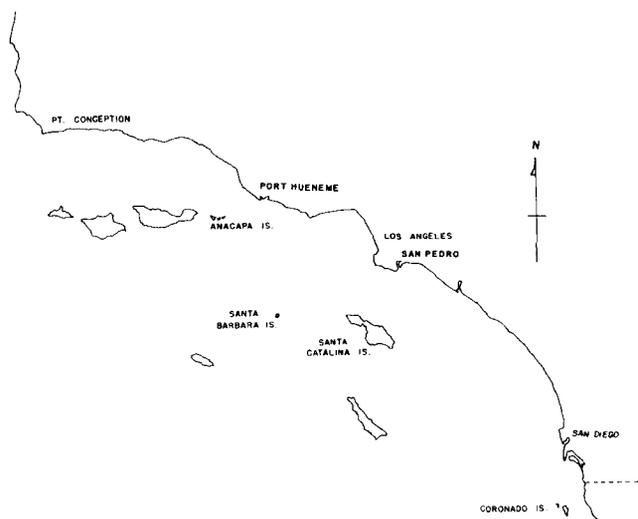


Figure 1. Southern California Bight and offshore islands.

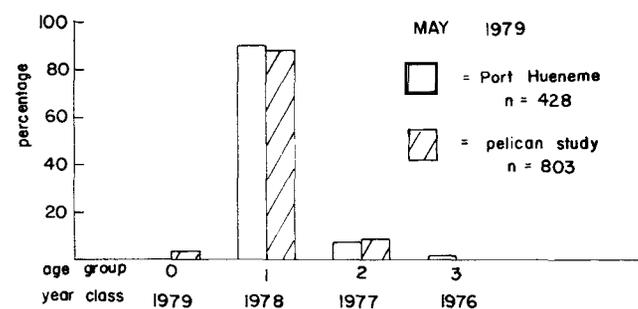


Figure 2. Age composition of northern anchovies taken from pelican food samples at Anacapa Island and from commercial fishery samples at Port Hueneme during 1979.

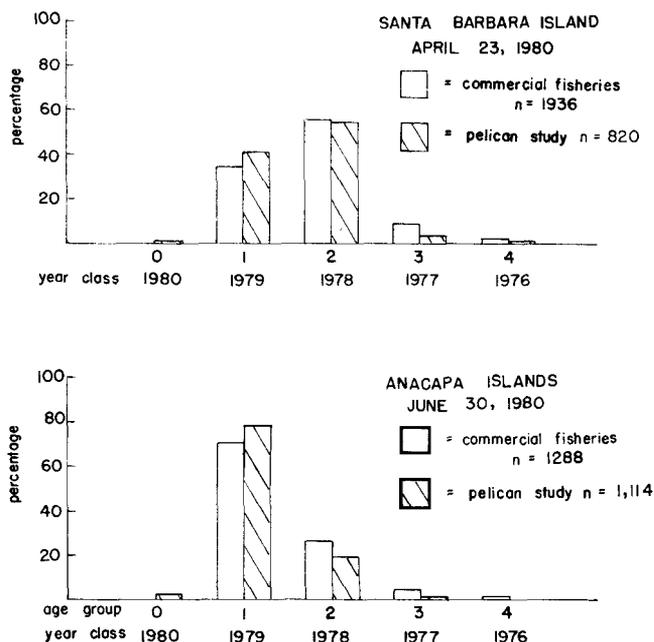


Figure 3. Age composition of northern anchovies taken from pelican food samples (Santa Barbara Island and Anacapa Island) and from commercial fishery samples (San Pedro) during 1980.

anchovy catches. Data were available for 1980 only. Lengths from Santa Barbara Island samples ($n = 113$) were compared with those in the commercial catch, ($n = 494$). Length frequencies in samples from both sources exhibited strong similarities and displayed a bimodal distribution near 95 mm (3.7 inches) and 120 mm (4.7 inches) SL, with means of 110.5 mm (4.3 inches) for the pelican study and 113 mm (4.4 inches) for the commercial data (Figure 4). When tested by the Kolmogorov-Smirnov test for significance, the two sets of data were found to be not significant at the 1% level. The largest cumulative difference was 0.15 which did not exceed the 1% critical value of 0.17, thus concluding that the data were statistically similar. Lengths from anchovies taken from pelicans at Anacapa Island ($n = 172$) when compared with commercial data ($n = 644$) for the same month were nearly identical in length frequency distribution with a single mode at 100 mm and a mean of 103 mm (4 inches) SL (Figure 4). The Kolmogorov-Smirnov test for significance also indicated no significance between samples at the 1% level, with the largest cumulative difference of 0.06 being far below the critical value of 0.14.

DISCUSSION

Numerous variables may affect the results from each sampling method. The pelican's ability to sample anchovies is limited by its foraging range from the colony (about 30 to 50 km, CDFG unpublished data).

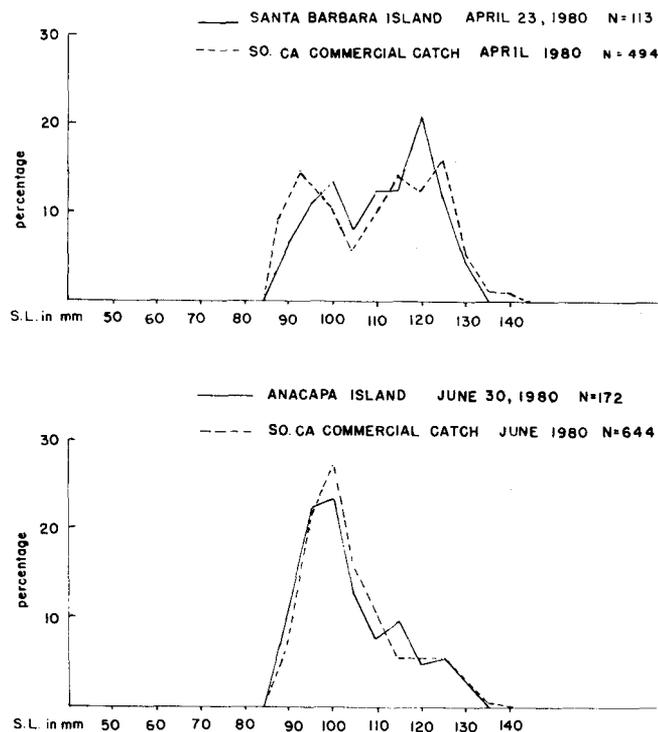


Figure 4. Length distributions of northern anchovies taken from pelican food samples (Santa Barbara Island and Anacapa Island) and from commercial fishery samples (San Pedro) during 1980.

The birds, of course, are not constrained by legal size limits, seasons, or closures. Their foraging behavior necessitates the pursuit of fish near the water surface during daylight, but the fish need not be present in commercial-size schools.

The commercial fishery, in contrast, is less limited by range but must catch legal-size fish in season outside closures. This sampling method would be affected by gear bias (e.g. mesh size). Fishing by purse seine on commercial-size schools occurs farther beneath the surface, primarily at night.

Although the differences in fishing techniques seem substantial, samples taken from both sources (for the same general area and time period) were significantly correlated by means of the Kolmogorov-Smirnov method. The potential for interaction between pelican and the anchovy fishery is supported by these findings, but this subject is discussed elsewhere (Anderson et al. 1980). A thorough examination of results and statistical analyses will be pursued when additional data are available.

CONCLUSION

This technique may provide an opportunity to examine the northern anchovy population in the event that there was no fishery or that conventional means of sampling were not available. We believe that the use

of the California brown pelican as a sampling instrument has merit and that this technique has potential as a practical alternate means of sampling the northern anchovy population for age and length composition.

ACKNOWLEDGMENTS

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SEASONAL GROWTH PATTERNS OF CALIFORNIA STOCKS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, PACIFIC MACKEREL, *SCOMBER JAPONICUS*, AND JACK MACKEREL, *TRACHURUS SYMMETRICUS*

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ABSTRACT

Market sample data obtained from the California Department of Fish and Game were analyzed to show number, mean length, and mean weight of fish by age and month for northern anchovy, *Engraulis mordax*, Pacific mackerel, *Scomber japonicus*, and jack mackerel, *Trachurus symmetricus*. In addition, maximum and minimum lengths and weights and their standard deviations were calculated.

Graphs showing the relationship between age and length and between age and weight were produced for each of these three species. The graphs show that the age-length relationships of Pacific mackerel, jack mackerel, and northern anchovy landed in southern California and of northern anchovy landed in central California are adequately described by the von Bertalanffy growth curve. These graphs also show considerable seasonal variation in the age-weight relationships. These seasonal fluctuations may be related to the occurrence of spawning and feeding relationships. Analysis of the growth in weight suggests that a size limit would be expected to increase yields of Pacific mackerel, but not of jack mackerel or northern anchovy.

RESUMEN

Datos de muestras de anchoveta del norte, *Engraulis mordax*, macarela, *Scomber japonicus*, y macarela caballa, *Trachurus symmetricus*, colectadas en el mercado por el California Department of Fish and Game, se analizaron para mostrar número, longitud media, y peso medio de los peces por edad y por mes. Adicionalmente, se calcularon las longitudes y los pesos máximos y mínimos y sus desviaciones estándar.

Se produjeron gráficas para cada una de estas tres especies, mostrando la relación entre edad y longitud y entre edad y peso. Las gráficas muestran que para la macarela, macarela caballa y anchoveta del norte desembarcadas en el sur de California, y para la anchoveta del norte desembarcada en California central, las relaciones entre edad y longitud están descritas

adecuadamente por la curva de crecimiento de von Bertalanffy. Estas gráficas también muestran considerable variación estacional en las relaciones entre edad y peso. Estas variaciones estacionales pueden estar relacionadas con desove y alimentación. El análisis del crecimiento en peso sugiere que con un tamaño límite se puede esperar un aumento en los rendimientos de macarela, pero no así para macarela caballa ni anchoveta del norte.

INTRODUCTION

The purpose of this study is to describe the seasonal growth patterns of northern anchovy, *Engraulis mordax*, jack mackerel, *Trachurus symmetricus*, and Pacific mackerel, *Scomber japonicus* and to explore what these seasonal growth patterns suggest in terms of managing these fisheries.

Data for the study were provided by the California Department of Fish and Game (CDFG). Part of the data had been used previously to describe von Bertalanffy growth equations for northern anchovy (Spratt 1975), jack mackerel (Wine and Knaggs 1975), and Pacific mackerel (Knaggs and Parrish 1973). In our study, computer programs were developed to calculate and graph growth statistics for these three species.

At the time the market samples were taken, northern anchovy had a quota, a 5-inch size limit, and a closed season during summer. These regulations were established by the State of California. No such regulations existed for Pacific mackerel and jack mackerel. Currently, the Pacific Fisheries Management Council has established a quota, a 5-inch size limit, and a closed season for northern anchovy. The State of California has established a quota, a 10-inch size limit, and a closed season for Pacific mackerel. There are no such regulations for jack mackerel.

METHODS

Description of Data Base

Data for this study were obtained by the CDFG through their programs for sampling and aging commercial catches of northern anchovy, jack mackerel, and Pacific mackerel. Sampling procedures for north-

ern anchovy have been described by Collins (1969). However, the sampling procedures for the jack mackerel and Pacific mackerel data have not been published.

Data for northern anchovy were taken from landings in San Pedro and Monterey. The samples from the San Pedro landings consist of 58,347 fish and include the 1966/67 season and the 1968/69 through 1978/79 seasons. The samples from the Monterey landings consist of 4,902 fish and include seasons 1966/67 through 1969/70 and seasons 1971/72 through 1977/78. In southern California, at the time these samples were taken, the anchovy season opened in September and closed during June, July, and August. However, during the 1978/79 season, the anchovy season closed during July and August. In central California, the anchovy season opened in August and closed during June and July.

The data for jack mackerel and Pacific mackerel were taken from landings in San Pedro. The jack mackerel samples include seasons 1966/67 through 1970/71, and consist of 20,109 fish. The Pacific mackerel samples include seasons 1962/63 through 1973/74 and consist of 7,005 fish. During this period of time there was a severe decline in the population of Pacific mackerel. Landings were extremely limited, and few fish were sampled. Finally, in 1970, the State of California put a moratorium on Pacific mackerel landings, which continued until 1977.

The individual fish data include date of capture, length, weight (g), sex, maturity, annuli (rings), and year class. Jack mackerel and Pacific mackerel lengths were recorded as fork length (FL), and northern anchovy lengths were recorded as standard length (SL).

For the purpose of portraying the data, it is assumed that all fish are born in the same month of the year. The spawning season for both jack mackerel and Pacific mackerel is March through October, with the majority of spawning taking place April through August (Knaggs and Parrish 1973; Wine and Knaggs 1975). For this study, May will be considered the birth month of both jack mackerel and Pacific mackerel. Northern anchovy has a year round spawning season, with the majority of spawning taking place in February and March (Ahlstrom 1966). For northern anchovy, February will be considered the birth month.

In Pacific mackerel (Fitch 1951) and jack mackerel, rings are laid down on the otoliths near the time of the birthday and, thus, can be used as a measure of age. In northern anchovy, however, rings are laid down during the spring, with the majority laid down by June 1st (Collins and Spratt 1969). Therefore, in our study ages of northern anchovy were calculated based on rings and date of capture.

Data Analysis

A computer program was developed to calculate the number, the mean length, and the mean weight of fish by age and by month. The program also calculated maximum and minimum lengths, maximum and minimum weights, standard deviations of lengths, and standard deviation of weights by age and by month. Standard deviations were not calculated if there were less than ten observations. This program also produced graphs of age-length and age-weight relationships.

In order to more clearly describe the seasonal fluctuations in weight, the proportion of growth by month was calculated for each of the three species. The September mean weight was taken as a starting point because this is the month the fish are recruited to the fishery. The proportion was calculated by dividing each monthly mean weight of each age group by its corresponding September mean weight. This procedure resulted in an overlap of age groups. To avoid bias resulting from small numbers of fish at the older ages, the proportions were weighted by the number of fish. These calculations were made for younger fish (mostly immatures), for older fish (mostly adults), and for the total number of fish.

RESULTS

The relationships between age and length and between age and weight for northern anchovy, jack mackerel, and Pacific mackerel are shown in the following tables and figures. When expressed graphically the seasonal fluctuations in growth in weight, and to a lesser degree growth in length, are evident. Growth in weight has different seasonal patterns in the three species, and it also differs between anchovy landed in Monterey and San Pedro.

Seasonal Distribution of Catch by Age

The summaries of the number and mean length of fish by age and month for northern anchovy landed in San Pedro and Monterey show considerable differences in the age structure and the seasonality of the fisheries in the two regions. The data for northern anchovy sampled in San Pedro show that a very small percentage of the fish were less than one year old (3.2%); the bulk of the fish (83.8%) consisted of ages 1-3 (Table 1). One-year-old fish comprised 26% of the fish sampled; 33.8% of the fish were two years old, and 24% were three years old. The highest percentages of catch occurred in fall and early winter (October through January), with a small peak during the spring (April and May). Landings were low during the peak of the spawning season (February and March) and during the summer due to the closed season. A

TABLE 1

Number (N), Mean Standard Length mm (\bar{X}), and Percentage of Fish by Age and Month for Northern Anchovy Sampled in San Pedro.

AGE		FEB	MAR	APR	MAY	JUN*	JUL	AUG	SEP	OCT	NOV	DEC	JAN	SUBTOTAL	% BY AGE
0	N	0	0	0	0	0	0	0	52	297	280	575	665	1869	.032
	\bar{X}	0	0	0	0	0	0	0	104	103	106	104	105		
1	N	684	1778	1842	1870	519	0	0	707	2059	1610	2016	2091	15176	.260
	\bar{X}	104	106	109	112	110	0	0	117	117	119	117	116		
2	N	1236	993	1526	1592	75	0	0	1585	3630	3514	3348	2234	19733	.338
	\bar{X}	113	116	117	118	119	0	0	121	123	124	124	122		
3	N	970	662	1700	1593	31	0	0	999	1743	2717	2187	1422	14024	.240
	\bar{X}	119	125	125	123	129	0	0	124	127	129	129	130		
4	N	409	554	1306	639	2	0	0	186	500	896	620	454	5566	.095
	\bar{X}	127	133	132	130	131	0	0	129	131	133	133	138		
5	N	110	348	591	180	0	0	0	25	63	125	88	95	1625	.028
	\bar{X}	136	139	138	138	0	0	0	133	136	136	138	144		
6	N	32	97	132	33	0	0	0	3	7	12	6	6	328	.006
	\bar{X}	141	146	144	145	0	0	0	144	136	142	142	156		
7	N	2	8	10	3	0	0	0	0	1	0	0	0	24	.0004
	\bar{X}	162	151	147	147	0	0	0	0	124	0	0	0		
8	N	0	1	1	0	0	0	0	0	0	0	0	0	2	.00003
	\bar{X}	0	147	172	0	0	0	0	0	0	0	0	0		
SUBTOTAL		3443	4441	7108	5910	627	0	0	3557	8300	9154	8840	6967	58347	
% BY MONTH		.059	.076	.122	.101	.011	0	0	.061	.142	.157	.152	.119		

*Represents only one season of data (1978/79)

small percentage (7.4%) of the anchovies sampled in Monterey were age group 0; most (83.7%) were age groups 1-4 (Table 2). The 1- to 4-year-old fish comprised 17.4%, 22.2%, 27.4%, and 16.7%, respectively, of the sampled catch. Peak landings occurred in the late summer and fall (August through November).

A comparison of the anchovy landings in the two areas shows that the fish landed in Monterey tend to be older than those landed in San Pedro. The median age in the Monterey samples was three, and the median age in the San Pedro samples was two. Peak landings in Monterey occurred earlier in the season and were

more seasonally concentrated than those in San Pedro. In Monterey, 66% of the sampled catch was landed during the September-November period, whereas in San Pedro, 45.1% was landed during October-December.

The San Pedro landings of jack mackerel consisted primarily of young fish; 27.3% of the fish sampled were less than one year old, 49.5% were one-year-old fish, and 16.5% were two-year-old fish (Table 3). Only 6.6% of the fish were age three and older. The dominance of young fish in the catch is influenced by the fact that the bulk of the adult stock is not available

TABLE 2

Number (N), Mean Standard Length mm (\bar{X}), and Percentage of Fish by Age and Month for Northern Anchovy Sampled in Monterey.

AGE		FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	SUBTOTAL	% BY AGE
0	N	0	0	0	0	0	0	6	45	46	252	11	4	364	.074
	\bar{X}	0	0	0	0	0	0	110	110	109	112	109	122		
1	N	1	28	19	11	0	0	175	228	242	112	15	21	852	.174
	\bar{X}	124	108	114	110	0	0	121	123	123	122	127	124		
2	N	7	46	52	14	0	0	122	275	295	152	65	60	1088	.222
	\bar{X}	126	120	125	126	0	0	131	133	131	133	132	132		
3	N	18	54	61	17	0	0	135	246	381	234	98	100	1344	.274
	\bar{X}	136	124	135	133	0	0	139	141	139	138	137	138		
4	N	22	55	47	1	0	0	71	141	188	153	72	67	817	.167
	\bar{X}	144	146	147	134	0	0	146	147	146	143	141	145		
5	N	23	14	29	2	0	0	28	78	62	63	24	22	345	.070
	\bar{X}	149	146	151	135	0	0	153	152	151	149	145	151		
6	N	7	9	20	0	0	0	4	24	6	6	5	1	82	.017
	\bar{X}	155	152	155	0	0	0	155	161	153	153	152	154		
7	N	0	0	5	0	0	0	0	3	0	2	0	0	10	.002
	\bar{X}	0	0	155	0	0	0	0	158	0	165	0	0		
SUBTOTAL		78	206	233	45	0	0	541	1040	1220	974	290	275	4902	
% BY MONTH		.016	.042	.048	.009	0	0	.110	.212	.249	.199	.059	.056		

TABLE 3
 Number (N), Mean Fork Length mm (\bar{X}), and Percentage of Fish by Age and Month for Jack Mackerel Sampled in San Pedro.

AGE		MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	SUBTOTAL	% BY AGE
0	N	0	0	0	1	16	265	274	629	770	809	1507	1219	5490	.273
	\bar{X}	0	0	0	187	156	160	166	171	172	172	180	180		
1	N	1560	1868	904	1091	1175	1144	687	742	171	253	227	135	9957	.495
	\bar{X}	183	186	186	198	201	210	213	214	215	219	218	225		
2	N	589	506	351	200	168	427	264	243	100	134	199	144	3325	.165
	\bar{X}	227	230	228	233	237	238	235	235	241	242	243	249		
3	N	218	205	123	29	57	184	29	8	26	60	41	22	1002	.050
	\bar{X}	249	259	249	275	278	274	282	297	279	265	263	278		
4	N	43	61	28	3	33	48	10	5	18	17	14	7	287	.014
	\bar{X}	271	273	270	282	298	302	308	311	301	292	297	335		
5	N	3	4	5	1	1	8	4	2	2	12	1	0	43	.002
	\bar{X}	324	304	289	327	302	342	357	330	325	320	330	0		
6	N	1	0	0	0	0	0	1	0	0	1	1	0	4	.0002
	\bar{X}	345	0	0	0	0	0	362	0	0	317	325	0		
7	N	0	0	1	0	0	0	0	0	0	0	0	0	1	.00005
	\bar{X}	0	0	335	0	0	0	0	0	0	0	0	0		
SUBTOTAL		2414	2644	1412	1325	1450	2076	1269	1629	1087	1286	1990	1527	20109	
% BY MONTH		.120	.131	.070	.066	.072	.103	.063	.081	.054	.064	.099	.076		

to the San Pedro purse seine fleet. Adult fish occur farther offshore and to the north of the fleet's fishing grounds (Blunt 1969). In addition, the absence of a size limit allows the take of small jack mackerel, which were apparently available to the fishery year round, since the data show no sharp peaks in monthly landings.

Pacific mackerel landings in San Pedro were dominated by age groups zero and one, 38.6% and 28.2% respectively (Table 4). The remaining percentage, 33.2%, was widely distributed among the other ages. In contrast to jack mackerel, older Pacific mackerel

are available to the purse seine fishery as evidenced by the higher percentages of two- to six-year olds in the data. In addition, Fitch (1951) reported that the early fishery was dominated by two- to six-year olds. Catches of Pacific mackerel show strong seasonality, with a sharp peak in October/November. A second, minor peak, composed primarily of juveniles, occurred in May.

Growth in Length

The monthly distribution of lengths of northern anchovy in samples taken from the San Pedro and Mon-

TABLE 4
 Number (N), Mean Fork Length mm (\bar{X}), and Percentage of Fish by Age and Month for Pacific Mackerel Sampled in San Pedro.

AGE		MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	SUBTOTAL	% BY AGE
0	N	0	0	0	0	150	720	579	369	329	268	139	152	2706	.386
	\bar{X}	0	0	0	0	201	211	226	231	245	237	230	237		
1	N	697	326	273	220	173	167	72	12	5	15	4	12	1976	.282
	\bar{X}	266	272	280	282	278	298	301	301	292	308	291	305		
2	N	64	35	107	55	45	138	57	16	1	10	8	42	578	.083
	\bar{X}	301	309	310	314	313	320	323	321	305	324	323	328		
3	N	33	41	62	29	62	148	84	45	4	19	12	5	544	.078
	\bar{X}	331	333	334	331	332	336	339	339	341	337	340	353		
4	N	60	27	51	36	23	105	39	27	0	6	7	3	384	.055
	\bar{X}	348	351	356	358	358	359	363	354	0	357	356	363		
5	N	68	13	23	29	11	182	61	66	4	8	8	2	475	.068
	\bar{X}	369	373	375	375	372	377	381	378	391	383	380	379		
6	N	24	2	14	5	8	115	32	52	18	9	0	0	279	.040
	\bar{X}	384	381	397	383	389	385	388	387	408	394	0	0		
7	N	1	0	7	2	1	17	1	9	5	2	0	0	45	.006
	\bar{X}	398	0	400	394	393	400	410	385	408	413	0	0		
8	N	1	0	3	0	1	9	0	0	0	1	0	0	15	.002
	\bar{X}	408	0	419	0	428	411	0	0	0	385	0	0		
9	N	0	0	1	0	0	2	0	0	0	0	0	0	3	.0004
	\bar{X}	0	0	408	0	0	416	0	0	0	0	0	0		
SUBTOTAL		948	444	541	376	474	1603	925	596	366	338	178	216	7005	
% BY MONTH		.135	.063	.077	.054	.068	.229	.132	.085	.052	.048	.025	.031		

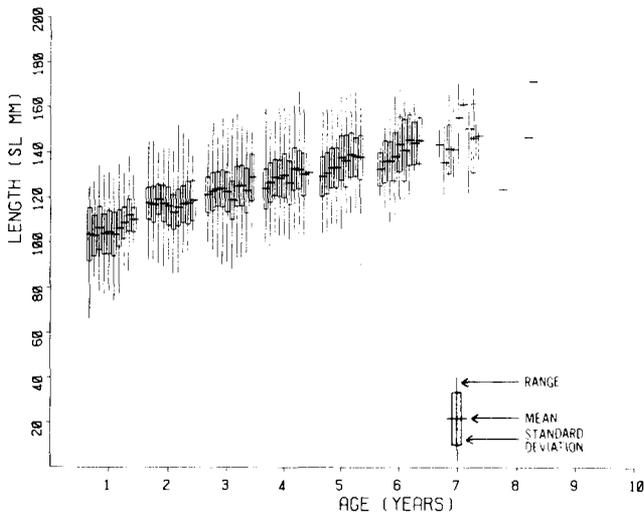


Figure 1. Monthly distribution (February-January) of the length of northern anchovy in samples taken from San Pedro (58,347 fish, 1966-78).

tery fisheries shows these fish have a slow growth rate, little seasonal fluctuations in mean standard length, and that anchovies landed in Monterey were larger than those landed in San Pedro. Young-of-the-year anchovies were recruited to the fishery in the fall (September-October). In San Pedro this occurred at a mean standard length of 103 mm (Figure 1, Table 1). By age four these fish had grown to a mean standard length of 130 mm. In Monterey, young-of-the-year anchovies were recruited to the fishery at a mean standard length of 109 mm and by age four had grown to a mean standard length of 146 mm (Figure 2, Table 2). At the time they entered the fishery, the anchovies landed in Monterey were 6 mm longer than the anchovies landed in San Pedro. This difference in stan-

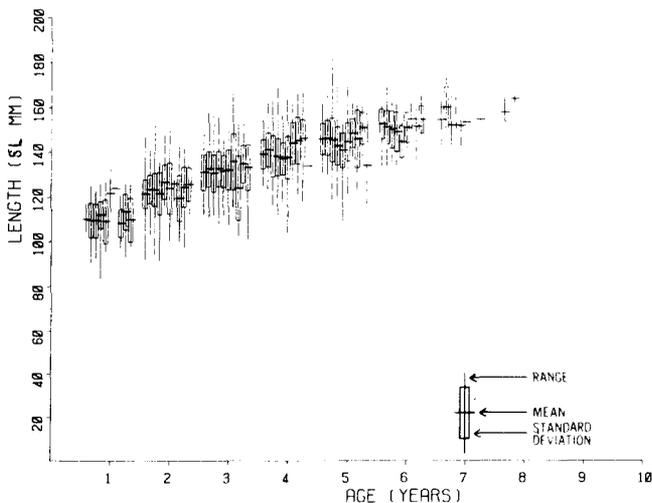


Figure 2. Monthly distribution (February-January) of the length of northern anchovy in samples taken from Monterey (4,902 fish, 1966-77).

ard length had increased to 16 mm by age four. The growth curves of anchovies in the two regions are almost linear and free of fluctuations.

The growth of anchovy described in this study differs from other published studies in that growth to age one is more rapid and growth after this age is slower. Clark and Phillips (1952) found one-year-old anchovies in central California to be 92 mm in standard length, and Spratt (1975) found one-year-old anchovies in southern California to be 92 mm in standard length. Using February as the birth month, we found one-year-old anchovies to be about 110 mm in central California and 104 mm in southern California. We also found that at age four anchovies in central California were 144 mm and anchovies in southern California were 127 mm. Clark and Phillips, however, found that anchovies in central California were 152 mm at age four, and Spratt found that anchovies in southern California were 135 mm at age four. The most likely explanation for the differences in growth rates among these studies is that anchovies have different growth rates in different years. Spratt's data cover the years 1966-72 and consist of 677 aged fish. Clark and Phillips' data cover the years 1946-51 and consist of 211 aged fish. Our study covers the years 1966-78 and consists of 58,347 aged fish for southern California and 4,902 aged fish for central California.

Young-of-the-year jack mackerel first entered the fishery during September-October at a mean fork length of 158 mm and reached 300 mm by the time they were four years old (Figure 3, Table 3). Fish that were three years and older tended to exhibit seasonal fluctuations in mean fork length; growth was more rapid in the spring and summer than in the winter. Growth in length of jack mackerel is well described by

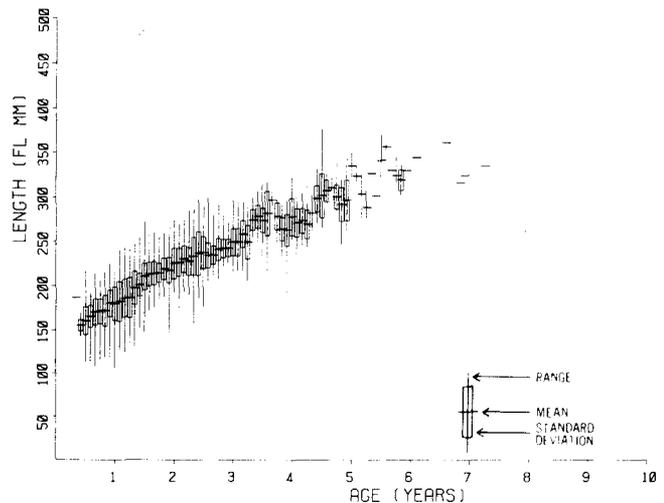


Figure 3. Monthly distribution (May-April) of the length of jack mackerel in samples taken from San Pedro (20,109 fish, 1966-70).

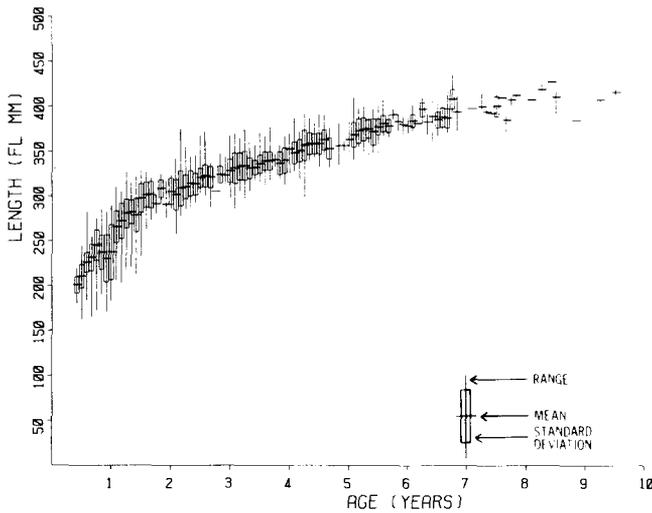


Figure 4. Monthly distribution (May-April) of the length of Pacific mackerel in samples taken from San Pedro (7,005 fish, 1962-73).

a von Bertalanffy growth equation (Wine and Knaggs 1975).

Young-of-the-year Pacific mackerel are recruited to the fishery in September-October at a mean fork length of 206 mm (Figure 4, Table 4). These fish attained a length of 359 mm by the time they were four years old. Growth was particularly rapid during the spring and summer for one-year-old fish. Growth in length of Pacific mackerel appears to exhibit a close fit to a typical von Bertalanffy growth equation (Knaggs and Parrish, 1973).

Growth in length of jack mackerel and Pacific mackerel have several differences. Pacific mackerel initially have a faster rate of growth than jack mackerel. Although both enter the fishery in September (at about six months of age), Pacific mackerel have a mean fork length of 206 mm, whereas jack mackerel have a mean fork length of only 158 mm. Growth in Pacific mackerel is very rapid to about two years of age, then decreases somewhat in older fish. Jack mackerel, however, maintain a moderate, almost linear, growth rate. In addition, Pacific mackerel growth in length displays seasonality in one-year-old fish, whereas jack mackerel growth displays seasonality in fish three years and older.

Growth in Weight

The monthly distribution of northern anchovy weights in samples taken from the San Pedro fishery indicates that anchovies first entered the fishery at a mean weight of 11.1 g and by age four had increased to a mean weight of 23.2 g (Figure 5, Table 5).¹ In a

¹The total numbers of fish in Tables 1-4 are different from those in Tables 5-8 because some fish were not weighed.

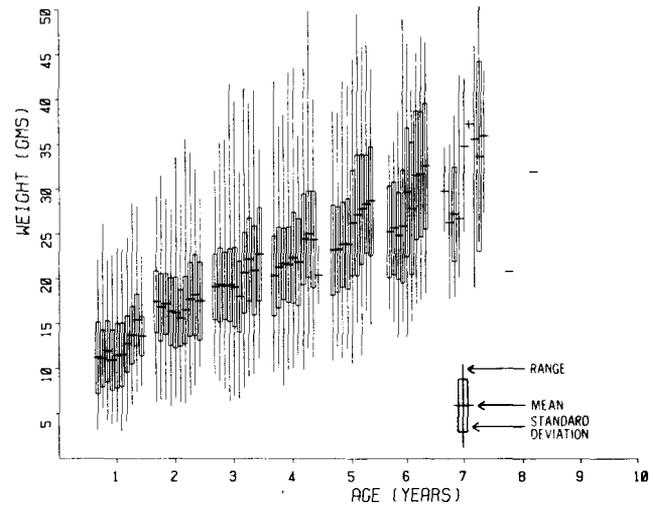


Figure 5. Monthly distribution (February-January) of the weight of northern anchovy in samples taken from San Pedro (58,296 fish, 1966-78).

period of four years, these fish had increased their weight by a factor of 2.1. Growth in weight shows a step-like fluctuation with no growth during the fall and winter months, followed by a spurt of growth beginning in late winter or early spring, which continues through early summer. Although there are no data over the summer months, it appears that younger fish (ages 1 and 2) increased in weight over these months, whereas older fish (ages 3+) lost weight over this period.

Northern anchovies were recruited to the Monterey fishery at a mean weight of 15.5 g (Figure 6, Table 6). By age four, they had increased to a mean weight of

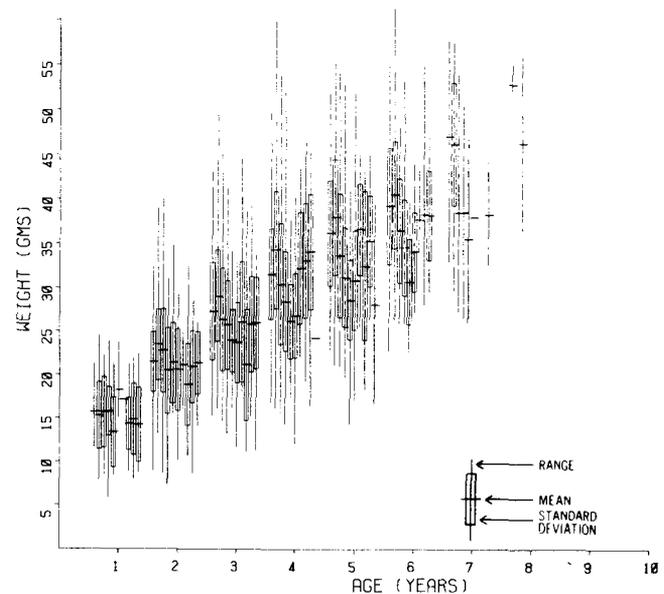


Figure 6. Monthly distribution (February-January) of the weight of northern anchovy in samples taken from Monterey (4,807 fish, 1966-77).

TABLE 5
 Number (N), Mean Weight g (\bar{X}), and Percentage of Fish by Age and Month for Northern Anchovy Sampled in San Pedro.

AGE		FEB	MAR	APR	MAY	JUN*	JUL	AUG	SEP	OCT	NOV	DEC	JAN	SUBTOTAL	% BY AGE
0	N	0	0	0	0	0	0	0	52	297	280	575	665	1869	.032
	\bar{X}	0	0	0	0	0	0	0	11.2	11.1	12.0	11.0	11.4		
1	N	684	1778	1842	1870	519	0	0	707	2059	1610	2016	2091	15176	.260
	\bar{X}	11.6	12.8	13.7	15.4	13.6	0	0	17.4	16.8	17.2	16.3	16.2		
2	N	1236	993	1517	1592	75	0	0	1585	3630	3514	3348	2234	19724	.338
	\bar{X}	15.6	16.5	17.7	18.3	17.5	0	0	19.1	19.3	19.2	19.3	19.1		
3	N	970	662	1683	1593	31	0	0	999	1743	2717	2187	1422	14007	.240
	\bar{X}	18.0	20.7	22.2	20.9	22.7	0	0	20.3	21.3	21.7	21.6	22.3		
4	N	409	554	1288	639	2	0	0	186	500	896	620	454	5548	.095
	\bar{X}	21.8	24.4	25.0	24.4	20.4	0	0	23.2	23.2	23.8	23.9	26.3		
5	N	110	348	586	180	0	0	0	25	63	125	88	95	1620	.028
	\bar{X}	27.1	27.8	28.4	28.7	0	0	0	25.2	25.7	24.8	25.8	29.6		
6	N	32	97	130	33	0	0	0	3	7	12	6	6	326	.006
	\bar{X}	27.8	31.5	31.6	32.5	0	0	0	29.7	26.3	27.2	26.7	34.7		
7	N	2	8	10	3	0	0	0	0	1	0	0	0	24	.0004
	\bar{X}	37.2	35.5	33.6	35.9	0	0	0	0	18.1	0	0	0		
8	N	0	1	1	0	0	0	0	0	0	0	0	0	2	.00003
	\bar{X}	0	31.9	58.2	0	0	0	0	0	0	0	0	0		
SUBTOTAL		3443	4441	7057	5910	627	0	0	3557	8300	9154	8840	6967	58296	
% BY MONTH		.059	.076	.121	.101	.011	0	0	.061	.142	.157	.152	.120		

*Represents only one season of data (1978/79)

35.7 g. These fish had increased their weight by a factor of 2.3 in four years. The growth of Monterey anchovies shows significant seasonal fluctuations. During the fall to mid-winter months, prior to the peak spawning period, there is a loss in mean weight, which is more pronounced in fish three years and older. Growth appears to be erratic from mid-winter to spring, and finally, from spring to fall, there is a marked spurt in growth.

There are differences in the growth in weight of anchovies in the two areas. At the time they entered the fishery, the anchovies landed in Monterey were

4.4 g heavier than those landed in San Pedro. This difference in weight had increased to 12.5 g by age four. In addition, the anchovies landed in Monterey have different seasonal fluctuations from those landed in San Pedro.

Jack mackerel increased their weight by a factor of 7.6 over a period of four years. Young-of-the-year fish entered the fishery at a mean weight of 42 g and reached a mean weight of 319 g by the time they were four years old (Figure 7, Table 7). Jack mackerel have a moderate rate of growth with little seasonality until age three. For fish three years and older, there is an

TABLE 6
 Number (N), Mean Weight g (\bar{X}), and Percentage of Fish by Age and Month for Northern Anchovy Sampled in Monterey.

AGE		FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	SUBTOTAL	% BY AGE
0	N	0	0	0	0	0	0	6	45	46	252	11	4	364	.076
	\bar{X}	0	0	0	0	0	0	15.7	15.3	15.7	15.8	13.4	18.2		
1	N	1	28	19	11	0	0	175	228	240	112	15	21	850	.177
	\bar{X}	17.1	14.3	14.9	14.2	0	0	21.4	23.4	22.8	20.4	21.3	20.5		
2	N	7	46	52	14	0	0	122	275	279	152	65	60	1072	.223
	\bar{X}	21.1	18.9	20.9	21.3	0	0	27.2	29.0	26.3	25.7	23.9	23.7		
3	N	18	54	61	17	0	0	135	246	339	234	98	100	1302	.271
	\bar{X}	26.0	21.1	25.7	25.9	0	0	31.5	34.3	30.3	28.4	26.1	26.8		
4	N	22	55	47	1	0	0	71	141	163	153	72	67	792	.165
	\bar{X}	32.1	33.0	34.0	24.1	0	0	36.1	37.9	33.6	31.1	28.6	30.8		
5	N	23	14	29	2	0	0	28	78	53	63	24	22	336	.070
	\bar{X}	36.6	32.4	35.3	28.1	0	0	39.2	40.4	36.4	34.5	30.6	34.0		
6	N	7	9	20	0	0	0	4	24	5	6	5	1	81	.017
	\bar{X}	37.6	38.2	38.1	0	0	0	47.0	46.2	38.4	38.5	35.5	37.9		
7	N	0	0	5	0	0	0	0	3	0	2	0	0	10	.002
	\bar{X}	0	0	38.2	0	0	0	0	52.8	0	46.2	0	0		
SUBTOTAL		78	206	233	45	0	0	541	1040	1125	974	290	275	4807	
% BY MONTH		.016	.043	.048	.009	0	0	.113	.216	.234	.203	.060	.057		

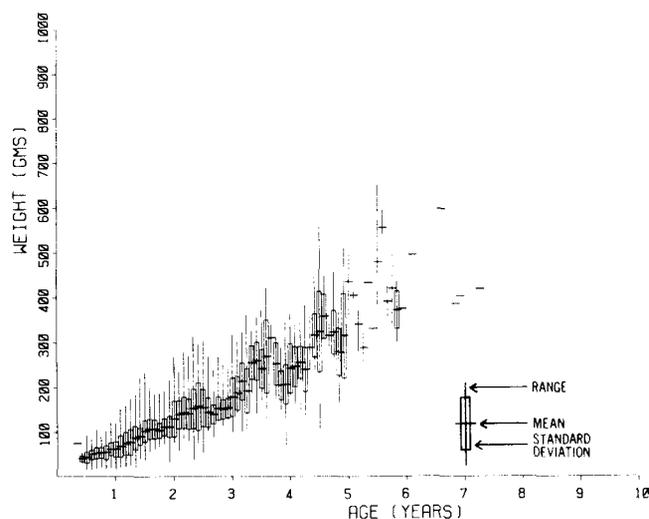


Figure 7. Monthly distribution (May-April) of the weight of jack mackerel in samples taken from San Pedro (20,068 fish, 1966-70).

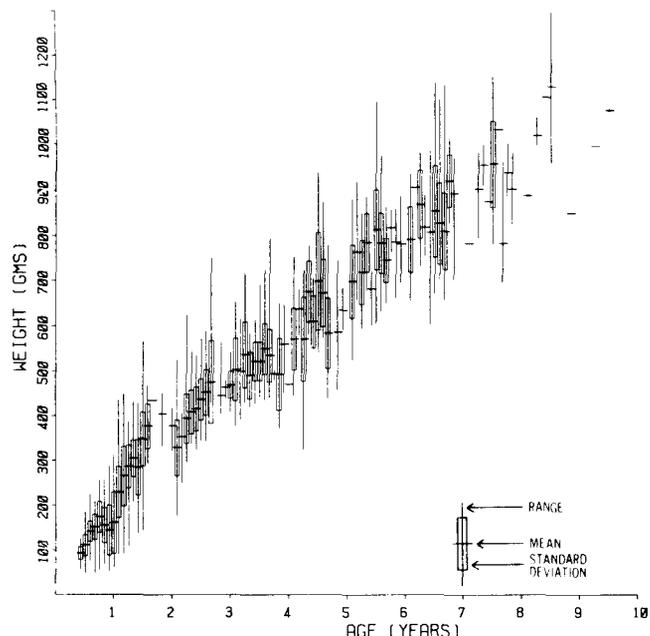


Figure 8. Monthly distribution (May-April) of the weight of Pacific mackerel in samples taken from San Pedro (6,054 fish, 1962-73).

increase in mean weight from late spring to late fall, followed by a loss in mean weight from winter to early spring.

Pacific mackerel entered the fishery at a mean weight of 102 g (Figure 8, Table 8). By age four, they had increased to a mean weight of 654 g, which represents an increase of 6.4 times the starting weight during this four-year period. Pacific mackerel, age groups 0-2, show a high growth rate and marked seasonal fluctuations. In these fish, a spurt of growth occurs from the spring to mid-winter months, followed by a small loss in weight during the mid-winter to spring months. For older fish (ages 3+), the number of fish

per month was not sufficient to show a distinct seasonal pattern.

There are several differences between the growth in weight of Pacific mackerel and jack mackerel. Pacific mackerel grow faster than jack mackerel, especially during their first few years. They enter into the fishery at a heavier weight (102 g) than jack mackerel (42 g) and seem to maintain this heavier weight overall. Pacific mackerel show seasonality in growth im-

TABLE 7
 Number (N), Mean Weight g (\bar{X}), and Percentage of Fish by Age and Month for Jack Mackerel Sampled in San Pedro.

AGE		MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	SUBTOTAL	% BY AGE
0	N	0	0	0	1	16	224	274	629	770	809	1507	1219	5449	.272
	\bar{X}	0	0	0	74	40	43	49	52	53	54	61	61		
1	N	1560	1868	904	1091	1175	1144	687	742	171	253	227	135	9957	.496
	\bar{X}	67	73	76	86	90	102	106	106	103	111	111	129		
2	N	589	506	351	200	168	427	264	243	100	134	199	144	3325	.166
	\bar{X}	139	143	140	152	157	154	143	139	152	150	153	177		
3	N	218	205	123	29	57	184	29	8	26	60	41	22	1002	.050
	\bar{X}	187	214	192	255	259	241	269	310	252	204	206	242		
4	N	43	61	28	3	33	48	10	5	18	17	14	7	287	.014
	\bar{X}	246	255	239	288	315	323	357	314	322	278	315	434		
5	N	3	4	5	1	1	8	4	2	2	12	1	0	43	.002
	\bar{X}	404	340	288	431	330	478	554	390	419	371	374	0		
6	N	1	0	0	0	0	0	1	0	0	1	1	0	4	.0002
	\bar{X}	494	0	0	0	0	0	596	0	0	385	402	0		
7	N	0	0	1	0	0	0	0	0	0	0	0	0	1	.00005
	\bar{X}	0	0	418	0	0	0	0	0	0	0	0	0		
SUBTOTAL		2414	2644	1412	1325	1450	2035	1269	1629	1087	1286	1990	1527	20068	
% BY MONTH		.120	.132	.070	.066	.072	.101	.063	.081	.054	.064	.099	.076		

TABLE 8
 Number (N), Mean Weight g (\bar{X}), and Percentage of Fish by Age and Month for Pacific Mackerel Sampled in San Pedro.

AGE		MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	SUBTOTAL	% BY AGE
0	N	0	0	0	0	150	720	576	369	329	260	138	150	2692	.445
	\bar{X}	0	0	0	0	93	111	141	151	174	155	144	161		
1	N	685	305	231	199	153	115	51	1	0	6	0	5	1751	.289
	\bar{X}	229	265	286	304	284	348	377	434	0	404	0	377		
2	N	41	9	78	32	32	110	41	11	0	6	6	24	390	.064
	\bar{X}	329	353	394	408	415	436	452	474	0	444	463	468		
3	N	17	8	20	13	50	114	63	39	4	15	9	1	353	.058
	\bar{X}	502	499	536	490	521	521	549	534	493	492	559	470		
4	N	47	6	12	13	11	38	22	23	0	4	7	0	183	.030
	\bar{X}	570	637	570	675	609	698	672	583	0	585	634	0		
5	N	64	6	13	21	8	131	52	66	4	4	8	0	377	.062
	\bar{X}	698	763	718	784	681	813	783	745	817	785	781	0		
6	N	23	1	13	5	7	87	32	52	18	9	0	0	247	.041
	\bar{X}	791	907	869	818	807	854	827	809	922	893	0	0		
7	N	1	0	7	2	1	16	1	9	5	2	0	0	44	.007
	\bar{X}	782	0	903	957	875	959	1036	782	939	904	0	0		
8	N	1	0	3	0	1	8	0	0	0	1	0	0	14	.002
	\bar{X}	889	0	1023	0	1109	1133	0	0	0	849	0	0		
9	N	0	0	1	0	0	2	0	0	0	0	0	0	3	.0005
	\bar{X}	0	0	998	0	0	1080	0	0	0	0	0	0		
SUBTOTAL		879	335	378	285	413	1341	838	570	360	307	168	180	6054	
% BY MONTH		.145	.055	.062	.047	.068	.222	.138	.094	.059	.051	.028	.030		

mediately after entering the fishery, whereas jack mackerel show little seasonality until age three.

Proportion of Growth in Weight by Month

Growth in weight of northern anchovy is highly seasonal, and the pattern of growth differs between the fish landed at San Pedro and those landed at Monterey. The San Pedro anchovies achieved nearly all of their annual increase in weight during the period of February to May (Figure 9A, Table 9). However, the pattern of growth is somewhat different in young and old fish. Younger fish, age groups 0-1, showed a slight decrease in weight from September to February, while older fish, ages 2+, showed a small weight gain. The young fish grew rapidly from February to May and essentially maintained their weight until September, while older fish grew rapidly from February to April, but lost about half of this increase in weight by September. At the end of a year, the San Pedro anchovies had an 18% increase in weight. However, the younger fish exhibited much more growth than the older fish (24% versus 8%). In the Monterey fishery, anchovies lost weight from September to May, and gained weight May to September (Figure 9B, Table 9). The younger fish, age groups 0-1, showed a similar seasonal pattern, but they had a more rapid growth rate from May to September. (Notice that there were few young fish sampled from December to May.) The older fish, ages 2+, showed a marked weight loss (23%) from September to De-

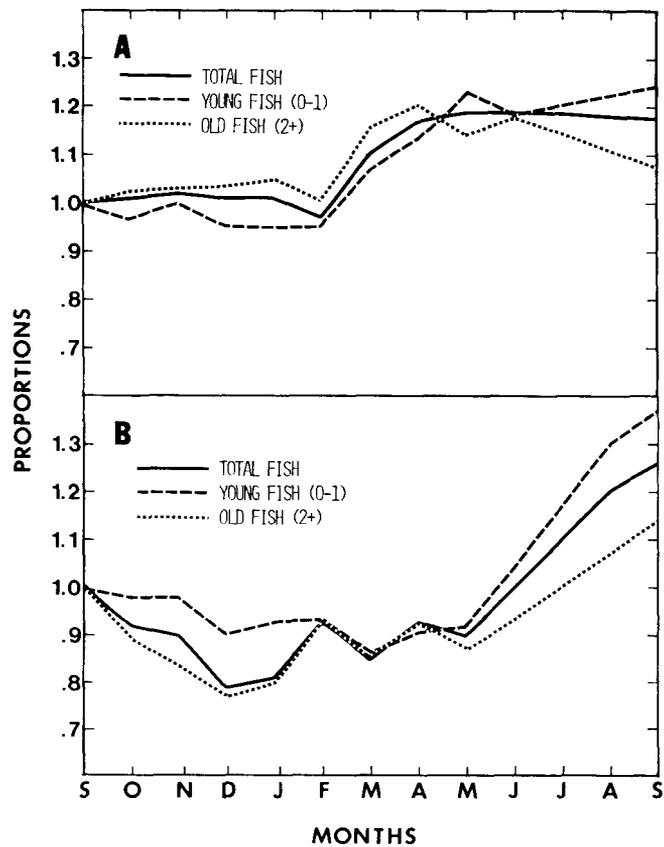


Figure 9. Proportion of growth in weight by month for (A) northern anchovy sampled in San Pedro (no data for July and August) and (B) northern anchovy sampled in Monterey (no data for June and July).

TABLE 9
 Seasonal Variation in the Weight* of Northern Anchovy, Jack Mackerel, and Pacific Mackerel.

	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
San Pedro anchovy													
Young (0-1)	1.00	.97	1.00	.95	.95	.95	1.07	1.13	1.23	1.19			1.24
Old (2+)	1.00	1.02	1.03	1.03	1.05	1.00	1.16	1.20	1.14	1.18			1.08
Total	1.00	1.01	1.02	1.01	1.01	.97	1.10	1.17	1.19	1.19			1.18
Monterey anchovy													
Young (0-1)	1.00	.98	.98	.90	.93	.93	.86	.91	.92			1.30	1.37
Old (2+)	1.00	.89	.84	.77	.80	.94	.85	.93	.87			1.07	1.14
Total	1.00	.92	.90	.79	.81	.93	.85	.93	.90			1.20	1.26
Jack mackerel													
Young (0-2)	1.00	1.09	1.13	1.18	1.26	1.28	1.43	1.48	1.60	1.74	1.75	2.07	2.16
Old (3+)	1.00	.97	1.12	1.13	1.01	.85	.85	1.04	.98	.99	.92	1.18	1.21
Total	1.00	1.08	1.13	1.18	1.25	1.25	1.42	1.47	1.59	1.72	1.73	2.07	2.14
Pacific mackerel													
Young (0-1)	1.00	1.20	1.50	1.62	1.86	1.66	1.53	1.72	2.39	2.80	2.65	3.02	2.78
Old (2+)	1.00	1.09	1.09	1.03	1.14	1.02	1.09	1.12	1.14	1.23	1.20	1.25	1.22
Total	1.00	1.16	1.40	1.42	1.81	1.58	1.47	1.63	2.17	2.70	2.39	2.68	2.32

*Expressed as a proportion of the September mean weight.

ember, much of which was regained between December and February; little change in weight occurred during the February to May period. All of their net annual increase in weight occurred from May to the following September. At the end of a year, the anchovies landed in Monterey showed a 26% increase in weight; young fish showed a 37% increase while the older fish showed a 14% increase. A comparison of the growth patterns of anchovies in the two regions shows that San Pedro anchovies increased in net weight from February to May and the Monterey anchovies increased in net weight from May to September. Other than the increase in weight that occurred from February to May, the anchovies in the San Pedro fishery showed little variation in weight. In the Monterey fishery, however, anchovies showed a loss in weight from September to May. At the end of a year, young anchovies at Monterey showed a 54% greater increase in weight than young anchovies at San Pedro; older anchovies at Monterey showed a 75% greater increase than those at San Pedro.

As previously mentioned, there are considerable differences in the growth patterns of jack and Pacific mackerel; growth is also different in the young and older individuals of both species. The data on these two species are heavily biased toward young fish, and therefore, the growth pattern of combined young and old fish is essentially the same as that for young fish. The ages chosen to represent young and old fish in jack mackerel differ from those chosen in the other two species. The natural break between the steady growth rate of young jack mackerel and the seasonal growth of older jack mackerel occurs between the ages of two and three (Figure 7).

The growth pattern for young jack mackerel, age

groups 0-2, shows a steady increase in weight all year long (Figure 10A, Table 9). The older fish, ages 3+, showed an increase in weight from September to December, followed by a loss in weight from December

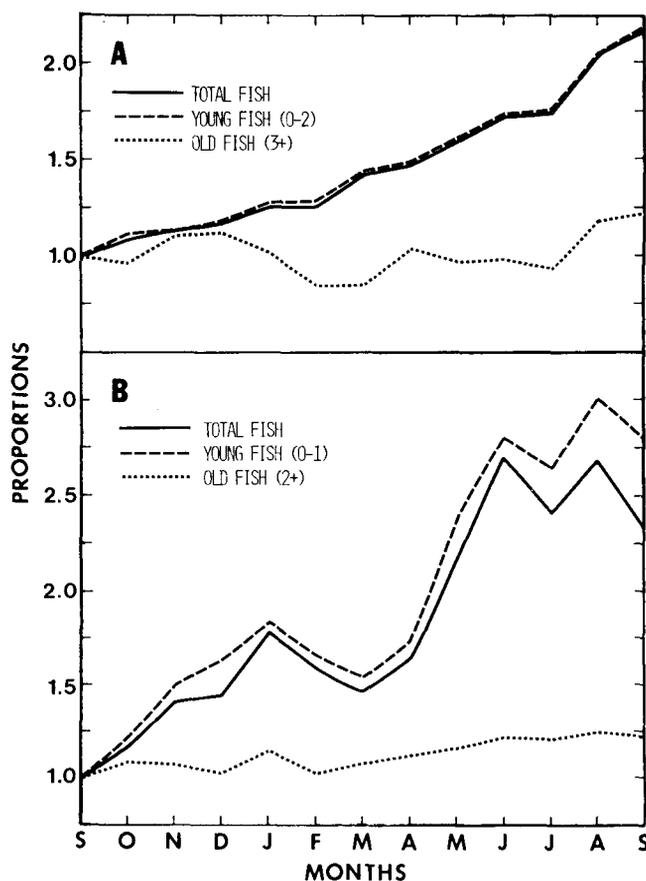


Figure 10. Proportion of growth in weight by month for (A) jack mackerel sampled in San Pedro and (B) Pacific mackerel sampled in San Pedro.

to February/March. There is little net growth from February to July. Essentially all of the net increase in weight occurs from July to September. At the end of a year, the older fish showed a 21% net increase in weight, while the younger fish showed a 116% net increase in weight.

The growth pattern for young Pacific mackerel, age groups 0-1, shows tremendous growth all year long except for a small loss in weight from January to March (Figure 10B, Table 9). The older fish, ages 2+, showed a general increase in weight from September to January. Then there is a loss in weight during late winter followed by a period of steady growth from spring to the following September. Young Pacific mackerel showed an annual net increase in weight of 178%, while the older fish showed an annual net increase of 22%. The seasonal growth patterns of jack mackerel and Pacific mackerel show that both young and old Pacific mackerel and older jack mackerel have a loss in weight from approximately winter to spring. Both young jack mackerel and young Pacific mackerel grow very quickly, but the annual growth of young Pacific mackerel is 53% greater than young jack mackerel. Older Pacific mackerel showed a 5% greater annual increase in weight than older jack mackerel.

DISCUSSION

The data presented for the seasonal distributions of lengths show that growth in length is relatively free of seasonal variation in the California stocks of northern anchovy, jack mackerel, and Pacific mackerel. The exceptions to this occur in jack mackerel older than three years, and in young-of-the-year and yearling Pacific mackerel, where growth in length is more rapid in the spring and summer than in the winter. Other than these minor exceptions, growth in length of these species is adequately described by von Bertalanffy growth equations. The situation for growth in weight is another matter; seasonal variation in growth is very large and can vary with age and geographical area.

Anchovies in California gain nearly all of their annual net increase in weight during a short period of the year. In southern California, growth begins in February and extends until April or May. Young fish essentially maintain this same weight until the next February, while older fish lose more than half of the weight gained by September. Anchovies in central California achieve their annual net increase in weight three to four months later than those in southern California. The net increase in weight starts in the period from May to July and extends to September. During the next winter, much or all of this increase

will be lost, depending on the age of the fish. It should be noted that anchovies landed in San Pedro are from the central stock, whereas those landed in Monterey are probably from both the central and northern stocks (Vrooman et al. 1981).

Jack mackerel less than three years of age show little seasonality in growth in weight, whereas jack mackerel older than three years and post-recruit Pacific mackerel have weight losses during the late winter or early spring and weight gains during the rest of the year. The most rapid increase in weight in Pacific mackerel occurs when they are one year old, during the spring and summer. In jack mackerel the most rapid increase in weight occurs when they are three years old, also during the spring and summer. In jack mackerel this period marks the transition from a steady increase in weight to seasonal increases. In both Pacific and jack mackerel this rapid increase in weight occurs when the fish are about 250 mm in fork length. It appears that at this length there is a change in some life history feature, possibly in feeding habits, which results in a rapid increase in weight.

One of the major uses of data on the growth of commercially important fishes is the application of this information to fisheries management. The principal relationship of interest is that between the age and the total weight of an individual cohort. If fishing effort is large, it is theoretically possible to maximize yields by protecting the cohort from harvesting as long as the total weight of the cohort is increasing. The more quickly the cohort is gaining weight the more likely are there to be economic benefits from protection of younger fish. The relative advantage or disadvantage of a size limit can be readily observed by comparing the observed growth in weight with the growth that would be necessary to maintain a constant cohort weight.

The annual mortality rate for northern anchovy is about 66% per year ($Z = 1.1$, MacCall 1974). Without a fishery the number of fish in a cohort would be expected to decline annually by two-thirds. In order to maintain a constant cohort weight, anchovies would have to triple their weight each year; as shown earlier, anchovies do not triple their weight even in four years. The largest annual anchovy growth rate observed in our study was the 55% increase in weight achieved by age group zero fish at San Pedro. This indicates that the growth rate of post-recruit anchovies is not sufficient to maintain the cohort biomass. If younger fish were not protected by regulations, the age composition of the catch would be expected to approximate that of the population. That is, the numbers of fish in each succeeding age group would decline by two-thirds or more (depending on the size of the fishery). The age

composition of northern anchovy in the San Pedro fishery does not approach this decay rate until the transition from age three to four. The observed proportions of age groups zero to four (0.03, 0.26, 0.33, 0.24, 0.09) indicate that the present regulations provide almost total protection for young-of-the-year fish, considerable protection for yearlings, and some protection for two-year-old-fish.

The data presented in this study suggest that, in anchovy, maximum cohort weight occurs before recruitment to the fishery. Therefore, the size limit provides protection to cohorts for at least two years beyond the time they achieve maximum biomass. Small pelagic fishes are subject to recruitment overfishing (Cushing 1975), and in the absence of any other controls a size limit could be a desirable regulation for preventing this. However, when protection against recruitment overfishing is provided by an annual quota based on the spawning stock size, as in the case with the California anchovy fishery, the principal effect of a size limit is to increase the total effort and costs necessary to harvest the quota.

The use of growth information as a tool for fisheries management of jack mackerel is affected by the lack of good estimates for their natural mortality rate. It is also influenced by the fact that jack mackerel are increasingly unavailable to the fishery after age two. If, for want of a better estimate, it is assumed that young jack mackerel (age 0-2) have a mortality rate equal to that of Pacific mackerel ($M = 0.5$, Parrish and MacCall 1978), in the absence of a fishery, about 40% of the fish will die each year. To maintain a constant cohort weight, young jack mackerel would have to gain about 67% of their weight each year. In their first year in the fishery, age group zero in September to age group one in September, jack mackerel increased in weight by about 125%. In their second and third years in the fishery the increase was about 74% and 64%. This growth rate implies that it might be possible to increase the yields of jack mackerel by protecting fish less than one year old. However, before it could be determined if a size limit would be economically beneficial, it would be necessary to have a good estimate of natural mortality. It would also be necessary to evaluate whether the probability of capturing jack mackerel, before they become unavailable to the purse-seine fishery, is high enough to warrant protection of young fish.

Pacific mackerel have the fastest growth of the three species discussed. They more than triple their weight during their first year in the fishery. In their second and third years in the fishery they increase their weight by 46% and 26%. The annual mortality rate of Pacific mackerel is about 40% per year ($M = 0.5$, Parrish and

MacCall 1978). Maximum cohort weight occurs about two years after recruitment. However, after the fish have been in the fishery for one year, the cohort biomass does not increase greatly (i.e. growth at 46% and mortality at 40%). Growth is particularly quick during the yearling spring and summer. A size limit that would protect Pacific mackerel until they have completed this growth spurt would be expected to increase yields.

The growth patterns of northern anchovy, jack mackerel, and Pacific mackerel described in this study suggest different management strategies. Maximum cohort biomass occurs before the anchovy enter the purse-seine fishery. Therefore, growth overfishing is unlikely to occur in this species even without a size limit or mesh-size limitation. Pacific mackerel are subject to growth overfishing, and the question is as yet unresolved for jack mackerel.

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AGE-COMPOSITION CHANGES IN THE ANCHOVY, *ENGRAULIS MORDAX*, CENTRAL POPULATION

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ABSTRACT

Age composition sampling of anchovy reduction fishery landings detected major changes in the past four years (1977-1980). Weak year classes spawned in 1974 and 1975, a large increase of a major predator, and greatly increased catches by the combined Mexico-California reduction fisheries have caused a major change to a much younger anchovy population. Prior to 1977, the fisheries exploited mostly 2- and 3-year-old fish with substantial catches of older fish. Since 1977, ages 0 and 1 have heavily dominated catches, and older age groups have diminished. Under the present high fishing pressure nearing 400,000 tons per year, failure of two successive year classes could depress anchovy stocks to undesirably low levels.

RESUMEN

Por medio de los muestreos tomados de los desembarques de la pesquería de reducción de anchoveta para determinar la composición en edades, se descubrieron grandes cambios durante los últimos cuatro años (1977-1980). Pequeñas generaciones desovadas en 1974 y 1975, la población aumentada de un depredador importante, y el aumento en las capturas de las pesquerías de reducción combinadas de México y California han sido causas de un cambio mayor en una población mucho más joven de anchoveta. Antes de 1977, las pesquerías explotaban por la mayor parte a peces de 2 y 3 años con capturas substanciales de peces de más edad. Desde 1977, los peces de edades 0 y 1 han dominado las capturas, y se han disminuido los grupos de más edad. Bajo la alta explotación actual, acercándose a 400,000 tons. anuales, el fracaso de dos generaciones sucesivas podría deprimir las existencias de anchoveta hasta niveles muy bajos y desfavorables.

INTRODUCTION

The California Department of Fish and Game has routinely sampled the anchovy reduction fishery of

southern California since its inception in 1965. The basic objective of this sampling program is to monitor the impact of the fishery on population age structure and to assess year class strength.

Until recent years, no major changes in anchovy age composition were detected by the reduction fishery sampling. During the four years of 1977-1980 there was a pronounced shift to a much higher proportion of young age groups and fewer large old fish. Concurrent with this change the combined anchovy catch of California and Mexico reached a record high of 386,000 short tons in 1980, and a major predator, the Pacific mackerel, *Scomber japonicus*, has greatly increased in numbers.

METHODS

Anchovy reduction fishery landings at San Pedro, southern California, are sampled during the fishery season, which was from September 15 to May 15 for the years 1965-1978, and since 1978, from September 15 to June 30, with a closure February 1 to March 31. A maximum of 30 samples, each weighing 250 grams, is randomly drawn from each 5,000 short tons landed.

Age determination is made from otoliths by the method described by Collins and Spratt (1969). Age composition of individual 5,000-ton strata are combined to estimate the age composition of the fishery season landings. Age and size composition of reduction seasons' landings of all southern California and most Mexican landings have been published since inception of the California fishery (Collins 1969, 1971; Chavez et al. 1977; Spratt 1972, 1973a, b; Sunada 1975, 1976, 1977, 1979a, b, in press; Sunada and Silva 1980).

Due to sampling bias, the true age composition of the anchovy central population has not been determinable by fishery catches, which undersample ages 0 and 1 and slightly undersample old age groups (Mais 1974). For reasons not clearly understood, the youngest age groups are not fully recruited to the purse seine-based fishery. It must be kept in mind that these data reflect age composition of the fishery catch and

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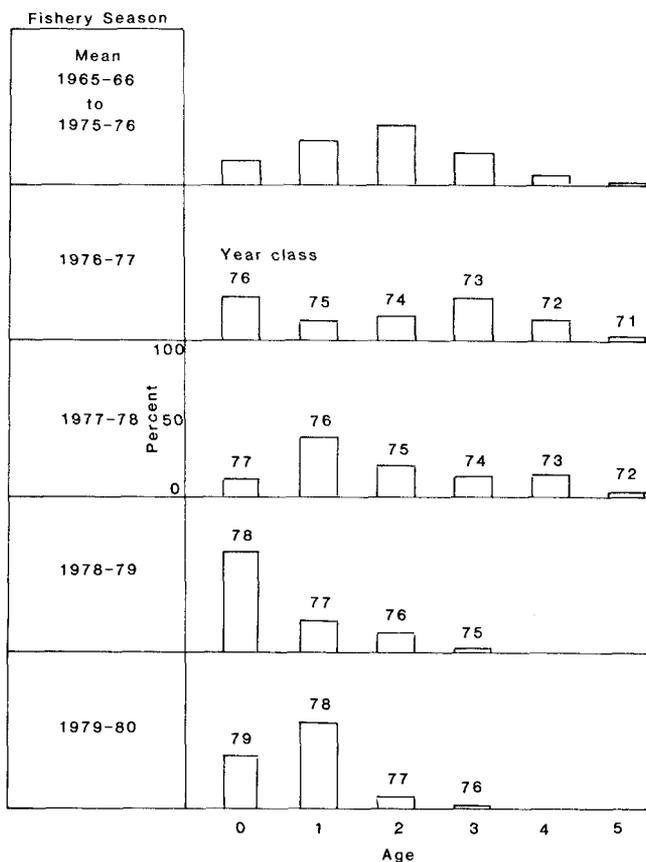


Figure 1. Age composition of California anchovy reduction fishery, by numbers of fish.

not the population. Their chief value is as an index of population age-structure change.

RESULTS

Fishery Age Composition 1965 to 1976

During the first 11 fishery seasons, no major changes in age composition occurred. A typical season catch/age composition consisted mainly of 1, 2, and 3-year-old fish, a relatively low percentage of age 0, and progressively much diminished percentages of 4-year-olds and older (Table 1). The mean age composition for the first 10 seasons (there was an insignificant catch in 1967-68 season) was 10% age 0 (range 2.4-27.0%), 27% age 1 (range 10.5-50.8%), 37% age 2 (range 22.4-48.5%), 20% age 3 (range 8.2-34.0%), 5% age 4 (range 1.5-12.0%), and 1% age 5 (range 0.1-3.2%), (Figure 1, Table 1). The relatively low percentages of ages 0 and 1 strongly indicate these age groups are not fully vulnerable to the fishery. Age 1 fish exceeded Age 2 in only two of the 11 seasons.

In these first 11 years, the California reduction catch fluctuated considerably until reaching a maxi-

TABLE 1
Age Composition¹ of Anchovy Reduction Fishery of Southern California

Season	Age						
	0	1	2	3	4	5	6
1965-66	4.5	14.7	48.5	23.4	7.5	1.3	0.1
1966-67	6.9	22.9	38.1	23.0	7.5	1.4	0.2
1967-68	1.4	12.6	26.3	30.7	19.3	9.1	6.6
1968-69	18.5	45.9	22.4	8.2	4.3	0.6	0.1
1969-70	27.0	27.8	35.2	8.3	1.5	0.1	Tr
1970-71	4.0	32.1	40.2	20.1	3.1	0.5	Tr
1971-72	11.3	51.0	26.8	8.4	2.4	0.2	0
1972-73	9.5	25.9	47.6	14.2	2.3	0.4	Tr
1973-74	6.9	20.2	35.3	30.8	6.2	0.6	Tr
1974-75	4.6	18.5	39.5	26.4	9.6	1.3	0.1
1975-76	2.4	10.5	37.7	34.0	12.0	3.2	0.2
1976-77	27.8	12.0	16.2	27.9	13.4	2.5	0.2
1977-78	10.5	37.7	20.3	14.0	14.1	2.4	0.2
1978-79	65.1	19.6	13.1	1.6	0.5	0.1	0
1979-80	34.5	55.2	8.8	1.3	0	0	0

¹Percent of age group by numbers of fish.

imum of 156,000 short tons in 1975 (Table 2). The Mexican catch earlier was much lower but sharply increased after 1973. By 1975 the combined California-Mexico catch was 217,000 tons (Table 2).

Fishery Age Composition 1977 to 1980

Weak year classes spawned in 1974 and 1975 apparently were the cause of a major change in catch age composition when these year classes became fully recruited to the fishery. In the 1976-77 season, the 1974 year class as 2-year-olds comprised only 16% of the catch, the lowest contribution of any previous year class at this age. This was also the only season thus far that more 3-year-old fish (1973 year class) were caught than 2-year-olds (Figure 1).

TABLE 2
Annual Catch Record¹ of California and Mexican Anchovy Fisheries

Year	California	Mexico	Total
1965	0.2	10	10
1966	27	15	42
1967	32	23	55
1968	14	16	30
1969	65	4	69
1970	93	31	124
1971	44	22	66
1972	67	34	101
1973	131	17	148
1974	81	48	129
1975	156	61	217
1976	122	79	201
1977	110	157	267
1978	11	143	154
1979	56	272	328
1980	47	339	386
	1,056	1,271	2,327

¹In 1,000 short tons. Sources: California landings, California Department of Fish and Game; Mexico landings, Instituto Nacional de Pesca, 1965-1978, and Departamento de Pesca, 1979-80.

The 1975 year class comprised the second lowest (20%) of 2-year-olds up to that time in the 1977-78 season (Figure 1). This was also the only season there was a higher percentage of 4-year-olds (1973 year class) than 3-year-olds (1974 year class).

By the 1978-79 season, the weak 1974 and 1975 year classes as 3- and 4-year-olds had nearly disappeared from the fishery. The 1976 year class, which appeared strongly at ages 0 and 1, faded at age 2. Age 0 fish (1978 year class), for the first time in the history of the fishery, became the dominant (64%) age group in the catch (Figure 1). The highest percentage of any previous age 0 fish (1976 year class) was 28%. Ages 0 and 1 combined comprised over 84% of the age composition for this season (Figure 1).

The dominance of young fish continued and intensified in the 1979-80 season. Nearly 90% of the catch was composed of ages 0 (1979 year class) and 1 (1978 year class). Ages 2 (1977 year class) and 3 (1976 year class) comprised the lowest percentages for these age groups in the history of the fishery (Figure 1).

The age composition of these last two seasons' catches is radically different from the previous 12. The young age groups, which previously were considered not fully recruited, now grossly dominate the fishery.

Most California landings from 1965-1977 were heavily weighted toward the fall portion of the fishery season. Fall landings during this period were composed mainly of the older age groups (2, 3, and 4+ year olds) with few 1-year-olds and almost no fish of the incoming year class (age 0). The younger age groups normally appeared in spring landings. In the 3 seasons, 1978-79, 1979-80, and 1980-81, fall landings have been poor relative to those of spring and have contained an abnormally high proportion of young fish. This was particularly true of the 1978 year class, which was prevalent in California and Mexican catches during the fall of 1978.

During the 1977 to 1980 period, the commercial catch fluctuated greatly. The California catch plummeted from 110,000 tons in 1977 to 11,000 tons in 1978, increased to 56,000 tons in 1979, and was 47,000 tons in 1980 (Table 2). Since 1979, fishing seasons were approximately six weeks longer than in previous years. The Mexican catch fluctuated less with a slight dip from 1977 to 1978 and a substantial increase to 339,000 tons in 1980 (Table 2). The combined California-Mexico 1980 catch of 386,000 tons is the highest to date. The Mexican fishery has surpassed and greatly exceeded the California fishery the past

four years (Table 2). Some of the Mexican catch is comprised of a southern stock not exploited by California fishermen.

Virtual Population of Year Classes 1968 to 1977

The California reduction catch of each year class during its lifetime was estimated for year classes 1968 through 1977 (Table 3). The fishing fleet and effort did not fluctuate much while these year classes were in the fishery; so these catches or virtual populations should be a rough index of year-class strength. These data show the 1972 year class to be the strongest, with a catch of 142,000 tons, and the 1977 year class the weakest, with a catch of 22,000 tons. Strong successive 1970-1973 year classes produced the high California catch levels sustained from 1972 to 1977 (Figure 2, Table 2). Of the four year classes following 1973, three were weak (1974, 1975, and 1977) and one (1976) was mediocre (Figure 2). These year classes have been in the fishery during the three fishing seasons (1977-78, 1978-79, and 1979-80) of much reduced California catches and during the period when age composition shifted toward younger fish. They have also been present when acoustic, larvae, and egg production surveys have indicated a smaller anchovy population (Mais 1978, 1979, 1980; Stauffer 1980; Stauffer and Parker 1980).

Some assessment of year class strength can also be derived from the Mexican catch of the 1976 and later year classes when that fishery became fully geared up. The catch of the 1976 year class in California was mediocre relative to those of other year classes taken

TABLE 3
Anchovy Reduction Catch¹ by Year Class: 1968-1980

Year class	Catch (in short tons)		Total
	California	Mexico	
1968	67,000	—	67,000
1969	82,000	—	82,000
1970	119,000	7,000	126,000
1971	119,000	23,000	142,000
1972	142,000	61,000	203,000
1973	123,000	71,000	194,000
1974	48,000	58,000	106,000
1975	33,000	41,000	74,000
1976	66,000	152,000	218,000
1977	22,000	72,000	94,000
1978	48,000 ²	409,000 ³	457,000
1979	still in fishery		
1979	12,000 ²	155,000 ³	167,000
1980	—	101,000 ³	101,000

¹Data from California Department Fish and Game Fishery Monitoring and Instituto Nacional de Pesca, Mexico.

²To June 15, 1980.

³To January 1, 1981, extrapolated from California catch data.

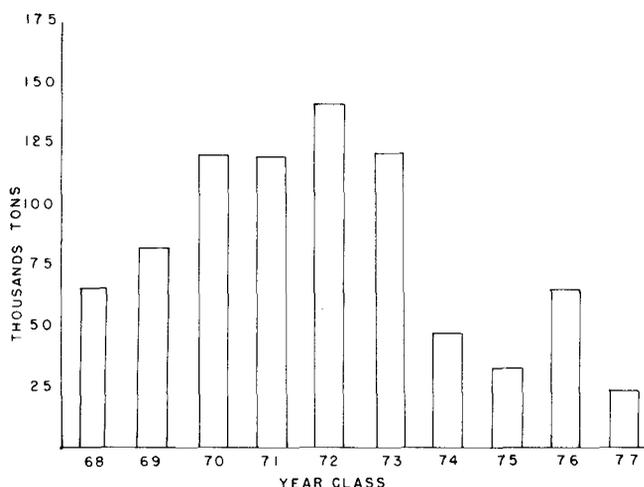


Figure 2. California anchovy reduction catch by year classes 1968 to 1977.

in California. This year class, however, appeared strongly in the Mexican catch of 1977 and 1978. More fish of the 1976 year class were taken (152,000 tons) in Mexico than the strong 1972 year class (142,000 tons) in the California catch. The weakness of the 1977 year class was also reflected in the Mexican catch of 72,000 tons relative to the 1976 and 1978 year class catches of 152,000 and 409,000 tons respectively (Table 3). The Mexican catch of 1978 year class thus far greatly exceeds that of any preceding year class in either California or Mexico. This year class will contribute more than 450,000 tons to the combined California and Mexico fisheries during its lifetime and must be ranked one of the strongest of all to date (Table 3). However, its relative strength may have been exaggerated by the increased effort by the Mexican fishery since 1976.

Year Class Catch by Age

The catch of each year class by age also strongly indicates that the fishery has shifted sharply in recent years to very heavy exploitation of year classes in the

younger age groups and a much diminished catch of older fish of the same year class. In the California fishery the proportion of catch of age 0 fish ranged from 2.7 to 26.7% from year classes 1968 to 1975, with a mean of 9.4% (Table 4). The catch percentage of this age group for the 1976 and 1977 year classes was 45 and 36% respectively. There has been a drastic decline in catches of these year classes as 3-year-olds and older. The range of percent of catches as 3-year-olds for year classes, 1968-1974, was 6.7 to 33.9% with a mean of 22.5%. The range of this category for the 1975-1977 year classes was 0.5 to 3.2% with a mean of 2.4%. The highest percentage of these last 3 year classes is less than half the lowest percentage of the seven earlier year classes. There was essentially no catch of 4- and 5-year-old fish of 1974-1977 year classes (Table 4).

Cumulative catch at age for the 1972 and 1977 year classes illustrates this change (Figure 3). The 1972 cumulative catch curve for year classes is typical of those of 1968-1973 with relatively small contribution of age groups 0 and 1, major contribution of 2 and 3, and measurable quantities of 4- and 5-year-old fish. The catch curve of the 1977 year class is typical of those of recent years with high contribution of ages 0 and 1, low contribution of ages 2 and 3, and no catch of 4- and 5-year-olds.

The combined contribution of 0- and 1-year-olds expressed as a percentage of year class catch were plotted against a similar combination of 3- and 4-year-olds for the 1968-1977 year classes (Figure 4). The catch percentage of the younger group ranged between 20 and 25% for the strong 1970-1973 year classes and from 40 to 87% for the weak 1974, 1975, and 1977 year classes. This same combined age group comprised 88% of the mediocre to strong 1976 year class.

TABLE 4
 California Anchovy Reduction Catch of Year Classes 1968-1977 by Age Group.

Year class	Catch ¹	Catch Percent by Age Group						Total
		0	1	2	3	4	5	
1968	67,166	7.2	33.7	47.9	6.7	2.7	1.8	100%
1969	81,573	26.7	31.5	17.2	13.3	9.2	1.9	100
1970	119,000	2.7	22.5	30.3	31.2	9.4	3.8	100
1971	118,356	5.1	16.4	36.0	26.0	14.3	2.2	100
1972	141,740	5.0	17.2	32.4	33.9	10.0	1.3	100
1973	122,897	6.8	17.5	42.8	24.1	8.8	0	100
1974	47,837	11.1	31.0	35.8	22.0	0	0	100
1975	32,514	10.4	39.6	46.7	3.2	0	0	100
1976	65,555	45.0	43.3	11.2	0.5	0	0	100
1977	21,719	36.3	51.4	11.3	1.0	0	0	100

¹Short tons; data from California Department of Fish Game Fishery Monitoring

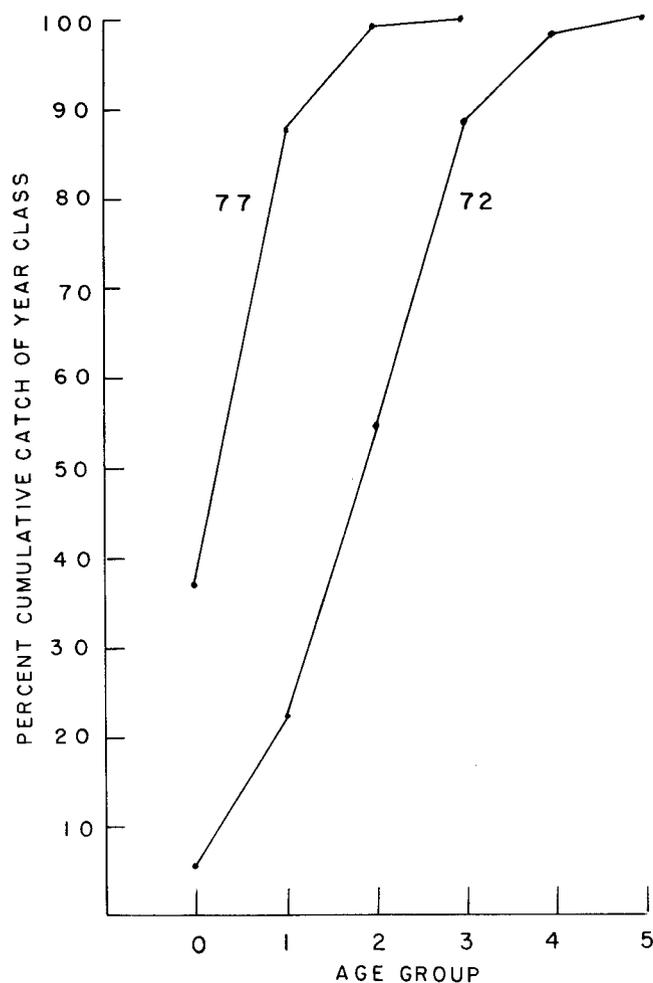


Figure 3. California cumulative catch by age of anchovy year classes 1972 and 1977.

The catch percentage of the older group ranged from 33 to 44% for the strong year classes (1970-1973) and from 1% to 22% for the weak ones (1974, 1975, and 1977). The contribution of this age group by the 1976 year class was only 0.5% (Figure 4).

DISCUSSION

The main questions raised by the recent shift in the age structure of the central anchovy population are its causes and effects. Of the five year classes prior to and including 1978, three were weak (1974, 1975, and 1977), one was strong (1978), and the 1976 year class appeared strong in Mexico and mediocre in California. Concurrent with the shift to a younger population, there have been record high catches, principally by Mexico, a large increase in a major predator, the Pacific mackerel, and a decrease in the population size as estimated by acoustic, larvae, and egg production surveys.

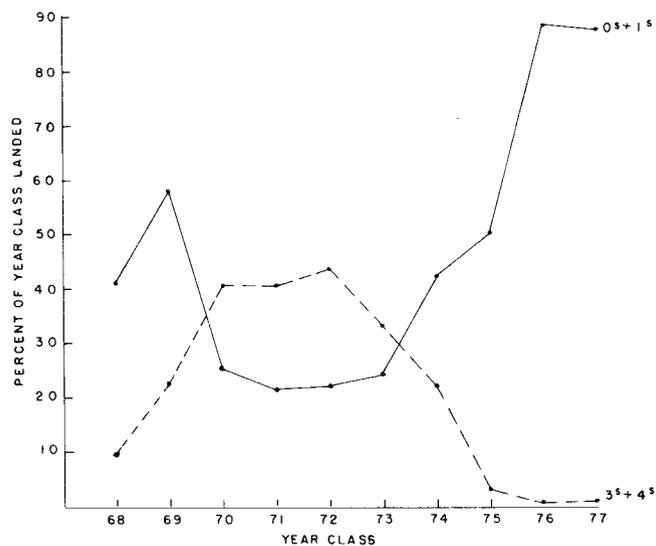


Figure 4. California anchovy reduction catch of year classes 1968-1977 at combined ages 0-1 and 3-4.

Based on data of past years, predation by Pacific mackerel alone has not resulted in a young and reduced anchovy population. In 1963, larvae surveys by the National Marine Fisheries Service estimated an all-time high of 4.66 million tons in the central stock of anchovy spawner biomass. This and the preceding 2 years also had high Pacific mackerel population ranging from 96,000 to 137,000 tons as estimated by Parrish and MacCall (1978). Although the Pacific mackerel population has increased greatly since 1976, recent population estimates (Klingbeil 1976, 1977, 1978, 1979, 1980) are lower than the 1961-63 period. Limited sea-survey midwater trawl data in 1963 indicated an adult anchovy age composition consisting mainly of 2-, 3-, and 4-year-old fish with 3-year-olds predominating, (Heimann 1969).

The relative weakness of three of the last five year classes (1974-1978) together with the combined mortality of the fishery and the Pacific mackerel predation are the most likely causes of age-structure shift and decrease in population size.

The 1978 year class appears to be very strong. If weak year classes were the cause of age-structure change, the 1978 year class should persist in the fishery at ages 4 and 5 and should shift the age structure back to the pattern of the early 1970's. If, however, this year class disappears after age 3, as did the 1976 and 1977 year classes, increased mortality, with the fishery the most likely source, must be considered the major cause of altered age structure.

The present anchovy fishery age composition and

the lower population levels the past three years should be viewed as a danger sign to the health of the central population and must be watched very closely. With the recent record high in California-Mexico catches, heavy exploitation of ages 0 and 1 and a scarcity of older fish, a failure of two consecutive year classes such as occurred in 1974 and 1975, could sharply reduce the population level to undesirably low levels.

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DESCRIPTION OF REARED LARVAE AND EARLY JUVENILES OF THE CALICO ROCKFISH, *SEBASTES DALLII*

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ABSTRACT

The developmental stages of the calico rockfish, *Sebastes dallii*, are described marking the first time that a species of eastern Pacific *Sebastes* has been reared from birth to pelagic juvenile. Larvae were obtained from a field-caught pregnant female and reared on wild zooplankton screened to a size range of 105-272 μm . Calico rockfish larvae are 5 mm long at birth and transform into pelagic juveniles by 20-mm length. The larvae are slender compared to those of most other described species and have a distinctive pattern of melanophores. Morphological and meristic features are described, with particular attention to the development of head spines. Rearing techniques are outlined and discussed.

RESUMEN

Se describen los estadios de desarrollo de *Sebastes dallii*, marcando la primera vez que se haya cultivado una especie de *Sebastes* del Pacífico oriental desde el parto hasta la etapa de juvenil pelágico. Se obtuvieron larvas de una hembra capturada en su hábitat, y se alimentaron de zooplancton que se cernió hasta obtener un rango de 105 a 272 μm . Las larvas de *Sebastes dallii* son 5 mm de largo al nacer y se convierten en juveniles pelágicos a los 20 mm de longitud. Estas larvas son más delgadas que las de la mayoría de otras especies descritas y tienen un patrón distintivo de melanóforos. Se describen sus características morfológicas y merísticas, con atención al desarrollo de las espinas de la cabeza. Se presentan y se discuten las técnicas de cultivo.

INTRODUCTION

Sebastes dallii is a small species of rockfish found in near coastal waters of 18- to 256-m depth from San Francisco, California, to Sebastian Viscaíno Bay, Baja California (Miller and Lea 1972). It occurs in a variety of habitats from rocky reefs (Turner et al., 1969) to soft shelf substrates (Mearns 1979). Because of its small size and slow growth rate (Chen 1971), calico rockfish are not fished commercially and constitute a minor fraction of the sport fishery (Crooke 1978; Wine 1979). Mearns (1979), however, has

shown that small juveniles of this species exhibit episodes of high recruitment to the coastal shelf of southern California, which suggests that they may be of ecological importance.

Sebastes dallii, like other species of *Sebastes*, is a fecund ovoviviparous fish whose larval stages are part of the ichthyoplankton. The larval and early juvenile stages of some *Sebastes* species have been described (Moser et al. 1977; Richardson and Laroche 1979; Laroche and Richardson 1980); however, little is known about the early life history stages of shallow-water coastal rockfish species. The difficulty in identifying larvae of nearshore fishes and the recent interest in coastal ichthyoplankton generated by environmental concerns stimulated us to rear larvae of these fishes to obtain voucher life history series. The life history series of *Sebastes dallii* described herein marks the first time a species of eastern Pacific rockfish has been reared from birth to juvenile.

MATERIALS AND METHODS

A pregnant 104-mm SL *Sebastes dallii* was collected by hook and line in shallow water south of the Coronado Islands, Baja California, on February 24, 1978. Larvae were freely running from the female at the time of capture. The larvae were immediately placed in 1-gallon jars of seawater where they began swimming towards the surface. The larvae were transported to the laboratory in an ice chest and placed in a 400-liter cylindrical black culture container within six hours of capture. At this time, some larvae appeared neutrally buoyant, as they maintained their position in the water column with little effort. Many larvae sank to the bottom, and mortality of these larvae over the next two days was probably 100%. The viable larvae had considerable amounts of yolk left, although not as much as those that sank to the bottom. Food was added to the cultures after four days in captivity. The food consisted of live plankton collected from Mission Bay, San Diego, with a 70- μm -mesh plankton net. The zooplankton was first screened through a 272- μm -mesh screen and collected on a 105- μm -mesh screen to select for smaller copepodites and nauplii. The initial densities of food organisms were copepods, 2/ml; copepodites, 4.6/ml; nauplii, 3.9/ml; polychaete larvae, 1.1/ml; and rotifers, 3.9/ml. A liter of a dense

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culture of algae, *Tetraselmis suecica*, was added daily as food for the zooplankton. The culture container was illuminated from above by four 40-W daylight fluorescent bulbs at 0.9 m from the surface. When the density of nauplii fell below 1/ml, additional zooplankton was added to the culture. As the larvae grew larger, larger zooplankton were added to the tanks. Moribund larvae and detritus were siphoned from the bottom of the container daily. Filtered seawater was added to maintain the culture volume at approximately 400 liters.

Larvae were removed from the culture tank over a period of 60 days and preserved in 4% buffered formaldehyde for subsequent analysis of morphometry and pigmentation and for meristic and osteological analysis. A series was cleared in a graded series of KOH-glycerin solutions and was stained with Alizarin Red-S. Terminology and methods of description follow those of Moser et al. (1977) and Moser and Ahlstrom (1978).

DESCRIPTION OF DEVELOPMENT

General Development

Larvae of *S. dallii* are released during winter and spring and are about 5.0 mm long at birth (Figure 1). Notochord flexion occurs between 6.2 and 8.0 mm, and the larvae have transformed into pelagic juveniles by 20.0 mm (Table 1). The larvae are comparatively slender with a relatively small head and large eyes. They develop a complex and distinctive pattern of

melanophores (Figure 1) of which the postanal lateral series may prove to be diagnostic when the larvae of other nearshore species of *Sebastes* become known.

The slender terete pelagic juveniles (Figure 1E) resemble those of *S. jordani* in form and pigmentation (see Moser et al., 1977 for comparison). Mearns (1979) has shown that the juveniles become demersal in early summer at a length of 20-25 mm standard length (SL). A 36.6-mm benthic juvenile collected by otter trawl has the adult pigment pattern (see Phillips 1957).

Morphology

Larvae and pelagic juveniles of *S. dallii*, like those of *S. jordani*, are slender-bodied compared to other species (Table 2). Other features shared with *S. jordani* are a comparatively small head and short snout-to-anus distance. The latter character, of course, is not as marked as in the shortbelly rockfish, *S. jordani*. Eye diameter is greater in *S. dallii* than in the other species studied.

Spine formation in larvae of *S. dallii* (Table 3) follows in general the pattern described for other species (Moser 1972; Moser and Ahlstrom 1978; Richardson and Laroche 1979; Laroche and Richardson 1980). In *S. dallii*, the pterotics, 2nd and 4th anterior preoperculars, 1st and 4th upper infraorbitals, 1st lower infraorbital, lower posttemporals, and nuchals are present in larvae but are lost in subsequent juvenile stages. The cleithral spine is present in pelagic juveniles but becomes minute and finally lost in benthic juveniles.

TABLE 1
 Measurements of Reared Larvae¹ of *Sebastes dallii*.

Standard length in mm (age in days)	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
5.1 (1)	2.2	1.1	0.21	0.45	1.0	0.29	0.16	—	—
5.3 (3)	2.2	1.2	0.35	0.45	1.0	0.29	0.25	—	—
5.4 (5)	2.3	1.2	0.31	0.43	1.0	0.28	0.35	—	—
5.5(11)	2.3	1.2	0.34	0.46	0.87	0.31	0.35	—	—
5.6(10)	2.4	1.2	0.31	0.46	0.85	0.33	0.35	—	—
5.7 (8)	2.4	1.3	0.33	0.51	0.96	0.34	0.42	—	—
5.9(10)	2.5	1.4	0.35	0.54	1.1	0.35	0.41	—	—
6.2(15)	2.6	1.5	0.40	0.53	1.0	0.34	0.46	—	—

6.5(32)	2.8	1.6	0.43	0.60	1.2	0.50	0.44	—	—
6.9(32)	3.1	1.8	0.57	0.65	1.4	0.52	0.63	0.02	—
7.0(32)	3.1	1.8	0.52	0.66	1.3	0.49	0.60	0.08	—
7.1(33)	3.3	1.9	0.55	0.73	1.5	0.54	0.59	0.10	—
7.3(33)	3.5	2.1	0.56	0.83	1.7	0.65	0.60	0.16	4.1
8.0(20)	3.8	2.1	0.58	0.79	1.8	0.61	0.70	0.13	4.4

7.3(38)	3.6	2.2	0.68	0.85	1.8	0.64	0.64	0.17	4.2
8.6(26)	4.2	2.4	0.72	0.88	1.9	0.70	0.83	0.22	4.8
9.4(28)	4.5	2.8	0.80	1.0	2.1	1.1	1.0	0.27	5.3
9.8(42)	5.1	3.2	1.0	1.1	2.2	1.2	1.0	0.34	5.7
10.1(49)	5.7	3.2	1.0	1.2	2.8	1.4	1.1	0.86	5.9
20.2(60)	11.7	6.1	2.0	2.1	5.1	4.7	1.7	3.3	12.3
21.7(60)	12.2	6.3	2.1	2.1	5.5	5.2	1.8	3.2	12.8

¹Specimens between dashed lines are undergoing notochord flexion.

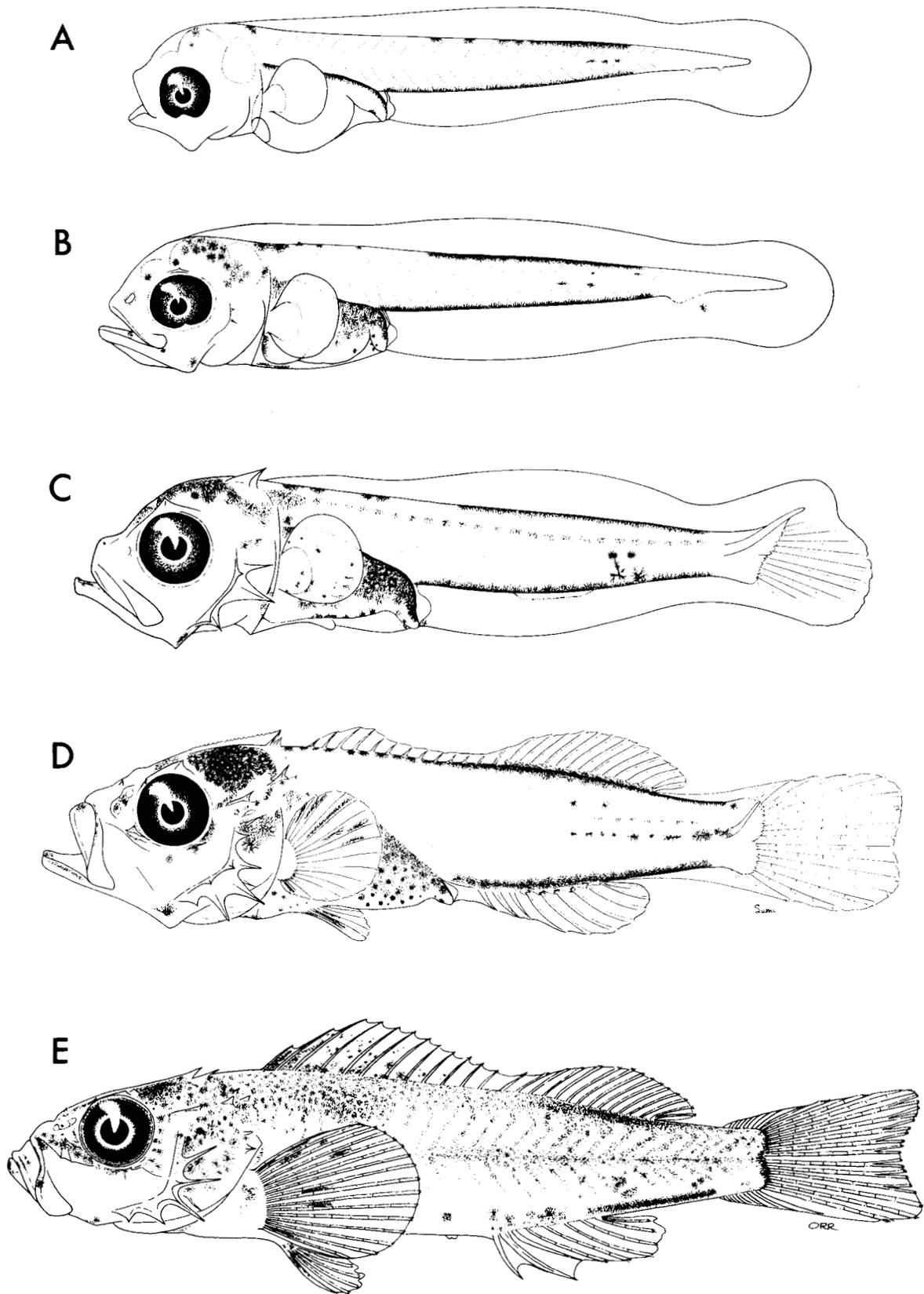


Figure 1. Reared specimens of *Sebastes dallii*: A. 5.1-mm larva (Day 1); B. 6.2-mm larva (Day 15); C. 7.1-mm larva (Day 33); D. 10.1-mm larva (Day 49); E. 21.7-mm pelagic juvenile (Day 60).

TABLE 2
 Comparative Morphometry of Five Species of *Sebastes*¹

Species	Snout to anus distance		Head length		Snout length		Eye diameter		Body depth		Pectoral fin length		Pectoral fin base depth		Pelvic fin length		
	Body length	Head length	Head length	Body length	Head length	Body length	Head length	Body length	Body length	Body length	Body length	Body length	Body length	Body length	Body length	Body length	
<i>S. dallii</i>	A	42.4±0.52(42-43)	22.6±1.06(21-24)	25.6±3.02(19-29)	38.0±1.85(35-41)	17.6±1.85(15-20)	5.6±0.52(5-6)	5.9±1.36(3-7)	—	—	—	—	—	—	—	—	—
	B	45.7 2.07(43-48)	26.5 1.38(25-29)	28.7 1.86(27-32)	37.8 1.33(36-40)	20.7 2.07(18-23)	8.0 0.63(7-9)	8.3 0.82(7-9)	—	—	—	—	—	—	—	—	—
	C	50.8 3.27(48-56)	30.6 1.95(28-33)	30.4 0.89(29-31)	36.8 1.92(34-39)	23.8 2.68(22-28)	11.0 2.45(9-14)	10.2 0.84(9-11)	—	—	—	—	—	—	—	—	—
	D	57.0 1.41(56-58)	29.5 0.71(29-30)	33.0 0.00(33)	33.5 0.71(33-34)	25.0 0.00(25)	23.5 0.71(23-24)	8.0 0.00(8)	—	—	—	—	—	—	—	—	—
<i>S. jordani</i>	A	36.5 0.84(36-38)	22.3 1.51(21-25)	26.8 3.43(23-31)	37.7 0.82(36-38)	17.0 1.26(16-19)	6.7 0.52(6-7)	6.5 0.55(6-7)	—	—	—	—	—	—	—	—	—
	B	42.4 1.67(41-45)	28.4 2.19(26-30)	35.5 1.29(34-37)	32.2 2.50(29-35)	21.0 1.00(20-22)	8.4 1.14(7-10)	7.8 0.45(7-8)	—	—	—	—	—	—	—	—	—
	C	51.0 2.86(46-54)	32.3 1.44(31-36)	34.4 1.98(31-39)	29.3 2.10(27-34)	23.8 1.19(22-26)	16.8 3.25(11-20)	7.9 1.00(7-10)	—	—	—	—	—	—	—	—	—
	D	53.3 1.03(52-55)	31.2 1.94(28-33)	34.0 2.83(30-38)	26.5 1.52(24-28)	22.2 0.84(21-23)	20.5 1.05(19-22)	7.0 0.00(7)	—	—	—	—	—	—	—	—	—
<i>S. levis</i>	A	39.6 2.30(37-44)	24.7 1.60(23-28)	30.7 2.63(27-35)	33.1 2.67(29-36)	21.7 1.11(20-23)	17.4 5.29(11-24)	10.9 1.57(8-13)	—	—	—	—	—	—	—	—	—
	B	48.9 3.44(45-56)	30.5 1.85(28-33)	34.8 0.87(34-36)	32.5 1.77(30-35)	28.5 3.51(24-35)	34.9 6.96(24-46)	12.9 0.64(12-14)	—	—	—	—	—	—	—	—	—
	C	59.2 2.87(57-63)	35.0 2.00(34-38)	30.2 2.22(28-33)	30.5 1.73(28-32)	34.0 1.41(33-36)	45.0 3.74(41-50)	11.2 0.96(10-12)	—	—	—	—	—	—	—	—	—
	D	63.0 0.82(62-64)	33.8 0.96(33-35)	30.5 2.38(28-33)	27.0 3.37(25-32)	35.0 1.41(34-37)	40.8 7.09(32-47)	10.2 0.96(9-11)	—	—	—	—	—	—	—	—	—
<i>S. macdonaldi</i>	A	42.4 3.53(36-47)	27.6 2.25(24-31)	30.6 4.16(25-36)	34.6 2.34(31-37)	23.1 3.99(13-27)	8.4 1.21(6-10)	—	—	—	—	—	—	—	—	—	—
	B	51.8 3.56(48-56)	35.6 1.52(34-38)	34.0 4.00(30-38)	32.0 1.41(31-34)	31.6 2.07(30-35)	13.0 1.22(12-15)	—	—	—	—	—	—	—	—	—	—
	C	60.3 3.06(55-64)	37.5 1.84(34-41)	32.9 3.00(29-37)	33.0 1.33(31-35)	34.4 1.17(33-36)	19.3 3.65(15-26)	—	—	—	—	—	—	—	—	—	—
	D	64.2 2.44(61-68)	35.1 2.37(32-38)	27.9 2.09(25-32)	30.7 2.74(26-34)	31.4 1.59(30-34)	30.4 1.74(28-34)	—	—	—	—	—	—	—	—	—	—
<i>S. paucispinis</i>	A	41.0 2.74(37-44)	26.8 2.28(24-29)	27.4 3.21(24-32)	32.8 3.77(29-37)	19.6 1.67(17-21)	16.4 4.56(11-21)	9.0 0.71(8-10)	—	—	—	—	—	—	—	—	—
	B	44.8 3.70(40-49)	29.6 1.95(27-32)	30.6 1.82(29-33)	30.2 1.64(29-33)	23.0 1.41(21-24)	27.2 2.49(25-31)	9.0 0.71(8-10)	—	—	—	—	—	—	—	—	—
	C	57.3 3.82(51-61)	37.1 1.07(36-39)	32.2 0.98(31-33)	31.3 1.70(28-33)	29.6 0.98(28-31)	35.7 1.25(34-37)	7.6 0.53(7-8)	—	—	—	—	—	—	—	—	—
	D	62.3 2.73(60-66)	36.2 1.72(33-38)	30.5 2.95(26-33)	27.8 1.72(26-30)	27.3 0.52(27-28)	28.2 3.40(25-34)	6.0 0.89(5-7)	—	—	—	—	—	—	—	—	—

¹A = preflexion larvae; B = larvae undergoing notochord flexion; C = postflexion larvae; D = pelagic juveniles

TABLE 3
 Sequence of Development of Head Spines¹ of *Sebastes dallii*.

Spine	Length of specimen (mm)																
	5.6	5.9	6.0	6.3	6.4	7.1	7.3	8.0	8.6	9.8	10.1	20.2	36.6	49.1	53.0	67.5	
Pterotic	X														0	0	0
2nd anterior preopercular	X													0	0	0	0
3rd posterior preopercular	X																
Postocular		X															
2nd posterior preopercular				X													
Parietal					X												
4th anterior preopercular						X						0	0	0	0	0	0
4th posterior preopercular							X										
Lower posttemporal									X								0
Lower opercular									X								
Interopercular									X								
1st upper infraorbital									X			0	0	0	0	0	0
3rd anterior preopercular									X/0	0	0	0	0	0	0	0	0
1st lower infraorbital										X				0	0	0	0
5th posterior preopercular										X							
Nuchal											X	0	0	0	0	0	0
Upper opercular											X						
Supracleithral											X						
Nasal											X						
Preocular											X						
1st posterior preopercular											X						
2nd lower infraorbital											X						
4th upper infraorbital											X		0	0	0	0	0
Cleithral												X					
Tympanic												X					
Upper posttemporal												X					
Subopercular													X				

¹Presence of spine is indicated by an "X" or continuous line. Absence of a spine is indicated by "0." In asymmetrical specimens, the condition of the left and right sides is separated by a slash.

The absence of supraocular and the 2nd and 3rd upper infraorbitals in larvae of *S. dallii* may be useful in identifying this species.

Fin Development

The pectoral fins of *S. dallii* larvae are the smallest of any species studied (Table 2; Richardson and Laroche 1979; Laroche and Richardson 1980). Rays begin ossifying at about 8.0 mm, and the full comple-

ment of 16-17 is present at 10.0 mm (Table 4). The pelvic fins begin to develop when the larvae reach 7.0-mm length, and they remain relatively small throughout the larval period (Table 2). Ossification of the rays begins in 9-mm larvae, and the full complement of I,5 rays is present at 10.1 mm. The cartilaginous radial elements and rays of the dorsal and anal fins appear in 7-mm larvae, and the ossification of the rays is initiated in 9-mm larvae. The 10-mm larva has

TABLE 4
 Meristics of Cleared and Stained Larvae of *Sebastes dallii*.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
5.9					1	1											
6.0					1	1											
6.2	1	1			2	2											
6.4	2	3			2	2											
7.1	3	4			3	3											
7.3	4	4			4	4											
8.0	7	8			6	6	7	7	1	2		10					20
8.6	8	7		2	7	7	11	11	1	2		12					23
9.8	8	7	3	4	7	7	15	15	1	2		14	II,6	IV,11	I,2	I,2	26
10.1	8	7	7	8	7	7	17	18	1	2	4	17	III,6	XIII,13	I,5	I,5	26
20.2	8	7	12	13	7	7	17	17	2	2	9	22	III,6	XIII,13	I,5	I,5	26

the adult complement of XIII, 13 dorsal and III,6 anal rays.

The caudal fin begins to form at about 6.0 mm with the appearance of some cartilaginous hypurals and principal rays. Ossification of the principal and procurrent rays is shown in Table 4. As described for *S. melanostomus*, the lowermost superior hypural and the uppermost inferior hypural each have two centers of ossification, which may reflect the ancestral condition of 3+3 hypurals in the family (Moser and Ahlstrom 1978).

Pigmentation

The pigment pattern of newborn larvae consists of a postanal series of melanophores along the dorsal and ventral midlines, a short postanal series along the horizontal myosepta, one to several spots at the nape, a patch of melanophores above the brain, an embedded melanophore in each otic region, and a series of melanophores along the dorsolateral surfaces of the gut on each side (Figure 1A).

For 50 newborn larvae the number of melanophores in the ventral postanal series ranged from 29 to 49 ($\bar{x} = 37.7 \pm 4.33$ SD), whereas the number in the dorsal series ranged from 7 to 19 ($\bar{x} = 13.7 \pm 2.74$ SD). The ventral series extended from the first to the 15th or 16th postanal myomere, and the dorsal series extended from the 4th or 5th to the 14th or 15th postanal myomere. The lateral postanal melanophores ranged from 1 to 6 ($\bar{x} = 2.3 \pm 1.20$ SD) on the left side and 0 to 5 ($\bar{x} = 1.8 \pm 1.13$ SD) on the right side. Four specimens lacked lateral melanophores on the right side.

Melanophores above the brain ranged from 1 to 9 ($\bar{x} = 4.2 \pm 1.79$ SD) whereas those on the nape ranged from 0 to 6 ($\bar{x} = 2.0 \pm 1.17$ SD). Two specimens lacked nape melanophores. Of the 50 specimens, 12 had otic melanophores on both sides, 14 lacked them on one side, and 24 lacked them on both sides.

The ventral postanal series remains throughout the larval period, but becomes divided into two lines on either side of the developing anal fin in 7-mm larvae. Anterior to the anal fin, the two lines become embedded and extend anterior to the anus. In some larvae, one to several melanophores may form just lateral to the posterior region of the ventral midline series. They appear in 80% of the specimens from 6.2 to 10.1 mm and, when maximally developed, appear as a bridge between the ventral midline series and the series along the horizontal septa (Figure 1C).

Melanophores are added anteriorly to the dorsal midline series and reach the level of the anus when the larvae are about 6.0 mm (Figure 1B). Thereafter,

melanophores are added irregularly in the zone between the occiput and the anterior end of the dorsal midline series. These melanophores form in two lines on either side of the dorsal midline. When the dorsal fin begins to form in 7-mm larvae, the postanal dorsal midline series begins to separate into two series on either side of the midline, and these become continuous with the more anterior dorsal pigment lines. The smallest specimen in which the dorsal pigment is continuous from occiput to caudal peduncle is 7.3 mm.

The lateral postanal melanophores persist throughout the larval period. For 37 specimens between 5.0 and 8.0 mm, the number of lateral melanophores on the left side ranged from 0 to 7 ($\bar{x} = 2.5 \pm 1.43$ SD), and those on the right side ranged from 0 to 5 ($\bar{x} = 2.6 \pm 1.26$ SD). Of the 37 specimens, only four lacked lateral melanophores on one side, and all had them on at least one side. Melanophores are added to the lateral series in larger larvae, and in the two pelagic juveniles the entire horizontal myoseptum is heavily pigmented, as are the myosepta above and below it. A zone of solid pigmentation covers the dorsal region of the body (Figure 1E).

Melanophores are added to the patch above the nape so that the entire nape is covered when the larvae reach 6.0 mm (Figure 1B). At this size the patch begins to be overlain by dorsal musculature, and simultaneously, embedded melanophores begin to appear over the posterior region of the vertebral column. Melanophores are added between this region and the embedded nape patch, and in larvae as small as 6.9 mm, the series of embedded melanophores above the vertebral column is complete (Figure 1C).

Melanophores are added above the brain so that in 6-mm larvae, where there are 12-14 melanophores, the dorsal surfaces of the optic and cerebellar lobes are solidly pigmented. Melanophores also begin to appear on the lateral and ventrolateral surfaces of the cerebellar and medullary regions, and by 7.0 mm these areas are solidly pigmented (Figure 1C). Melanophores appear on the dorsal surface of the olfactory lobes at about 5.5 mm and number from 1 to 3 until the larvae reach 7.0 mm, when the region becomes solidly pigmented.

Melanophores appear on the lower jaw in larvae about 5.5 mm long. One to several melanophores are present anteriorly on one or both sides of the jaw in about half the larvae up to 7.0 mm. More are added in larger larvae to cover the anterior curve of the lower jaw (Figure 1D). Melanophores also form posteriorly on the jaw. One or two may be present on each side in the region of the articular bone, and one or two may form in the angular region. Melanophores may be absent in either the angular or articular region on either

side, but at least one melanophore is present on the posterior lower jaw.

At about 7.0 mm, melanophores appear at the anterior region of the snout. In about half the larvae larger than 7.0 mm, one or two melanophores are present in the midline of the snout between the maxillaries. From one to three melanophores may form along the maxillaries lateral to the median snout region, with about half the specimens lacking them altogether on one or both sides. More appear at about 10.0 mm to form a streak along the upper portion of each maxillary (Figure 1D). Also, in 7-mm larvae, one or two melanophores may be present on each nasal flap. In larvae of about 10.0 mm, the nasal flaps become solidly pigmented. In larvae larger than 7.0 mm, one to several melanophores are usually present on the upper region of the opercle (Figure 1C) along with a single melanophore on the preopercle posterior to the eye. Melanophores in these regions increase in number at about 10.0 mm, and the entire upper half of the head is pigmented in the pelagic juveniles (Figure 1D, E).

The initial melanophore pattern of the gut region is augmented in larvae between 5.0 and 6.0 mm. The dorsolateral gut pigment increases to form a shield over the gut (Figure 1B). Also, pigment extends forward internally to form an embedded melanistic zone medial to the cleithra. On the ventral midline of the gut a preanal and cleithral melanophore are at each end of a series that can range up to 10 in number. When expanded they appear as a partial or complete line. In later stage larvae the dorsolateral shield extends ventrad and reaches the ventral midline in larvae larger than 8.0 mm.

The fins are lightly pigmented. The first pigment to form is a single melanophore in the future hypural region of the developing caudal fin (Figure 1B). It is present in about one third of the larvae larger than 5.2 mm. When the hypurals begin to develop, the melanophore is usually located at the posterior margin of the hypural plate between the superior and inferior groups of elements. At about 10.0 mm, additional melanophores form along the posterior margin of the plate and outline the entire posterior margin in the pelagic juveniles. Pigment appears on the pectoral fins in some 7-mm larvae, where one to several melanophores may be present on the dorsal and on the ventral region of the blade (Figure 1C). A maximum of 7 upper and 4 lower melanophores is present in larvae up to 10 mm and a maximum of 12 was present on the fin blades of the pelagic juveniles. A patch of melanophores begins to form on the medial surface of the pectoral base in 8-mm larvae and intensifies with development. Pigmentation first appears on the pelvic

fins in 8-mm larvae as a melanophore at the base and one to several on the fin blade. Melanophores are added to the blade in later stages but are restricted to the proximal region (Figure 1C). Pigmentation is present on the spinous dorsal fin in the two pelagic juveniles. The first two interradiation membranes of the spinous dorsal are solidly pigmented, and the membranes between the 3rd and 10th spinous rays have scattered pigmentation restricted to the proximal half of the fin (Figure 1E).

DISCUSSION

Although Japanese workers have successfully reared four species of western Pacific *Sebastes* (summarized in Moser et al. 1977), *S. dallii* is the first eastern Pacific species to be reared through to juveniles. Reasons for our previous lack of success in rearing larvae of several *Sebastes* species using a diet of *Artemia* nauplii (as used by the Japanese workers) and more recently a diet of the rotifer, *Brachionus plicatilis*, are open to speculation. One possibility is that *S. dallii*, being a moderately shallow species, has more robust larvae than those of the deeper water species used in previous rearing attempts. The four successfully reared western Pacific species are all shallow-water forms (Lo-chai Chen, personal communication). Also, the diet of wild zooplankton maintained at high densities during the first few days of feeding undoubtedly contributed to our success. *Artemia* nauplii are far from an optimally nutritional diet, and our experience with *Brachionus* was that even high densities of this organism did not elicit a feeding response in rockfish larvae.

Perhaps the most important factor in achieving success with *Sebastes* larvae is the stage of development at birth. Timing of birth in the wild appears to be precisely related to stage of development, perhaps by some biochemical or mechanical cue from the larvae, and capture of full-term females that are ready to give birth is a rare event. This raises the more general question of whether or not there is a maternal nutritional contribution in addition to the yolk. If this were true, one might speculate that such nutrition is critical to development of certain organ systems late in the pregnancy and that premature birth might impair organogenesis. Affirmation of this speculation must await future physiological studies on intraovarian development of *Sebastes*.

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EDDIES AND SPECIATION IN THE CALIFORNIA CURRENT

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ABSTRACT

Northern anchovy, Pacific sardine, and Pacific hake have population discontinuities in the vicinity of Punta Eugenia, Baja California. The same latitude has been described as a provincial boundary for several taxa, including coastal fishes, brachyurans, bryozoans, and molluscs. The distribution of wind stress over the surface waters of the California Current region has a persistent feature in the same area: the coastal impingement of a zone of surface water convergence, which elsewhere is parallel to the coast of the Californias and several hundred kilometers offshore. Semipermanent cyclonic eddies are evident north and south of Punta Eugenia, and it has been suggested that they play a role in the recruitment of pelagic larvae to the adult populations in these areas.

Limited communication between the eddies suggests a speciation mechanism that would be most effective on populations that time their spawning to coincide with strong eddy formation. One may also expect geminate species north and south of Punta Eugenia and few short-range endemics with long dispersal strategies along the coast of northern Baja California between the eddies.

RESUMEN

Existen discontinuidades en las poblaciones de anchoveta del norte, sardina y merluza en la zona de Punta Eugenia, Baja California. Esta latitud ha sido descrita como una frontera provincial de varios grupos taxonómicos, incluyendo peces costeros, braquiuros, briozoarios y moluscos. La distribución de esfuerzo del viento por las aguas de superficie de la región de la Corriente de California tiene una característica persistente en esta misma área, que es el encuentro con la costa de una zona de convergencia de aguas de superficie, que en otras partes ocurre paralela a la costa y a unos cientos de kilómetros afuera. Remolinos ciclónicos semipermanentes son evidentes al norte y al sur de Punta Eugenia, y se ha sugerido que éstos juegan un papel en el reclutamiento de larvas pelágicas a las poblaciones adultas en estas zonas.

La comunicación limitada entre los remolinos sugiere un mecanismo de especiación que sería más efectivo para poblaciones que fijan su época de desove

durante los períodos en que se forman fuertes remolinos. Puede esperarse encontrar especies geminadas al norte y al sur de Punta Eugenia y algunas especies endémicas de rango corto con estrategias de larga dispersión en la costa del norte de Baja California, entre los remolinos.

INTRODUCTION

Several coastal pelagic fish species display a population break in the vicinity of Punta Eugenia, Baja California. Distinct discontinuities in morphometric measurements, meristic counts, and proportion of selected protein polymorphs suggested restricted gene flow between populations north and south of approximately 28° N for *Engraulis mordax*, the northern anchovy (Hubbs 1925; McHugh 1951; Vrooman et al. in press), for *Sardinops caerulea*, the Pacific sardine (Clark 1947; McHugh 1950; Marr 1957, 1960; Sprague and Vrooman 1962; Vrooman 1964), and for *Merluccius productus*, the Pacific hake (Vrooman and Paloma 1977). Vrooman and Paloma (1977) referred to the southern population of *M. productus* as "dwarf hake" and suggested that it differs from *M. productus* and the more southern *M. angustimanus* at the species level. The southern populations of all three fishes (*Engraulis mordax*, *Sardinops caerulea*, and *Merluccius productus*) show similarities in some of the ways they differ from the northern population: growth is reduced after the first year resulting in a reduced maximum adult size, maturity occurs at an earlier age, and the life span is shorter; the southern forms have proportionally longer heads, longer snouts, and larger eyes.

The latitude of Punta Eugenia has been described as a provincial boundary for a wide variety of taxa including coastal fishes (Hubbs 1960), brachyurans (Garth 1960), bryozoans (Soule 1960), and molluscs (Hall 1964; Valentine 1966). These authors refer to a variously named warm-temperature fauna between Point Conception and Punta Eugenia and a distinct fauna of uncertain origin from Punta Eugenia south to Cabo San Lucas. Hubbs (1960) tentatively placed this region in the Panamic province but noted the "reduced tropical fauna," high endemism, and "insular characteristics" of the biota.

Superimposed on the distributions of coastal animals are the distributions of invertebrate species as-

sociated with oceanic water masses. The distribution of oceanic euphausiids and copepods, indicators of subarctic, equatorial, and central waters, have a common terminus at Punta Eugenia (Brinton 1962, 1967, 1973; Fleminger 1964, 1967). The junction of these distributions appears to move northward or southward in concert with temperature anomalies as described in CalCOFI Atlas Number 1 (Anonymous 1963) and by Wyllie and Lynn (1971), although shallow-water forms show a much clearer response than do deeper forms (Brinton 1960).

HYDROGRAPHY

The general hydrography off the coast of the Californias is determined by the California Current and is related to the anticyclonic circulation of the central North Pacific; however, significant features can be associated with local wind patterns and topography (Sverdrup et al. 1942; Smith 1968). Long-term monthly mean distributions of wind stress show alongshore flow throughout the year, weakest in the winter and strongest in the summer (Nelson 1977). Resolved on a 1° grid, however, net Ekman transport, proportional to and at right angles to the wind stress, shows considerable spatial variability. In general, an area of divergence parallels the coast, bounded by a zone of convergence 200-300 km from the coastline. The position of change from offshore divergence of surface water to convergence corresponds with the position of maximum wind stress, which intensifies, winter to summer, as the gradient between the semipermanent high pressure cell over the eastern Pacific Ocean and the low pressure cell over the southwest United States increases. The zone of convergence impinges the coasts at Punta Eugenia; this feature persists throughout the year and may preclude any poleward movement of water near the coast (Nelson 1977).

Surface current patterns, which describe cyclonic eddies in the Los Angeles Bight and southwest of Punta Eugenia, confirm Nelson's prediction (Bakun and Nelson 1977). Surface flow of the California Current appears to be diverted offshore at Point Conception and again at Punta Eugenia, while semipermanent eddies are apparent south of these headlands (Reid et al. 1958). Owen's (1980) description of baroclinic eddies and their persistence is in accord with this description.

DISCUSSION

The above-mentioned taxa have planktonic larval stages. The coastal eddies may play a role in recruitment to coastal adult populations by entraining a fraction of the larvae, thus offsetting to some extent

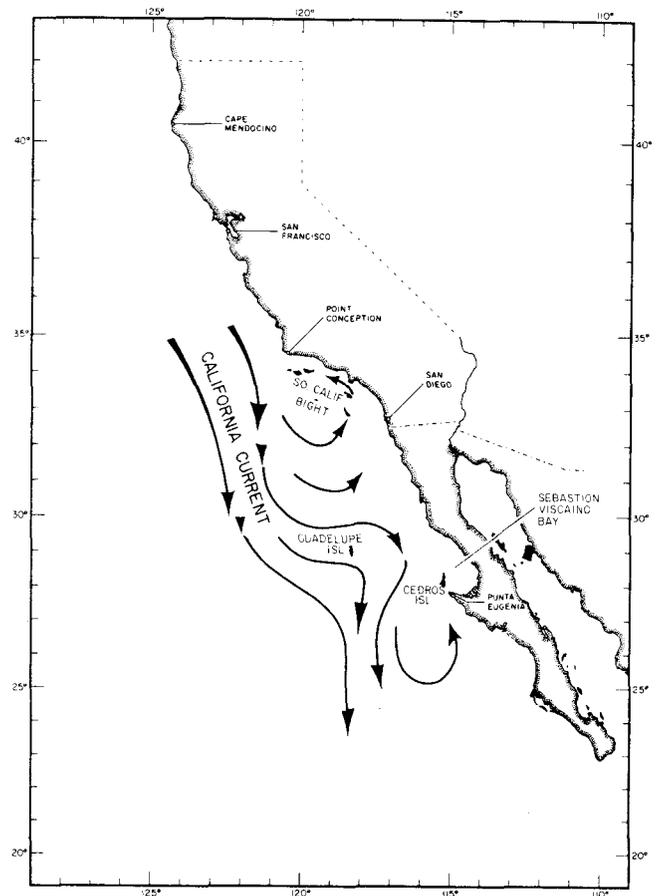


Figure 1. Large, persistent coastal eddies, south of Point Conception and Punta Eugenia, may entrain pelagic larvae and thus contribute to the recruitment to resident adult populations. Isolation of the eddies may constitute a speciation mechanism.

dispersion to the southwest via the California Current. Johnson (1960) has suggested such a mechanism for maintaining populations of *Panulirus interruptus*, the spiny lobster, in the Southern California Bight and southwest of Punta Eugenia. Boehlert (1977) recognized the possible importance of the Southern California Eddy to the recruitment of *Sebastes* spp., rockfishes. Early ichthyoplankton studies off the coast of the Californias found relatively few sardine eggs and larvae off northern Baja California and characterized these waters as a "marine desert" bounded by "rich" waters to the north and south (Anonymous 1952).

If the eddies are important to the process of recruitment, then the limited communication between them suggests a restricted gene flow between populations in the Southern California Bight and those south of Punta Eugenia. This postulated mechanism for speciation lends itself to several predictions:

1. Genetic differentiation between populations, within a species, should be greatest for those forms that time their spawning to coincide with

strong eddy formation as opposed to those forms that may time their spawning in response to other cycles (e.g. primary productivity).

2. There should be evidence of geminate species north and south of Punta Eugenia; e.g. *Labidocera trispinosa* and *L. johnsoni* (Fleminger 1975).
3. On the coast of northern Baja California, between the eddies, there should be a low proportion of dispersal types among sessile populations. A pelagic larval phase would imply dependence on long-range dispersal from the north; instead there should be selection for short pelagic phases or none at all.
4. The latitude of the hydrographic barrier may vary and be obscured by the convergence of oceanic water masses in the same general area which appears to be most pronounced in the upper layers.

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TROPHIC STRUCTURE AND THE CESIUM-POTASSIUM RATIO IN PELAGIC ECOSYSTEMS¹

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ABSTRACT

Collections of plankton and of pelagic squid, fishes, and marine mammals from the Southern California Bight and the eastern tropical Pacific were made to determine what, if any, relationships exist between trophic level and the cesium-potassium (Cs/K) ratio. Numerical trophic level assignments were computed independently from stomach content analysis data and were then compared to concentrations of Cs and K, as determined by atomic absorption spectrometry of muscle tissues, and to the Cs/K ratio, which was found to increase by a factor of 2.4 per trophic step. This increase is higher than that found in inshore food webs, suggesting that pelagic food webs may be more highly structured than those inshore. The need for more rigorous methods for making trophic level assignments is discussed.

RESUMEN

Se hicieron colecciones de plancton y de calamares pelágicos, peces y mamíferos marinos de la Bahía del Sur de California y del Pacífico oriental tropical para determinar qué relaciones, si las hay, existen entre el nivel trófico y la proporción de cesio a potasio (Cs/K). Asignaciones numéricas de niveles tróficos fueron computadas independientemente de los datos de análisis de contenidos estomacales, y después se compararon con concentraciones de Cs y K determinadas por espectrometría de absorción atómica de los tejidos musculares, y también con la proporción Cs/K, que aumentaba por un factor de 2.4 por etapa trófica. Este incremento es más alto que aquel que se ha encontrado en redes alimenticias cercanas a la costa, lo que sugiere que las redes alimenticias pelágicas pueden ser más estructuradas que las que se encuentran cerca de la costa. Se discute la necesidad de de-

sarrollar métodos más rigurosos para hacer asignaciones de niveles tróficos.

INTRODUCTION

It is not in the terrestrial experience continuously to inhale the young, eggs, sperm, food and excreta of all of our fellow creatures . . . Although it may seem repulsive to us, it, nevertheless, is the way of marine life. John D. Isaacs, Testimony before House Hearings, U.S. 92nd Congress, 24-25 May 1978.

The goal of this study was to determine the degree to which increased structure of pelagic marine food webs can lead to increasing concentrations of pollutants in marine animals. It is commonly assumed that marine food webs are as highly structured as those in terrestrial and freshwater ecosystems, an assumption that has led to public apprehension that pollutants will accumulate in seafood organisms via the feeding process. However, Isaacs (1972, 1973, 1976) proposed that with the exception of terrestrial expatriates (birds and mammals), marine food webs are largely unstructured, i.e. that they are composed of opportunistic, multidirectional feeders, and thus are not amenable to concentration of trace contaminants via the feeding process. Studies by Young (1970), Young et al. (1980), and Mearns and Young (1980), which included determination of cesium (Cs), potassium (K), and the ratio Cs/K in several coastal ecosystems and the Salton Sea, have given conflicting results. In the Salton Sea, Cs and the Cs/K ratio increased 2- to 3-fold per trophic step; in contrast, Cs and the Cs/K ratio in nearshore coastal ecosystems either did not increase with increase in trophic level (Gulf of California) or increased only slightly. Young et al. (1980) also included determination of Cs/K in a small group of fishes caught offshore in the San Pedro Channel; these data suggested that pelagic organisms produce trophic

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step increases in Cs/K ratios higher than those in the nearshore ecosystems.

METHODS

In this study we conducted a new survey of pelagic ecosystems. Our primary objective was to determine to what extent Cs/K ratios are related to trophic level assignments when those assignments are derived from food habits analyses of a suite of representative pelagic organisms. In addition, we felt that it would be useful to identify trophic relationships among major fishery species of the region—mainly anchovy, mackerel, bonito, tuna, and billfish.

A chemically independent quantitative method for assigning trophic levels to target species was developed. This is a simple numerical method based on the Index of Relative Importance (*IRI*) of food items (Pinkas et al. 1971).

To make sure the patterns we found were not unique to the Southern California Bight or its particular fauna, we decided to also make collections from a different ecosystem—the eastern tropical Pacific food web of tunas and pelagic sharks.

Field Sampling

In the Southern California Bight, collections of zooplankton, squid, teleosts, elasmobranchs, and mammals were taken during 1979 and 1980 from an area roughly bounded by San Miguel Island, San Nicholas Island, San Clemente Island, and San Diego. Zooplankton were sampled with a net of 0.3-mm mesh from three stations south of Point Dume. Some fish were taken by hook-and-line, but most of the fish specimens were taken by commercial fishermen and transferred directly with catch data to the Southern California Coastal Water Research Project (Table 1). In addition to the major pelagic fishes and invertebrates, we were able to collect tissues from five California sea lions (*Zalophus californianus*), a blue whale (*Balenoptera musculus*), and a white shark (*Carcharodon carcharias*, Table 1).

Quantities (25-50 g) of zooplankton, taken from each of three surface horizontal tows south of Point Dume on 21 August 1980, were quickly frozen in glass containers for chemical analyses; subsamples were fixed in formalin for taxonomic identification. Small and medium-sized fishes and the squid were returned on ice to the laboratory where they were frozen for later dissection. The mackerels and bonito were measured, weighed, and eviscerated and their stomach contents examined immediately or fixed in

formalin for later examination. Eviscerated bodies were then frozen for later tissue dissection. Large fishes were identified, measured, and where possible, weighed in the field or at dockside. Then one or more 0.5- to 1.0-kg chunks of muscle tissue from the anterior dorsal area were removed, returned to the laboratory on ice, and frozen for later tissue dissection.

Collections from the eastern tropical Pacific region were taken during Cruise 1089 aboard the *M/V Sarah Ann* under charter to the Inter-American Tropical Tuna Commission (IATTC) between 11 and 29 April 1980 (Table 1). Additional collections of flying fishes (*Exocoetus monocirrhus*), taken aboard the *M/V Enterprise* on Cruise 1083 during October and November 1978, were used in the chemical analyses.

As soon as possible after capture, the tunas, sharks, and other large fish were weighed to the nearest half-pound, measured to the nearest millimeter (fork length), and placed on a clean plastic-covered work area. A 0.5- to 1.0-kg chunk of white muscle was then cut from the dorsal area behind the head with a clean stainless steel knife and frozen in a clean labeled plastic bag. The entire stomach was removed from each fish, and individual bait fishes (consumed by the tunas during the fishing operation) were removed and discarded. If food organisms in the stomachs were found to be in very fresh condition, they were removed and frozen separately in clean plastic bags. Stomachs containing partially digested organisms were frozen intact in plastic bags. The whole squids, flying fishes, and frigate mackerels were also frozen in plastic bags.

Stomach Content Analysis

Stomach contents were analyzed in detail sufficient to compute one of several Indices of Relative Importance (*IRI*). Our requirements were (a) minimum of 15 positive stomachs, (b) a taxonomic description of each item in each stomach, (c) number of each item in each stomach, and (d) total volume or weight of each type of item in each stomach. For most fish, stomach contents were completely sorted by eye with aid of a dissection microscope. Contents of anchovy intestines and stomachs required use of a compound microscope in order to estimate the proportions of zooplanktonic and phytoplanktonic taxa. In general, then, organisms and other material were removed from the stomachs, rough sorted, identified to the lowest possible taxonomic level, and weighed by lowest taxonomic category to the nearest 0.1 g (squid beaks and small

TABLE 1

Common and Scientific Names, Months, Years, Locations and Methods of Capture of Zooplankton and Pelagic Squid, Elasmobranchs, Teleosts, and Mammals from the Southern California Bight and Eastern Tropical Pacific Ocean, 1978-80.

Common name	Scientific name	Month(s) captured	Location(s)	Method(s)
SOUTHERN CALIFORNIA BIGHT (32°40'-34°20'N; 118°20'-120°40'W)				
Zooplankton		August 1980	3-5 km S. of Pt. Dume	0.3-mm mesh net
Northern anchovy	<i>Engraulis mordax</i>	August-October 1980	Off Orange County and Port Hueneme	Commercial and bait seine
Market squid	<i>Loligo opalescens</i>	December 1979	Isthmus, Catalina Island	Commercial hoop net
Pacific sardine	<i>Sardinops sagax caeruleus</i>	May 1980	S. of Pt. Dume, Los Angeles County	Commercial seine
Jack mackerel	<i>Trachurus symmetricus</i>	January and June 1980	San Pedro Channel, Catalina Is.	Commercial seine, gill net
Pacific mackerel	<i>Scomber japonicus</i>	January 1980-January 1981	San Pedro Channel, Dago Bank, Catalina Is., Newport Beach	Commercial seine, gill net, jigging.
Pacific bonito	<i>Sarda chiliensis</i>	January and June 1980	King Harbor, Huntington Beach, Newport Beach	Hook and line, gill net
California barracuda	<i>Sphyræna argentea</i>	June 1980	Newport Beach, Orange County	Commercial gill net
California sea lion	<i>Zalophus californianus</i>	March-April 1980	Beaches, Los Angeles and Orange Counties	Taken by Los Angeles Co. Dept. Health Services.
Swordfish	<i>Xiphias gladius</i>	October-December 1980	San Miguel Is., San Clemente Is., Catalina Is., Oceanside	Commercial gill net
Blue shark	<i>Prionace glauca</i>	May 1980	Newport Beach, Avalon Bank	Commercial gill net
Thresher shark	<i>Alopias vulpinus</i>	September-October 1980	San Nicholas Is., Santa Barbara Is., Catalina Is., Oceanside	Commercial gill net
Mako shark	<i>Isurus oxyrinchus</i>	May-June 1980	San Pedro Channel, Avalon Bank, Newport Beach	Commercial gill net
White shark	<i>Carcharodon carcharias</i>	February 1980	Catalina Island	Commercial gill net
Blue whale	<i>Balenoptera musculus</i>	July 1980	140 km SW of San Diego	Collided with tanker, recovered in L.A. Harbor
EASTERN TROPICAL PACIFIC (5°-13°N; 81°-89°W, IATTC Cruise 1089)				
Zooplankton		April 1980	5°34'-12°27'N; 85°12'-89°32'W	0.6-mm mesh
Squid	<i>Symplectoteuthis ovalaniensis</i>	April 1980	5°56'-12°00'N; 81°45'-88°35'W	Rod and reel, dipnet
Flyingfish	<i>Oxyporhamphus micropterus</i>	April 1980	11°48'-12°18'N; 88°29'-89°34'W	Landed on deck, regurgitated
Frigate tuna	<i>Auxis thazard</i>	April 1980	11°14'-12°30'N; 87°52'-89°38'W	Jig line
Skipjack tuna	<i>Katsuwonus pelamis</i>	April 1980	5°39'-11°16'N; 81°42'-88°06'W	Live bait and pole, jig line
Yellowfin tuna	<i>Thunnus albacares</i>	April 1980	5°52'-11°16'N; 81°56'-88°06'W	Live bait and pole, jig
Silky shark	<i>Carcharhinus fulciformis</i>	April 1980	6°31'N; 85°01'W	Rod and reel
EASTERN TROPICAL PACIFIC (3°-4°S; 78°-84°W, IATTC Cruise 1086)				
Flying fish	<i>Exocoetus monocirrhus</i>	October-November 1978	3°-4°S; 78°-84°W	Dip net

items) or 1.0 g (whole organisms).

Stomachs of some of our specimens were empty (See RESULTS section for details.). Therefore we turned to the literature for additional data that could be used to compute *IRI* or otherwise help in making trophic level assignments. These data are included in the RESULTS section.

Assignments of Trophic Levels

Five trophic levels were used in this study:

- I. Primary Producers
- II. Herbivores (feed on I)
- III. Primary Carnivores (feed on II)
- IV. Secondary Carnivores (feed on III)
- V. Tertiary Carnivores (feed on IV)

This system (see Lindeman 1942; Odum 1971) was sometimes modified in order to permit intermediate assignments of trophic level.

For our calculations we assigned trophic levels to prey items, computed a weighted average prey trophic

level, and then assigned the predator to the next highest full trophic step. In order to assign prey trophic levels, we made some assumptions about the feeding habits of several kinds of organisms; for example, that both diatoms and dinoflagellates are primary producers (Trophic Level I) and that all small crustacea, including copepods, ostracods, mysids, amphipods, and euphausiids, are herbivores (Trophic Level II), even though there are many predatory forms in these groups.

In order to weight the data we computed the Pinkas et al. (1971) Index of Relative Importance:

$$IRI = \%F (\%N + \%V)$$

where *%F* = percent frequency of occurrence of prey item, *%N* = percent by numerical abundance of prey item, and *%V* = percent by weight or volume of prey item. By convention the resulting numbers, in terms of percent of total *IRI*, are hereinafter referred to in terms of their relative importance.

Dissection and Chemical Analysis

White muscle, sufficient to make 10 g or more of tissue, was dissected and placed in acid-washed vials (Jan et al. 1977) for determination of Cs and K (Young et al. 1980; Jan and Young, unpublished manuscript). For some species represented by large specimens (sea lions, mako shark, silky shark, and blue shark), we analyzed one tissue sample from each of four or five specimens. For the white shark and blue whale, we analyzed three replicate muscle samples from each. For all other teleosts, elasmobranchs, and squid we attempted to analyze five samples, each containing a composite of tissue dissected from ten different individuals taken largely from the same sites and dates. This approach was not always possible or sufficient, so that samples ranged from three to five and individuals (per final sample) from two (swordfish) to 35 (northern anchovy).

Cesium was reported in micrograms per wet kg ($\mu\text{g}/\text{wet kg}$) and K in units of milligrams per wet g ($\text{mg}/\text{wet g}$). The Cs/K ratio is therefore expressed as $\text{Cs}/\text{K} \times 10^{-6}$ and is compared with trophic level assignments and other biological and chemical variables.

RESULTS

Zooplankton Composition

The Southern California (Point Dume) zooplankton samples were numerically dominated by calanoid copepods, namely *Acartia tonsa* (75%), *Calanus pacificus* (10%), and the genus *Paracalanus* (8%, Table 2); less abundant (1% or less) were euphausiids and their young, cyclopoid copepods, the calanoid *Labidocera*, ostracods, and bryozoan larvae. The dominance of *Acartia* and the absence of forms such as chaetognaths suggested that we sampled a near-shore zooplankton community.

Zooplankton from the night tows in the eastern tropical Pacific collection area were also numerically dominated by calanoid copepods (55.8%, Table 3). Euphausiids were abundant (16.5%), and there was a wide variety of other oceanic zooplankton including chaetognaths, pteropods, heteropods, cyclopoid copepods, and decapod larvae and zoea.

Feeding Habits

Stomachs of pelagic organisms from both collection areas contained a wide variety of items ranging from phytoplankton to remains of fish, a bird, and marine mammals (Tables 2 and 3). In several species, stomachs were either completely empty (market

squid), unavailable (California sea lions and blue whale), or contained totally unrecognizable material (flying fish). We therefore used data from the literature, which are noted in footnotes to Tables 2 and 3.

Important items in stomachs of pelagic organisms from the Southern California Bight collections (Table 2) included zooplankton, northern anchovy, market squid, pelagic red crab, Pacific hake, Pacific mackerel, and pinnipeds. Plankton were important items, as defined by percent of total *IRI*, in the stomachs of several species of small fish. Northern anchovy stomachs contained, in order of importance, zooplankton (66% of total *IRI*; mainly *Acartia tonsa*) and unidentifiable matter (34% of total *IRI*); phytoplankton were relatively unimportant (less than 0.3% of total *IRI*) except in a few fish from Port Hueneme which contained diatoms (*Coscinodiscus*, *Thalassiosira*, and *Rhizosolenia*) and dinoflagellates (*Gymnodinium* and *Gonyaulax*). Zooplankton were also the most important items in stomachs of Pacific sardine (99.9% of total *IRI*) and jack mackerel (76.9% of total *IRI*). In the Pacific sardine, the zooplankton were mainly calanoid copepods (*Calanus pacificus* and *Labidocera*) and zoea. Stomachs from some of the jack mackerel also contained numerous scales and remains of a few polychaetes and squid.

Northern anchovy was the most important prey in stomachs of a group of larger fishes; in terms of percent of total *IRI*, anchovy accounted for 97.9% in Pacific bonito, 97.2% in thresher shark, 66.7% in California barracuda, 46.7% in Pacific mackerel, and 42.6% in swordfish. Food items of secondary importance in the last of these predators included zooplankton in Pacific mackerel (mysids, 35%), Pacific hake in swordfish (41.9%) and unidentifiable material in California barracuda (27.4%).

Blue shark stomachs contained squid as the most important item (64.3% of total *IRI*) and pelagic red crab (*Pleuroncodes planipes*) as the second most important item (25.2%). One blue shark also contained remains of a western meadowlark (*Sturnella neglecta*). In contrast, mako shark stomachs contained Pacific mackerel as the most important item (47.1% of total *IRI*) and unidentifiable fish remains and jack mackerel as the second and third most important items (27.2% and 25.8%, respectively). The white shark contained only two items, a young California sea lion and the remains of another pinniped, possibly a northern elephant seal (*Mirounga angustirostris*).

Stomachs of several species were either completely

TABLE 2
Trophic Spectrum for Some Pelagic Organisms¹ from the Southern California Bight.

PREDATOR	Zooplankton	Pelagic red crab	Northern anchovy	Pacific sardine	Market squid	Jack mackerel	Pacific mackerel	Pacific bonito	Pacific hake	California barracuda	Blue shark	Swordfish	Mako shark	Thresher shark	California Sea lion	White shark	Blue whale
Number examined	3 ²	100 ³	19	24	50 ⁴	50	49	29	16	28	16	17	5	14	(29) ⁵	1 ⁶	(38) ⁷
Number positive	—	100	19	24	0	21	34	16	14	12	15	15	5	9	(27)	1	(34)
Weight (g)	0.001 (est.)	5.0 (est.)	10.8	213	46.8	154	357	921	314	1250	28.8 × 10 ³	145 × 10 ³	16.8 × 10 ³	61.4 × 10 ³	35 × 10 ³	1.36 × 10 ⁶	28.6 × 10 ⁶
Deerfish/debris/mush	34.0				11.1	7.8	0.1	0.8	7.1	27.4							P
PHYTOPLANKTON																	
diatoms		20.7	0.25														
dinoflagellates		1.6	0.04														
ZOOPLANKTON																	
radiolarians		14.8															
foraminifera		25.5															
copepods, unidentified		3.6	55.0	98.9		52.0	0.2										P
calanoid	94.0		9.81														
harpacticoid		<1.0	0.47														
cyclopoid			0.21														
nauplii/cypris			0.04														
ostracods			0.06														
amphipods					0.6												P
mysids					3.1		34.6										
zoëa/megalops				1.0	61.2				4.5		25.2						
pelagic red crabs	5.0																
unidentified crustaceans		0.1			5.4	24.9	0.6					0.01					100
gastropods		1.4			16.6												
other small invertebrates	<1.0		0.06	<0.1			0.3				0.3						
tintinnids		15.4															
POLYCHAETES					1.4	5.2	0.3										
CEPHALOPODS						1.2		0.5									
squid, unidentified																	
market squid																	
FISH																	
fish eggs																	
tissue, unidentified parts																	
Northern anchovy				<0.1	0.6	8.2	17.4	0.8	2.4	5.9	8.0	6.7	27.2	2.0			49.7
Pacific argentine							46.7	97.9	1.2	66.7	2.1	42.6		97.2			14.3
mesopelagic, unidentified																	
Pacific hake																	
Jack mackerel																	
Pacific mackerel									7.2								10.7
BIRDS																	
Western meadowlark																	
MAMMALS																	
California sea lion																	50.0
Elephant seal																	50.0

¹Data are % of total Indices of Relative Importance (%IRI) unless otherwise noted (see below). Data are from our own zooplankton and stomach content analyses except as noted in footnotes 3 and 7. Samples from all except pelagic red crab and Pacific hake were analyzed for Cs and K; food habits for these species were included in order to compute trophic level assignments for their predators.

²Data represent percent numerical abundances estimated from samples at three sites south of Point Dume, August 1980.

³Data are percent numerical abundances observed by Aleman and Martinez (1976) from specimens trawled by the *A. de Humboldt* presumably off Baja California; they note that 20.7% of the food items were phytoplankton and 79.3% were zooplankton (including some dinoflagellates).

⁴All of our squid from Catalina had empty stomachs. Data are from Karpov and Cailliet (1978) from 52 *Loligo opalescens* taken in Monterey Bay spawning grounds between September 1975 and March 1976; numbers are "modified IRI" as described by these authors.

⁵Gut contents not available from our specimens; data combined from examinations by Scheffer and Neff (1948), Fiscus and Baines (1966), and Morejohn et al. (1978); Morejohn et al. (1978) list other fish and cephalopod species in addition to those cited in this table. These data are in general agreement with a recently published account by Antonellis and Fiscus (1980).

⁶White shark (*Carcharodon carcharias*) over 3.7 m (12 feet) prey on seals according to Snow (1980). They also consume other sharks, large and small fish, turtles, squid, crab, dead animals and other items such as potatoes, coal, dogs, a horse, and man according to D'Aubry (1964) and Walford (1935).

⁷Data are from Thompson (1940) from 38 blue whales (*Balaenoptera musculus*) received at Akutan, Alaska, in 1937; whales averaged 22.6 m. All specimens contained euphausiids; some had trace amounts of copepods. Of 268 whales reported by Nemoto (1959), 266 contained only euphausiids (*Thysanoessa* spp. and *Euphausia pacifica*), and two had a mixture of euphausiids and copepods (*Calanus* spp.).

TABLE 3
 Trophic Spectrum of Squid and Fishes from the Eastern Tropical Pacific Collected in 1978 (Flying fish) and in 1980 (Others).¹

	PREDATOR	Zooplankton	Flying fish	Squid	Frigate tuna	Skipjack tuna	Yellowfin tuna	Silky shark
	Number examined	11	35	78	2	44	36	4
	Number positive	—	35	15	2	18	27	2
PREY	Weight(g)	0.001	51.0	209	774	2,487	3,315	25.8 × 10 ³
	Detritus/debris/mush		p	8.2				
	PHYTOPLANKTON							
	ZOOPLANKTON							
	foraminifera	<0.1						
	copepods, unidentified		100 ²					
	calanoid	55.8						
	cyclopoid	5.0						
	ostracods	0.4						
	amphipods	1.8				0.8		
	zoëa/megalops	2.7					<0.1	
	stomatopod larvae	0.7				0.8		
	euphausiids	16.5						
	unidentified crustaceans	<0.1	+ ²	+				
	oikopleura	<0.1						
	gastropods, unidentified	0.9						
	pteropods	2.3				0.8		
	heteropods	1.3						
	bivalves	<0.1						
	siphonophores	0.8						
	chaetognaths	6.1						
	CEPHALOPODS							
	argonautidae					0.8	17.4	
	squid			13.9+			55.9	
	octopods						0.1	26.9
	FISH							
	unidentified fish/tissue/parts	0.2	tr ²	77.8		3.15	2.4	
	eggs	1.6						
	anchovy (unidentified)			+		1.6	0.3	
	myctophids			+			0.2	
	flying fish					39.0	22.6	
	seahorse						0.5	
	jacks						0.2	
	frigate tuna					53.1	0.1	73.1
	jack mackerel							
	triggerfish				p		0.1	
	nomeidae						0.2	

¹Numbers for zooplankton are per cent relative abundance; all others are per cent of total Indices of Relative Importance (IRI).

²Material in stomachs of our flying fish was unidentifiable. Data based on qualitative observations cited in Breder (1938), Parin (1950), and Parin (1960).

empty (market squid) or unavailable to us (California sea lions, pelagic red crabs, and the blue whale). Therefore, we used data from the literature (cited in Table 2). Karpov and Cailliet (1978) reported that crustaceans (mainly zoëa) were the most important items in stomachs of squid on winter spawning grounds in Monterey Bay (61.2% of their total IRI, Table 2); euphausiids were most important elsewhere and at other times of the year.

California sea lions apparently prey on a large variety of fishes and invertebrates; pooled data from several sources (cited in Table 2) indicate that unidentified fish, market squid, northern anchovy, and Pacific hake were important food items (49.7%, 14.5%, 14.3%, and 10.7% of total IRI respectively). Blue whale in the North Pacific were reported by

Thompson (1940) and Nemoto (1959) to feed on large euphausiids and incidentally on copepods (Table 2). Finally, Aleman and Martinez (1976) reported that small zooplankton occurred frequently in intestines of pelagic red crab from Baja California (Table 2).

Important items in the stomachs of organisms from the eastern tropical Pacific collections included crustaceans, squid, flying fish, argonauts, and frigate tuna (Table 3). Squid and argonauts were the most important items in stomachs of yellowfin tuna (55.9 and 17.4% of total IRI) whereas frigate tuna was the most important item in the stomachs of skipjack tuna (53.1% of total IRI). Flying fish were of secondary importance in yellowfin tuna (22.6%) and skipjack tuna (39.0%).

Frigate tuna and octopods were the most important

TABLE 4
 Summary of Weights, Lengths,¹ Number of Samples Analyzed, Resulting Concentrations of Cs and K, and the Cs/K Ratios
 in Specimens from Southern California Bight Collected in 1979 and 1980.

Predator	Number collected	Weight (g)		Length (cm)		Number of Chemical Samples	Cs ($\mu\text{g}/\text{wet kg}$)		K (mg/wet g)		Cs/K $\times 10^{-6}$	
		\bar{x}	R	\bar{x}	R		\bar{x}	R	\bar{x}	R	\bar{x}	R
Zooplankton	3 (tows)	—	—	—	—	3(r)	3.29(2.22-4.11)	1.58 (1.48-1.73)	2.07 (1.50-2.67)			
Northern anchovy	177	10.8 (5.7-14.9)		10.0 (8.7-11.3)		5(c,35)	7.62 (5.0 -11.7)	4.11 (3.88-4.33)	1.86 (1.29-2.96)			
Market squid	33	46.8 (37.9-53.5)		13.3 (12.7-14.3)		3(c,11)	<3.7 (<2.3-5.1)	1.63 (1.11-2.60)	<2.39 (1.96-<3.14)			
Pacific sardine	40	213 (190-220)		25.2 (22.3-26.0)		4(c,10)	16.9 (16.0-17.8)	4.22 (3.58-4.58)	4.82 (3.65-4.47)			
Jack mackerel	50	154 (59-215)		24.0 (17.4-26.9)		5(c,10)	25.6 (15.2-30.9)	4.24 (3.67-4.60)	5.73 (4.14-6.72)			
Pacific mackerel	49	357 (139-675)		29.7 (23.5-36.1)		5(c,10)	33.2 (28.3-37.5)	4.58 (4.43-4.82)	7.23 (6.14-8.28)			
Pacific bonito	29	921 (887-949)		41.9 (41.7-42.1)		2(c,10)	37.7 (25.6-49.8)	4.65 (4.48-4.82)	8.01 (5.71-10.3)			
Calif. barracuda	28	1250 (1060-1313)		58.0 (41.9-62.4)		5(c,3.2)	20.7 (15.0-28.9)	5.37 (5.0 -5.80)	4.20 (3.00-5.17)			
Calif. Sea lion	5	20 to 50 $\times 10^3$ est.		100-150 est.		5(s)	32.8 (16.0-44.6)	3.03 (2.21-4.30)	10.7 (7.24-14.2)			
Swordfish	10	145 (125-165) 10^3		N.M.		5(c,2)	58.4 (50.2-76.8)	4.80 (4.39-5.54)	12.3 (9.66-17.4)			
Blue shark	16	28.8 (23-35) 10^3		173 (150-185)		4(s)	43.9 (38.4-53.4)	3.33 (2.77-3.62)	13.2 (10.6-15.3)			
Mako shark	5	16.8 (11.2-25.0) 10^3		108 (91-120)		5(s)	91.8 (74.0-118)	4.65 (4.56-4.80)	19.7 (16.2-25.1)			
Thresher shark	14	61.4 (49.1-83.2) 10^3		229 (213-244)		4(c,3)	92.5 (57.3-129)	3.85 (3.50-4.28)	24.0 (16.3-27.3)			
White shark	1	1.36 $\times 10^6$		512		1(r)	105.0 (84.4-123)	3.30 (3.05-3.51)	31.7 (27.7-35.0)			
Blue whale	1	28.6 $\times 10^6$		1737		1(r)	41.7 (36.5-45.6)	3.81 (3.75-3.89)	11.0 (9.38-12.1)			

¹Weights and lengths are sample grand means with ranges (in parentheses; n = 1 to 5; see footnote 2).

²Each sample includes tissue from one or more specimens of the same species; number in parentheses is average number of specimens in a sample; s = single specimens only; r = replicates from a single specimen; c = composites.

items in stomachs of the silky sharks (73.1% and 26.9% of total IRI, respectively). Flying fish from both of our collections contained material, but it was totally unidentifiable; several reports (Table 3) suggest that copepods may be important food items.

Cesium, Potassium, and Cs/K Ratios

There were considerable variations in the concentrations of Cs and K and the Cs/K ratio in organisms from southern California (see Table 4). Cesium (sixth column, Table 4) varied approximately 32-fold from 3.29 $\mu\text{g}/\text{wet kg}$ in zooplankton to 105 $\mu\text{g}/\text{wet kg}$ in the white shark. In contrast, potassium (K) varied only about 3.4-fold from 1.58 mg/wet g in zooplankton and squid to 5.37 mg/wet g in barracuda. The Cs/K ratio varied about 17-fold from 1.86×10^{-6} in northern anchovy to 31.7×10^{-6} in the white shark.

Chemical variations similar to those of the Southern California Bight occurred in the eastern tropical Pacific fauna (Table 5). Cesium ranged 26-fold from an average of 4.35 $\mu\text{g}/\text{wet kg}$ in zooplankton to 114.5 $\mu\text{g}/\text{wet kg}$ in the silky shark. Potassium ranged 3.5-fold from 1.45 mg/wet g in the zooplankton to 5.01 mg/wet g in the silky shark. The Cs/K ratio varied 12-fold from 1.94×10^{-6} in the squid to 22.8×10^{-6} in the silky shark. In general, then, both ecosystems produced a variety of organisms that were similar with respect to the distribution in Cs/K.

Trophic Level Assignments and Relation to Cs/K Ratios

Table 6 presents three samples of trophic level assignments computed according to the steps indicated in the METHODS section. As indicated in A of Table

TABLE 5
 Summary of Weights, Lengths,¹ Number of Samples Analyzed, Resulting Concentrations of Cs and K, and the Cs/K Ratios in
 Specimens from the Eastern Tropical Pacific Collected in 1978 and 1980.

Predator	Number collected	Weight (g)		Length (cm)		Number ² of Chemical Samples	Cs ($\mu\text{g}/\text{wet kg}$)		K (mg/ wet g)		Cs/K $\times 10^{-6}$	
		\bar{x}	R	\bar{x}	R		\bar{x}	R	\bar{x}	R	\bar{x}	R
Zooplankton	11	—	—	—	—	5(s)	4.35 (2.77-6.15)	1.45 (0.80-1.98)	3.30 (1.54-5.35)			
Flyingfish	35	51.0 (29.0 - 71.7)		16.3 (14.1-18.2)		5(c,7)	20.2 (16.9-24.3)	2.91 (2.54-3.51)	7.00 (5.58-8.47)			
Squid	78	209 (162 - 275)		19.7 (19.0-21.5)		5(c,5)	4.89 (2.35-6.41)	3.12 (2.50-3.73)	1.94 (0.95-2.34)			
Frigate tuna	2	774 (757 - 791)		36.5 (36.0-37.0)		2(s)	32.5 (30.0-34.9)	3.67 (3.49-3.85)	8.90 (7.79-10.0)			
Skipjack tuna	44	2487 (2398-2675)		49.1 (48.0-51.5)		5(c,9)	37.5 (34.4-43.3)	4.38 (4.25-4.59)	8.59 (7.49-10.2)			
Yellowfin tuna	36	3315 (2757 -4219)		54.4 (50.5-59.2)		5(c,7)	60.5 (42.5-74.8)	4.79 (4.56-5.03)	12.7 (8.84-16.6)			
Silky shark	4	25.8 (7.72-31.8) $\times 10^3$		131. (93.0-168)		4(s)	114.5 (96.3-126)	5.01 (4.43-5.33)	22.8 (13.8-30.6)			

¹Weights and lengths are sample grand means with ranges (in parentheses; n = 1 to 5; see footnote 2).

²Each sample includes tissue from one or more specimens of the same species; number in parentheses is average number of specimens in a sample; s = single specimens only; c = composites.

6, the composite prey of northern anchovy resulted in a computed trophic level of 1.82, resulting in a computed trophic level assignment of 2.82 for the anchovy. This is equivalent to the conventional trophic level expression II → III, i.e. almost, but not quite, a primary carnivore. We made similar calculations for the remaining species of macroorganisms using our own *IRI* or *IRI* derived from literature sources (as reported in Tables 2 and 3).

These computed trophic levels are compiled together with the assumed trophic levels of the zooplankton in Table 7. As indicated, computed trophic level assignments ranged from 2.82 for northern anchovy to 5.02 for the white shark. The data cluster into several groups that each center about one of the conventional trophic level assignments. One group centers around Trophic Level III (or computed trophic level 3.00, i.e. primary carnivores) and includes northern anchovy, the blue whale, flying fish, Pacific sardine, market squid, and jack mackerel (range, 2.82 to 3.05; mean, 2.99). Several animals, including the larger squid (*Symplectoteuthis*), Pacific mackerel, and frigate tuna, are distinctly higher (range, 3.52 to 3.56; mean, 3.54) but midway between primary and secondary carnivores (Trophic Level III - IV). A third group centers about Trophic Level IV, i.e. secondary carnivores: California barracuda, Pacific bonito, two coastal sharks, swordfish, and pinnipeds (range 3.74 to 4.02; mean, 3.89). At a level intermediate between

full secondary and full tertiary carnivores (i.e. Trophic Level IV - V) are the yearling tunas, mako and silky sharks (4.23 to 4.55; mean, 4.37). Finally, because it contained nothing other than pinnipeds (centered around Trophic Level IV) in its stomach, the white shark produced a computed trophic level of 5.02 and thus centered on conventional Trophic Level V (tertiary carnivore).

The scatter diagram in Figure 1 shows that the Cs/K ratios generally increase with trophic level assignments (assumed and computed). The trend occurs irrespective of the source of the organisms (Southern California Bight or eastern tropical Pacific). Accordingly all data were combined for further statistical analysis.

Untransformed, these data produce a high correlation coefficient ($r = 0.753, p < 0.001$, Table 8). However, the regression line (dashed line, Figure 1) intercepts the Y-axis above Trophic Level 2.00 and thus predicts negative Cs/K ratios at lower trophic levels (i.e. $Cs/K = -10.1 \times 10^{-6}$ at computed Trophic Level I and -17.99 at the Cs/K intercept, Table 8). In contrast, \log_e transformation of the Cs/K ratio produces both a stronger correlation coefficient ($r = 0.776, p < 0.001$, Table 8) and a more realistic fit to the data points (no negative Cs/K ratios). This line (solid line in Figure 1) predicts a Cs/K ratio of 0.83×10^{-6} for computed Trophic Level I (primary producers), a value in close agreement with a mean Cs/K

TABLE 6
 Computation of Trophic Level Assignments for Northern Anchovy, Jack Mackerel, and Mako Shark.

Predator/prey	(1) Assumed or computed prey trophic level	(2) % <i>IRI</i>	(3) (1) × (2)/100	(4) Computed trophic level = (3) + 1	(5) Traditional trophic level assignment
A northern anchovy					
copepod	2.0	65	1.30		
detritus	1.5	34	0.51		
phytoplankton	1.0	1	0.01		
			1.82	2.82	II → III
B jack mackerel					
copepods	2.0	52	1.04		
Unidentified crustacean	2.0	24	0.48		
Unidentified matter	1.5	8	0.12		
Unidentified fish	3.0	8	0.24		
polychaetes	2.5	5	0.13		
squid	3.06	1	0.03		
			2.04	3.04	III
C mako shark					
Pacific mackerel	3.54	65	2.30		
jack mackerel	3.04 (from above)	19	0.58		
Unidentified fish	3.0	17	0.51		
			3.39	4.40	IV—V

TABLE 7

Summary of Locations of Capture, Cs/K Ratios, Assigned Trophic Levels (Assumed or Computed) and Conventional Expression of Assigned Trophic Levels for 22 Species of Pelagic Animals from the Southern California Bight and the Eastern Tropical Pacific, 1978 and 1980.

Species number ¹	Common Name	Location ²	Cs/K × 10 ⁻⁶	Assigned trophic level	Conventional trophic level
HERBIVORES (II)					
1	Coastal zooplankton	SCB	<2.07	2.00 ³	II
2	Oceanic zooplankton	ETP	3.30	2.00 ³	II
PRIMARY CARNIVORES (III)					
3	Northern anchovy	SCB	<1.86	2.82	II→III
4	Blue whale	SCB	11.0	3.00	III
5	Flying fish	ETP	7.00	3.00	III
6	Pacific sardine	SCB	4.02	3.01	III
7	Market squid	SCB	2.39	3.05	III
8	Jack mackerel	SCB	5.73	3.04	III
INTERMEDIATE (PRIMARY-SECONDARY) CARNIVORES (III-IV)					
9	Squid	ETP	1.94	3.52	III-IV
10	Pacific mackerel	SCB	7.23	3.54	III-IV
11	Frigate tuna	ETP	8.90	3.56	III-IV
SECONDARY CARNIVORES (IV)					
12	California barracuda	SCB	4.20	3.74	III→IV
13	Pacific bonito	SCB	8.01	3.80	III→IV
14	Thresher shark	SCB	24.0	3.82	III→IV
15	Swordfish	SCB	12.3	3.97	IV
16	Blue shark	SCB	13.2	4.00	IV
17	California sea lion	SCB	10.7	4.02	IV
INTERMEDIATE (SECONDARY-TERTIARY) CARNIVORES (IV-V)					
18	Yellowfin tuna	ETP	12.7	4.23	IV←V
19	Skipjack tuna	ETP	8.59	4.30	IV-V
20	Mako shark	SCB	19.7	4.39	IV-V
21	Silky shark	ETP	22.8	4.55	IV-V
TERTIARY CARNIVORE (V)					
22	White shark	SCB	31.7	5.02	V

¹Refers to numbers in Figure 1.

²SCB = Southern California Bight and adjacent waters; ETP = Eastern Tropical Pacific (oceanic)

³Assumed trophic level; all others computed from stomach contents data according to method described in text.

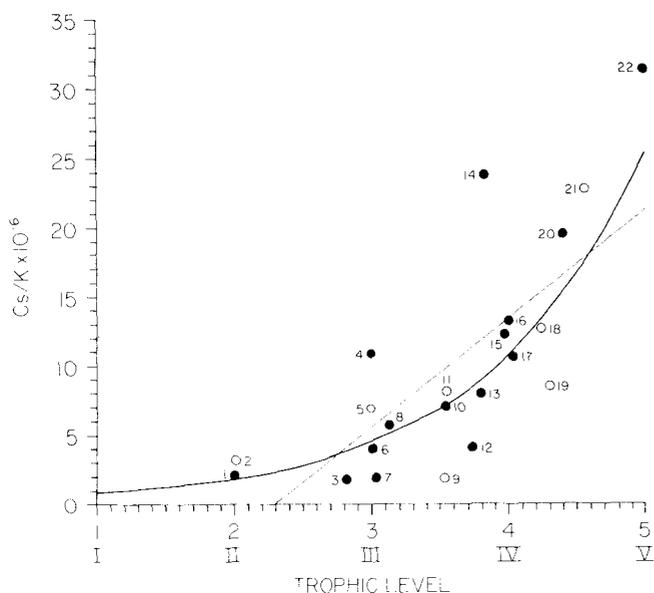


Figure 1. Scatter plot of mean Cs/K ratios against computed (arabic numerals) and traditional (Roman numerals) trophic level assignments. Data are for 22 species of coastal (closed circles) and oceanic (open circles) pelagic organisms. Refer to Table 7 for species identifications (numbered 1 through 22 above). Also shown are regression lines for raw (dashed line) and log₁₀-transformed (solid line) data; statistics for these lines are listed in Table 8.

ratio of 0.71 measured in giant kelp (*Macrocystis pyrifera*, Mearns and Young 1980).

The equation for the solid line in Figure 1 also predicts constant Cs/K increase factor of 2.35 per whole trophic step. This increase factor is similar to a value of 2.39 computed by grouping data around traditional trophic and intermediate trophic levels, calculating mean Cs/K ratios, and then computing Cs/K increase factors for whole trophic steps (Table 9). As shown in the last column in Table 9, these increase ratios vary from 1.98 between Trophic Levels III and II to 2.65 between Trophic Levels IV-V and III-IV. The average of the four increase ratios is 2.39±0.32 SD, a value in close agreement with that predicted from the curvilinear fit to all 22 data points (2.35).

DISCUSSION AND CONCLUSIONS

In animal tissues, the biological half-life of Cs is two to three times that of K (see Young 1970). Young (1970) has also shown that under equilibrium conditions food appears to be the major source of Cs to

TABLE 8
 Regression Statistics for Cs/K versus Trophic Level Computed Using Mean Values for Cs/K and All 22 Pelagic Organisms.

Comparison	<i>r</i>	<i>df</i>	<i>p</i>	<i>m</i>	<i>b</i>	Cs/K × 10 ⁻⁶
						Prediction for trophic level I
Cs/K vs. trophic level	0.753	20	<0.001	7.890	-17.99	-10.10
Log _e Cs/K vs. trophic level	0.776	20	<0.001	0.85430	-1.04078	-0.18648
Inverse Log _e Cs/K ¹	—	—	—	2.3497	0.3532	0.830

¹Log_e Cs/K returned to untransformed values.

TABLE 9
 Average Computed Trophic Levels, Weights, and Cs/K Ratios for Each of Six Intermediate or Full Trophic Levels, Together with Calculated Step Increases between Trophic Levels for Cs/K.

Trophic level	<i>N</i>	Computed trophic level		Weight (g)		Cs/K × 10 ⁻⁶		Calculated Increase ¹
		\bar{x}	<i>SD</i>	\bar{x}	<i>SD</i>	\bar{x}	<i>SD</i>	
II Herbivores	2	2.00	—	1 × 10 ⁻³	0	2.69 ± 0.89	—	
III Primary Carnivores	6	3.00 ± 0.10	—	4.77 ± 11.7 × 10 ⁶	—	5.33 ± 3.39	1.98/step	
III-IV Interm. Carnivores	3	3.54 ± 0.02	—	4.47 ± 2.93 × 10 ²	—	6.02 ± 3.63	—	
IV Secondary Carnivores	6	3.89 ± 0.12	—	4.54 ± 5.38 × 10 ⁴	—	12.07 ± 6.69	2.29/step	
IV-V Interm. Carnivores	4	4.37 ± 0.14	—	1.21 ± 1.13 × 10 ⁴	—	15.95 ± 6.47	2.65/step	
V Tertiary Carnivore	1	5.02	—	1.36 × 10 ⁶	—	31.7	2.63/step	

Average step increase in Cs/K = 2.39
 ± Standard deviation = 0.32

¹Computed only where there is data for a whole step: e.g. III/II = 5.33/2.69 = 1.98.

marine fish; a similar conclusion is reached when the argument is applied to K (D.R. Young, unpublished manuscript). On the assumption that this is also true for other types of marine organisms, this implies that the ratio of Cs to K in a marine predator should be two to three times higher than the ratio in its prey when both are in equilibrium. Thus in a linear food chain, such as once noted of the Salton Sea (Young 1970; Young et al. 1980), the Cs/K ratio should increase two to three-fold per trophic step. In fact, Young (1970) found the ratio to increase 2.5-fold in the Salton Sea. However, Isaacs (1972, 1973, 1976) postulated that marine food webs are not so structured; rather, they are composed of opportunistic, multidirectional feeders. A lack of increase in Cs/K ratio in several trophic steps in representatives of a nearshore food web in the Gulf of California (Young 1970; Young et al. 1980) was taken by Isaacs as evidence in support of this hypothesis.

In the present study, the Cs/K ratio in pelagic organisms from the eastern Pacific Ocean clearly increases with increase in trophic levels derived independently from gut content analysis. The Cs/K ratio increases by a factor of about 2.4 between trophic levels. In addition, a median increase factor of 2.3, computed from an earlier pilot study of representative pelagic fishes from the Southern California Bight (Young et al. 1980) agrees with the new data. Together or separately, these data do not support the hypothesis that pelagic food webs are unstructured.

However, we have also reported that considerably smaller increases in the ratio occur in nearshore and benthic food webs of the southern California mainland shelf (Young et al. 1980). As summarized in Table 10, the average increases in Cs/K were 1.52 in a benthic food web on the Palos Verdes Shelf, 1.40 in Los Angeles Harbor, and 1.23 in Upper Newport Bay. These data suggest that structure amenable to biomagnification of Cs increases as one leaves nearshore (detritus-based) food webs and enters offshore pelagic food webs.

Although the increase in Cs/K ratio with increase in trophic level is evident in our data, there are some

TABLE 10
 Comparison Cs/K Ratios and Step Increases in Cs/K Ratios (parentheses) in Four Marine Ecosystems.

Trophic level	Upper Newport Bay 1978 ¹	Los Angeles Harbor 1979 ²	Palos Verdes 1976 ¹	Pelagic 1980 ³
I	NA	0.71	NA	NA
II	NA	NA	NA	2.69
II-III	3.64	1.97	6.50	NA
III	NA	NA	NA	5.28 (1.98)
III-IV	5.53 (1.52)	3.05 (1.55)	9.93 (1.53)	6.02
IV	NA	NA	NA	12.07 (2.29)
IV-V	5.22 (0.94)	3.82 (1.25)	15.1 (1.52)	15.95 (2.65)
V	NA	NA	NA	31.7 (2.63)
Average increase	1.23	1.40	1.52	2.39

¹Young et al. 1980.

²Mearns and Young 1980.

³This study; Young et al. (1980) also reported a mean predator/prey increase factor of 2.42 for a small separate group of coastal pelagic fishes.

important deviations. Northern anchovy (primary carnivores) and both species of squid (primary to secondary carnivores) produced Cs/K ratios no higher than zooplankton (herbivores), whereas elasmobranchs (secondary and tertiary carnivores) produced high values when compared to fish of similar size (e.g. swordfish). It is possible the northern anchovy were feeding on phytoplankton for several months prior to capture; they are certainly capable of doing so, as noted by Miller (1976). Moreover, we have previously measured somewhat higher Cs/K ratios (mean 2.08×10^{-6}) in anchovy from Los Angeles Harbor (Young et al. 1980). The low Cs/K ratios in both squid species are also difficult to explain. It is possible we did not sample a tissue equivalent to the muscle in fish; however, the mantle is sufficiently active to be involved in propulsion of squid. Alternatively, the biological half-life of Cs may be much shorter in molluscs than in teleosts. Likewise, the biological half-life of Cs may be different (higher?) in elasmobranchs than in molluscs or teleosts. Although we have yet to fully investigate these possibilities, we can point out that we arrive at substantially the same general conclusions when we exclude all but the teleosts from our correlations. For example, regression of fish-only log-transformed Cs/K ratios with computed trophic levels significant ($r = 0.737$, $0.01 > p < 0.001$) and results in a Cs/K ratio increase of 2.23 per trophic step (Table 11).

Tables 3 and 4 suggest there may be some relation between the Cs/K ratio and size. Linear regression of untransformed data do not support this ($r = 0.054$, $p > 0.1$, Table 11); the lack of correlation is also obvious considering the six-order of magnitude range in weight between northern anchovy (10 g) and the blue whale (28.6×10^6 g), both of which are primary carnivores Trophic Level III. However, there is a significant correlation ($r = 0.741$, $p < 0.001$) when \log_e -transformed Cs/K ratios are regressed against \log_e -transformed weight data (Table 11). This

suggests there may be some connection between size (or size-related conditions such as growth rate or metabolic rate) and the Cs/K ratio. However, it can also be pointed out that this regression predicts a Cs/K ratio that is already too high for the blue whale (23.4 versus 11.0).

This study and a similar study in Los Angeles Harbor (Mearns and Young 1980) differ from most other studies on marine food webs in that an attempt has been made to objectively assign numerical values to trophic levels based on quantitative feeding habits data. There are hazards in doing this: for example, setting a numerical value for a trophic level disregards the omnivorous nature of some predators (as evident in Tables 2 and 3). Thus, we prefer to view the "computed trophic level" as an indicator of central tendency of food sources. Moreover, assigned prey trophic levels range 0.5 "trophic steps" around their central tendency for some predators. Thus, if this approach is to be used, we recommend reporting some measure of trophic dispersion such as that observed in true trophic spectra (e.g. Cailliet et al. 1979; Darnell 1961).

The studies done to date raise many questions that have yet to be thoroughly investigated. Factors such as growth rates, undiscovered food sources, (including seasonal variations), phylogenetic differences in biological half-lives of alkali metals (which may explain obvious deviations in squid and the three-fold range in K concentrations) have yet to be thoroughly explained. Nevertheless, the present study provides a new kind of focus on pelagic food webs and on some possible relationships among economically important species of pelagic fishes, their prey, and their predators. At present, we conclude that pelagic organisms live under conditions that are sufficient to promote accumulation of Cs in a pattern that is related to our concept of trophic structure. However, if relative change in the Cs/K ratio is indeed a measure of trophic structure, as proposed by Isaacs (1972, 1973, 1976), then these data support the hypothesis that pelagic

TABLE 11
 Regression Statistics for Cs/K versus Trophic Level for Teleosts only and for Cs/K versus Weight for all 22 Pelagic Organisms
 (Including \log_e -transformed Data).

Comparison	<i>r</i>	<i>df</i>	<i>p</i>	<i>m</i>	<i>b</i>	Cs/K $\times 10^{-6}$ Prediction
\log_e Cs/K vs. trophic level, teleosts only	0.737	9	$0.01 > p < 0.001$	0.80050	-0.97255	-0.17205
Inverse for \log_e Cs/K	—	—	—	2.227	0.378	0.845 for trophic level I
Cs/K vs. weight (g), all data	0.054	20	n.s. ¹	7.1×10^{-8}	10.05	—
\log_e Cs/K vs. \log_e weight (g), all data	0.741	20	< 0.001	0.11048	1.25613	3.15296
Inverse for \log_e Cs/K	—	—	—	1.117	3.512	23.4 for 38.6 mt blue whale

¹not significant ($p > 0.1$)

food webs are structured. However, we also note that Cs/K ratios increase in nearshore, harbor, and bay ecosystems much less than in pelagic ecosystems (factors of 1.52, 1.40, and 1.23 versus 2.35, respectively). In fact, the present data suggest that the ability of marine food webs to "biomagnify" Cs decreases with proximity to shore. Thus, it is possible that nearshore systems are indeed more like the "unstructured" food webs proposed by Isaacs (1972), whereas the pelagic systems are more like simplified, well-structured food webs such as noted of the Salton Sea (Isaacs 1972; Young 1970). Analyses are now in progress to determine which, if any, trace contaminants (metals and chlorinated hydrocarbons) also increase with trophic level.

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A COMPARISON OF EUPHAUSIID ABUNDANCES FROM BONGO AND 1-M CalCOFI NETS

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ABSTRACT

Abundances of 12 species of euphausiids were determined from net tows designed to compare catching capacities of a 1-m ring net having an anterior towing bridle and a bridleless Bongo sampler having nets of either 60- or 71-cm mouth width. Replicate tows consisted of the 1-m and the Bongo towed consecutively, obliquely to 210-m depth. Because many euphausiids migrate to considerable depths for the daytime, only nighttime samples were used in determining relative efficiencies of the nets.

For each species, determinations were made of differences between average abundances from Bongo and 1-m net samples. Abundances were compared at each 1-mm increment of body length. Larvae were more abundant when determined from samples from the 1-m net. Juveniles and adults were better retained by the Bongo. Total numbers differed little for most species.

After the larval phase, the ratio of Bongo catch to 1-m-net catch usually increased with body length until near maximum size. This led to significantly greater estimates of biomass from the Bongo samples. In the two species for which males and females were analysed separately, proportions of the sexes differed between the two nets.

The euphausiid data complement results on larval fishes that led to adoption of the Bongo as the standard CalCOFI net, replacing the 1-m net.

RESUMEN

Se determinaron las abundancias de doce especies de euphausiidos de unos lances de plancton diseñados para comparar la capacidad de captura de una red cónica de apertura de 1-m con una brida de remolque anterior, y un muestreador Bongo sin brida con redes de apertura o de 60 o de 71 cm. Los arrastres repetidos consistían de arrastres consecutivos de la red de 1 m y la Bongo, remolcadas oblicuamente a una profundidad de 210 m. Debido a que muchos euphausiidos migran a considerable profundidad durante el día, se usaron muestras tomadas de noche para determinar la eficacia relativa de las redes.

Para cada especie, se determinaron las diferencias entre las abundancias promedias de las muestras de la

Bongo y de la red de 1 m. Se compararon las abundancias a cada intervalo de 1 mm en la longitud del cuerpo de la larva. Las larvas de las muestras de la red de 1 m eran más abundantes. La red Bongo retuvo mejor a los juveniles y adultos. Había poca diferencia entre los números totales para la mayoría de las especies.

Después de la fase larval la proporción de captura por la Bongo a la captura por la red de 1 m generalmente incrementaba con la longitud del cuerpo de la larva hasta llegar casi al tamaño mínimo. Los muestreos por medio de la Bongo resultaron en mayores estimaciones de biomasa. Para las dos especies en que se analizaron por separado a los machos y las hembras, las proporciones de los sexos diferían entre las dos redes.

Estos datos de euphausiidos complementan los estudios sobre peces larvales, cuyos resultados causaron que se reemplazara la red de 1 m con la Bongo como la red estándar de CalCOFI.

INTRODUCTION

Among active zooplankters such as euphausiids, more individuals are expected to swim away from than toward the path of an approaching tow net because nets produce visual and pressure signals. Aron (1962) discussed the many gear-dependent problems of sampling the macroplankton, of which adult euphausiids are a conspicuous, often predominant part. The modest body of data relating to net avoidance has been critically analysed by Clutter and Anraku (1968), who concluded that, despite contradictory evidence, avoidance occurs among many organisms designated as plankton.

Avoidance is to be expected when a towing bridle is positioned in front of the mouth of a net, as in the 1-m ring net that was in use by CalCOFI during 1950-76 (Ahlstrom 1952). This has led to the design of samplers such as the Bongo net (McGowan and Brown 1966) in which the tow line extends upward rather than forward from the mouth of the net. A measure of avoidance, however relative, will be made here by comparing catches of euphausiids from these two nets.

Mackintosh (1934), observing from the deck of a ship, first reported that *Euphausia superba* moves rapidly away from an approaching plankton net. Effectiveness of an avoidance reaction must vary with

the speed at which a net is towed, even assuming the same filtration efficiency at different speeds. Hansen (1960) showed that in the North Sea more adult euphausiids are captured per unit volume of water by a high-speed net of small mouth width than by a slow, larger Hensen net. However, Tranter (1966), varying tow speed between 0.4 and 4.0 knots (21 and 210 cm/second), caught fewer euphausiids at higher speeds. Aron and Collard (1969) found that 10-18-mm specimens of three species of euphausiid were in equal numbers in nighttime Isaacs-Kidd midwater trawl tows comparing towing speeds of about 2 and 4 knots (105 and 210 cm/second).

In the present comparison, the two nets are towed at nearly equal speeds, 1.5-2.0 knots (75-105 cm/second).

Effects of size of net mouth were discussed by Aron (1962). Adult euphausiids dominated catches obtained by an Isaacs-Kidd midwater trawl but were rare in samples from the same area from a much smaller Clarke-Bumpus net. Neither of these nets have bridles extending directly forward from the mouth. However, no differences were found between euphausiid abundances sampled by bridled nets of 1.0- and 0.45-m mouth widths (Brinton 1962a) or among nets having mouth areas of 0.5, 0.25, and 0.05-m² (Tranter 1966). Conversely, McGowan and Fraundorf (1966) found clear differences between abundances of euphausiids from a largest net (mouth width of 1.4-m) and smallest net (0.2 m) of a six-net array but not between nets of more similar size. They also reported no differences in euphausiid species composition among the samples from the net-size comparison series. Sands (1978) reported that a Longhurst Frame of 0.09-m² mouth area (the frame and net of a Longhurst-Hardy Plankton Recorder; Longhurst et al. 1966) sampled most groups of plankton in a Norwegian fjord as well as or better than a Beyer Low-Speed Midwater Trawl of 1-m² mouth area, with the notable exception of the large euphausiid *Meganyctiphanes norvegica*.

For the present analysis, samples were obtained both from series in which nets were towed alternately during a period of several hours and from isolated pairs of tows. P.E. Smith of the National Marine Fisheries Service was particularly instrumental in initiating this net-comparison study and has demonstrated (unpublished data) that anchovy larvae of greater than about 12-mm length are significantly better sampled by the Bongo than by the 1-m net.

Like fish larvae, euphausiid crustaceans in the size range of about 5-25-mm body length are particularly active components of assemblages sampled by these plankton nets. The data are used to compare length-frequency (LF) distributions of euphausiids obtained

by the two methods of sampling. Smith's analysis of fish larvae in the 1975 samples, together with the results presented here on euphausiids, have already led to adoption of the Bongo net for standard use in CalCOFI plankton surveys. It would be useful to know whether or not correction factors could be appropriately applied to estimates of euphausiid abundance obtained using the 1-m net during 1950-76 (Brinton 1967b, 1973, 1976; Brinton and Wyllie 1976).

METHODS

The samples are from two periods.

1) In January and July of 1975, collections were made with a "Marmap" Bongo of 0.6-m mouth width towed alternately with a CalCOFI ring net of 1.0-m mouth width (Figure 1). Both nets were of 333- μ m mesh width. The same type of digital flowmeter was used in both nets. At each of three localities in the California Current, a daylight series consisting of five tows with each net was followed by a similar nighttime series. Tows were oblique to a depth of 210 m. During each 12-hour period of sampling, the ship followed a drogue positioned at 10-m depth. The northernmost locality (Figure 2) was near 35°N, 122°W, off central California within the cold-water regime of the current (CalCOFI Station 73.60 for winter series; Station 70.60 for summer series). The more southerly, warm-water localities were 30°N, 118.5°W (Station 103.60) and near 25°N, 114°W (Station 137.50, winter series; Station 133.46, summer series), both off Baja California.

2) From December of 1977 through August of 1978, during the course of seven CalCOFI survey cruises, a total of 61 pairs of samples—one sample from the 1-m ring net and one from a Bongo net of 0.71-m mouth width—were obtained at numerous stations off California and Baja California.

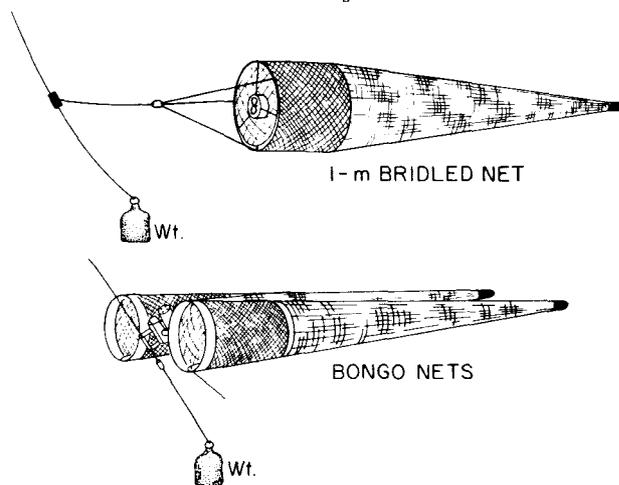


Figure 1. The 1-m plankton net, equipped with anterior towing bridle, and the Bongo frame, towed by upward-extending cable.

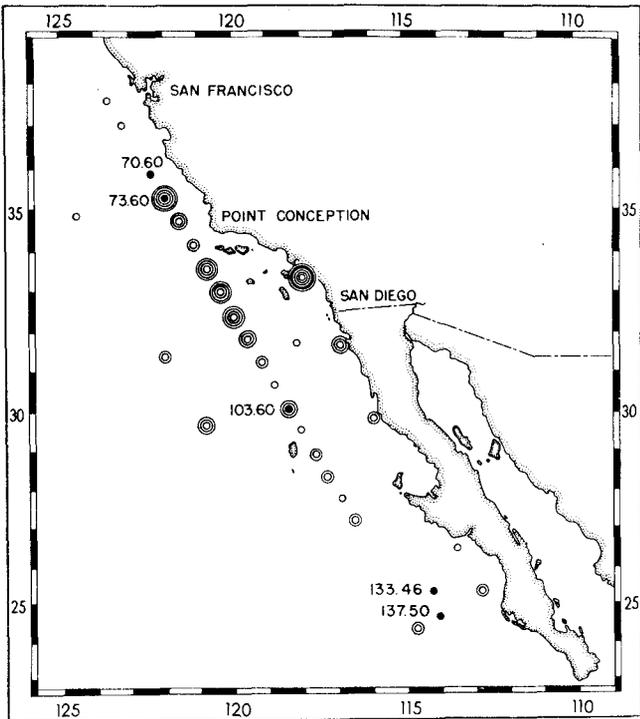


Figure 2. Localities in the California Current at which the nighttime tows used in this comparison of the Bongo and 1-m net were made. At the position of each solid circle, there were six nighttime and six daytime pairs of replicate tows in either January or July 1975. An open circle indicates a pair of tows from one of the CalCOFI Cruises during 1977-78, and concentric circles represent pairs from two or more of the cruises.

The present analysis deals only with nighttime pairs of samples, except in the case of the abundant *Euphausia pacifica*: the 1975 daytime data for this species is included to illustrate the character of day-night differences in abundance within the 0-210-m layer. Such differences reflect a combination of the effects of vertical migration and avoidance. Samples obtained at night are generally more useful for estimating euphausiid abundances because all growth stages are then in the upper layer of the ocean.

Samples were subsampled using the Folsom splitter. Analysis of the relatively large 1975 samples were of 1/32 fractions. The 1977-78 samples were examined following the method described in Brinton (1979), in which progressively larger fractions of a sample are examined for the increasingly rarer sizes of a given euphausiid species.

Twelve species were considered to be sufficiently abundant in enough of the paired samples to permit combining data among stations. A mean length-frequency distribution of a species was determined from all catches from each type of net.

Euphausia pacifica and *Nematoscelis difficilis* were particularly abundant in the mid-part of their ranges off central California, sampled during the winter and

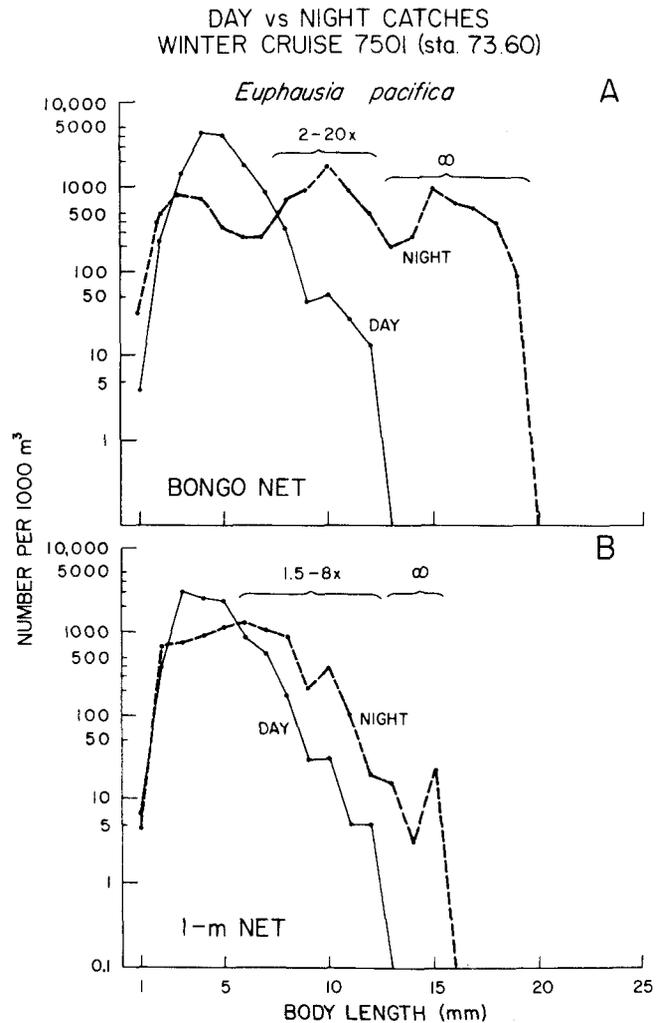


Figure 3. Length-frequency (LF) distributions of *Euphausia pacifica* from the day-night series of January, 1975, in which Bongo and 1-m net tows were alternated, yielding six daylight and six nighttime pairs of samples. Each LF curve is the mean of the six catches. Day and night abundances: A. from Bongo net; B. from 1-m net. Night/day catch ratios are indicated.

summer series of 1975. Therefore, these two species will be examined in most detail.

RESULTS

Day versus Night Catches, *Euphausia pacifica*

The mean length frequency (LF) for the five nighttime Bongo samples from the central California locality, Station 73.60, in January (Figure 3A) extends from 1-mm larvae through 19-mm adults. The five daytime Bongo tows captured specimens only in the range of 1-12 mm. In the 8-12-mm size range, nighttime abundances were 2 to 20 times greater than daytime estimates. These larger nighttime catches of *E. pacifica* may be attributed (1) to the deeper (>210-m) daytime levels of some large juveniles and adults due to vertical migration (Brinton 1967a) and (2) to differential day-night avoidance of the net by those 8-

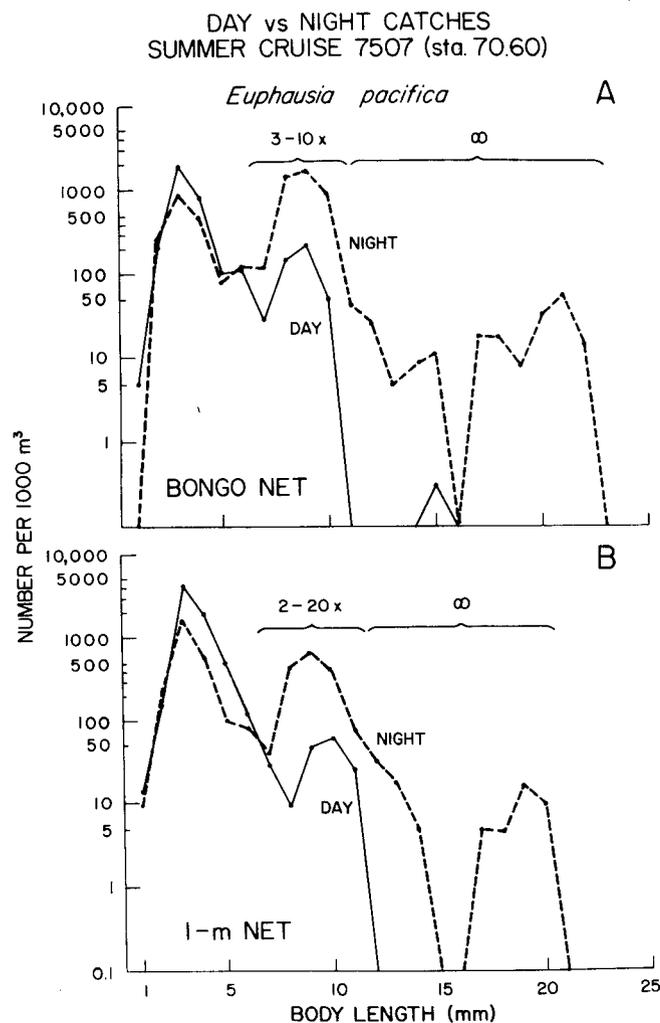


Figure 4. Length-frequency (LF) distributions of *Euphausia pacifica* from the day-night series of July, 1975, in which Bongo and 1-m net tows were alternated, yielding six daylight and six nighttime pairs of samples. Each LF curve is the mean of the six catches. Day and night abundances: A. from Bongo net; B. from 1-m net. Night/day catch ratios are indicated.

12-mm individuals that were above 210-m at all times. On the other hand, small 3-7-mm *E. pacifica* were better sampled by day than by night.

Like the Bongo net, the 1-m net caught 1-12-mm *E. pacifica* in the daytime (Figure 3B), but only 1-15-mm at night, compared to 1-19-mm for the Bongo.

In the summer-daytime samples (Figure 4), *E. pacifica* of 1-10 mm or 1-11 mm were caught by the 1-m net, compared to 1-12 mm by both nets in the winter-daytime samples. However, the summer-nighttime Bongo samples showed that the population then included specimens of up to 22 mm. The daytime sampling by both nets is relatively inefficient for 7-10-mm or 7-11-mm *E. pacifica* and is essentially nil for larger sizes. As in the winter, the summer sampling of 3-6-mm specimens was more effective in the daytime than at night.

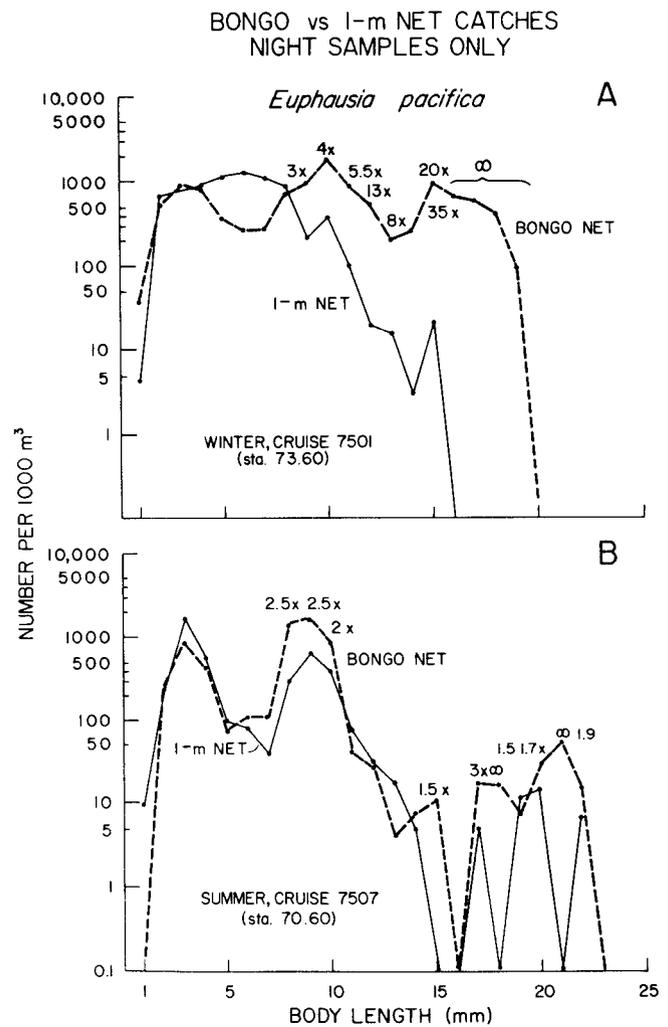


Figure 5. Mean LF distributions of *Euphausia pacifica* from nighttime series: A. January 1975; B. July 1975, during which Bongo and 1-m net tows were alternated. Bongo/1-m-net catch ratios are indicated at body lengths where Bongo catch was the greater.

Bongo versus 1-m Net, Nighttime, *E. pacifica*

Relative efficiencies of the Bongo and 1-m nets become particularly evident when the nighttime catch curves are compared directly (Figure 5).

During the winter series (Figure 5A), at body lengths >8 mm, a nearly direct relationship was seen between body length and capability of *E. pacifica* to avoid the 1-m net: at 9 mm, the Bongo catch was three times that of the 1-m net; at 15 mm it was 35 times greater, and for sizes greater than 15 mm, avoidance of the 1-m net was total. A seasonal difference in the response of *E. pacifica* to the net may be inferred from an apparently greater capacity of large juveniles and adults to avoid the 1-m net during the winter series. The summer curves for the two nets (Figure 5B) were more nearly the same through the size range of 2-14 mm, and catches of larger adults

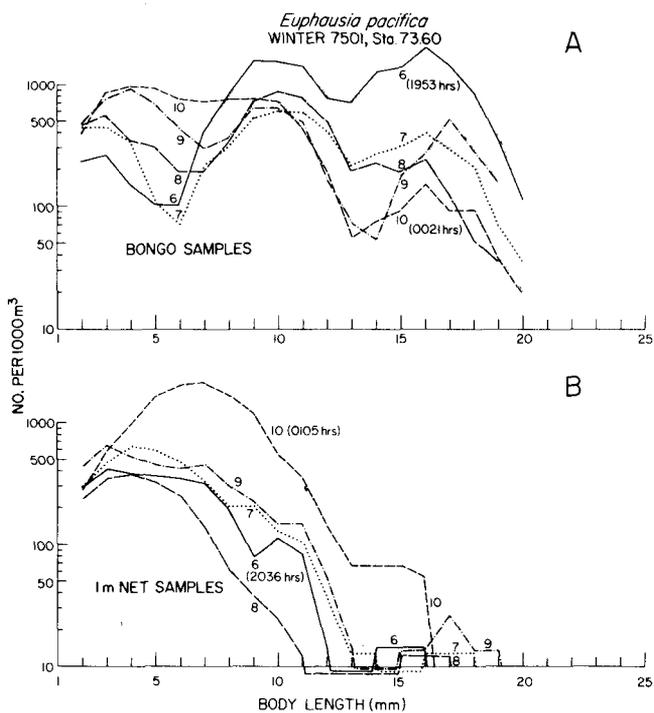


Figure 6. LF distribution of *Euphausia pacifica* from nighttime pairs of net-comparison tows, numbered 6 to 10, comprising the January (winter) 1975 series: A. Bongo; B. 1-m net samples.

usually differed by factors of <3 . However, because the larger *E. pacifica* were 20 times more abundant in the winter than in the summer samples, the relative importance of season, population density, or other factors to avoidance capability are unclear from these samples alone.

The mean LF distributions in Figure 5 are based on the individual winter and summer samples in Figures 6 and 7. Of the three distinct modes in the curves representing the winter Bongo samples (Figure 6A), the one at 3-4 mm was also clear and of similar magnitude in four of the five 1-m net samples (Figure 6B). The mode at 9-11 mm was small in all 1-m net samples, discernible only as shoulder to a major mode. The mode at 14-18 mm appeared regularly in the 1-m net samples but as a low peak representing few individuals, compared to abundances of 100 to $>1,000/1,000\text{ m}^3$ in the Bongo samples.

The summer Bongo series also recorded three modes (Figure 7A). Two were just as clear in the 1-m net samples (Figure 7B), though the 8-10-mm mode was based on abundances about one-half as great as those caught by the Bongo. The Bongo mode for large adults 18-22 mm in length was discernible in three of the five 1-m net samples.

Hourly Time Change in *E. pacifica* Population Structure

The five winter-nighttime Bongo samples obtained during 1953-0021 hours (Figure 6A) show (1) near

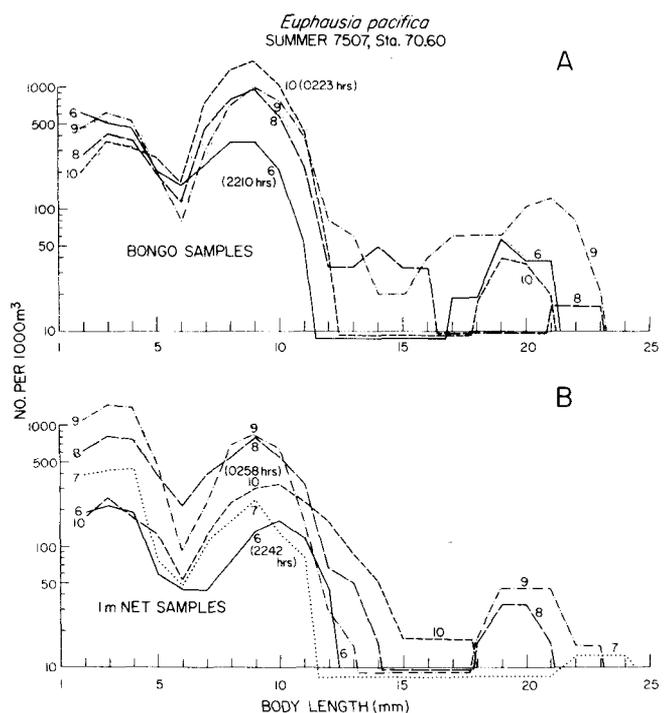


Figure 7. LF distribution of *Euphausia pacifica* from nighttime pairs of net-comparison tows, numbered 6 to 10, comprising the July (summer) 1975 series: A. Bongo; B. 1-m net samples. Bongo sample Number 7 was lost.

constancy with time in numbers of the 2-3-mm larvae and 7-12-mm juvenile-adults; (2) an increasing number of 4-6-mm specimens, until a factor of 10 separates the last tow, Number 10, from the first, Number 6; and (3) a decrease in numbers of 13-mm adults during the same 4½-hour period.

Bongo and 1-m net sampling alternated at half-hour intervals. Nevertheless, the Bongo curves are more similar among themselves than to any from the 1-m net (Figure 6B). Of the latter, Numbers 6-9 were most alike, whereas the final tow of the night, 1-m net Number 10, caught relatively numerous 4-16-mm specimens, much as the first tow of the night, Bongo Number 6, had caught particularly numerous specimens of 9-20 mm.

Effects of Bongo Mouth Width on Catch of *E. pacifica*

The 1975 winter and summer series compared the 1-m net with Bongo nets of 60-cm mouth width. The December 1977-August 1978 comparisons employed Bongo nets of 71-cm mouth width, designed so that the combined mouth area of the tandem nets equals the 0.785-m² mouth area of the 1-m net. An analysis to determine whether there is a difference in effectiveness—versus the 1-m net—between the two sizes of Bongos is limited by the substantial difference (Figure 5) between results of the winter and summer net-comparison series of 1975, both of which employed the smaller Bongo. During the winter series, the

Bongo caught significantly more *E. pacifica*, in relation to the 1-m net catch, than during the summer. This difference is still evident when the most atypical sample of each five-sample winter set (Figures 6A,B; Bongo sample Number 6 and 1-m-net sample Number 10) is omitted from the computation of mean LF distributions (Figure 8A). Therefore, combining 1975 winter and summer data on 60-m Bongo versus 1-m net appears unjustified for purposes of comparison with the 1977-78 data on 71-cm Bongo versus 1-m net. Such combining of data could have prompted the inference that the smaller Bongo is more efficient than the larger.

Nevertheless, the summer 1975 data for small Bongo and 1-m net (Figure 8B) closely resemble the 1977-78 data for large Bongo and 1-m net (Figure 8C, all seasons combined), when ratio of Bongo catch to 1-m net catch is plotted as a function of body length of *E. pacifica* (Figure 8D). In both series, the greatest relative Bongo net efficiency is at body lengths of 6-11, 14-18, and 21-22 mm. The magnitude of the ratios is similar. Only the anomalous data from the 1975 winter deter a conclusion that the different sized Bongo nets are equally effective samplers of *E. pacifica*.

Effects of Season, the 1977-78 Data, *E. pacifica*

The better ability of juvenile and adult *E. pacifica* to avoid the 1-m net during the 1975 winter series (Figure 8A), compared with the summer (Figure 8B), prompts examination of seasonal aspects of data from the 1977-78 period. Bongo/1-m-net catch ratios show the spring and summer curves to be roughly parallel (Figure 9).

Although represented as a mean of only eight stations of paired net tows, the 1977-78 winter data differ from that of the other seasons, as in 1975. In this instance, however, the anomaly in the winter data is the near equality of the two nets as catchers of juveniles and adults. In addition, 1-5-mm larvae were better sampled by the 1-m net by factors as great as 4-8 during the winter, though absolute numbers of these larvae were then low compared with spring and summer. Reasons for these inconsistencies in the winter data are not evident.

Male, Female, and Life-Phase Abundances versus Net Type, *E. pacifica*

Males and females are plotted separately (Figure 10A) in the adult segments of catch curves expressing mean LF distributions for the net-comparison stations at which *E. pacifica* occurred. The Bongo net tended to catch more males than females, and the 1-m net caught relatively more females.

Because there were more adult *E. pacifica* in the

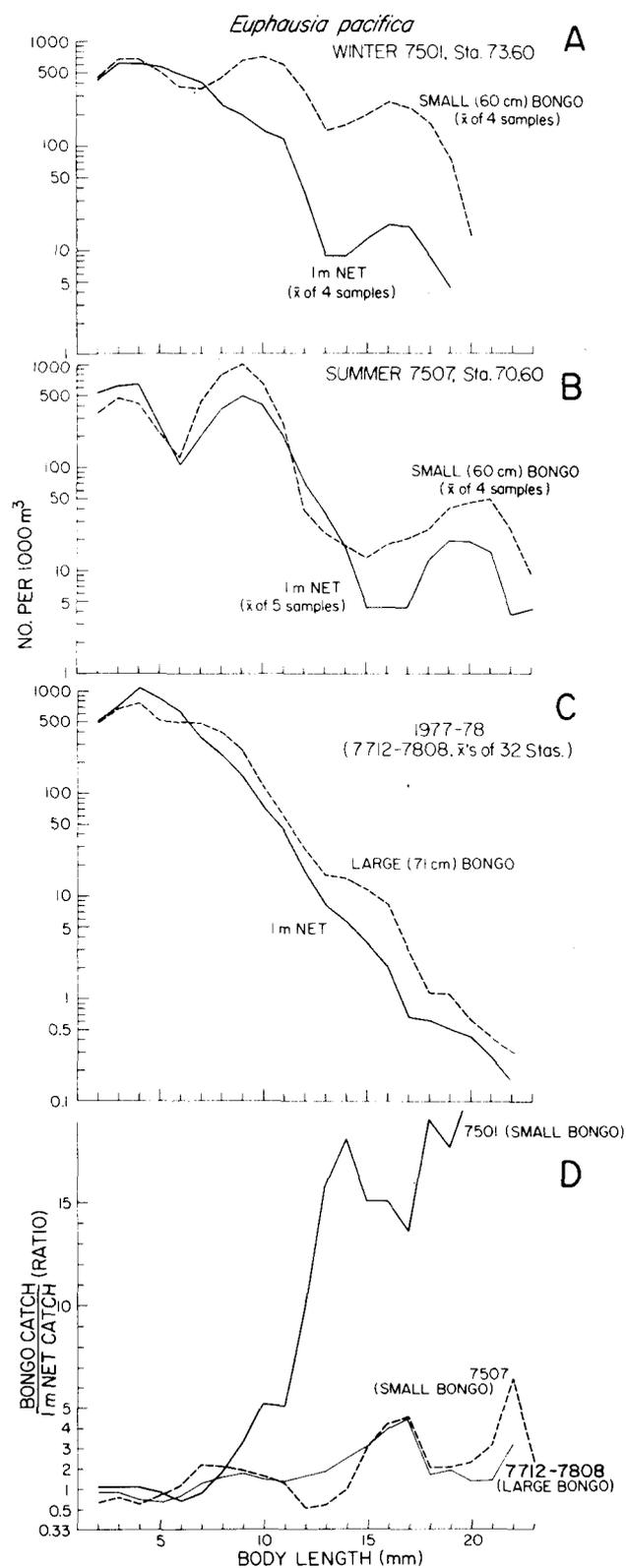


Figure 8. Mean LF distributions of *Euphausia pacifica* (3-point running averages): A. winter 1975 series, comparing 60-cm Bongo catches with 1-m net catches, omitting aberrant pairs Numbers 6 and 10 (Figure 6); B. summer 1975 series, also comparing 60-cm Bongo with 1-m net; C. 1977-78 pairs of tows, comparing 71-cm Bongo with 1-m net; D. Bongo/1-m-net catch ratios for the above.

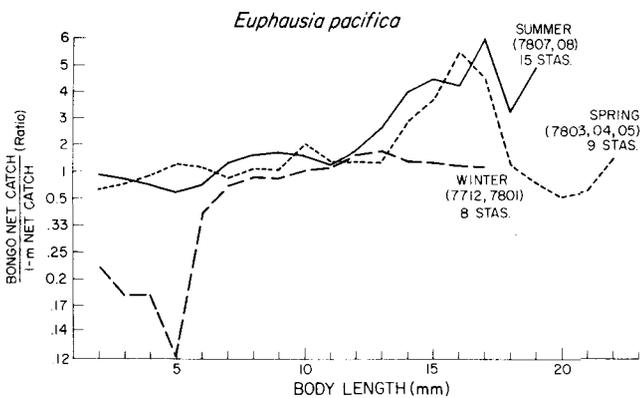


Figure 9. Mean Bongo/1-m-net catch ratios for *Euphausia pacifica* comparing winter, spring, and summer net-comparison sampling during 1977-78.

Bongo samples, it is supposed that the Bongo data provide the better description of a real population, in which males are narrowly in the majority, particularly in the range of 13-20-mm body length.

It appears unlikely that the apparent male predominance in the Bongo samples is due to a better capability of females to avoid that net. The 1-m net with its anterior bridle presents the more obvious stimulus to

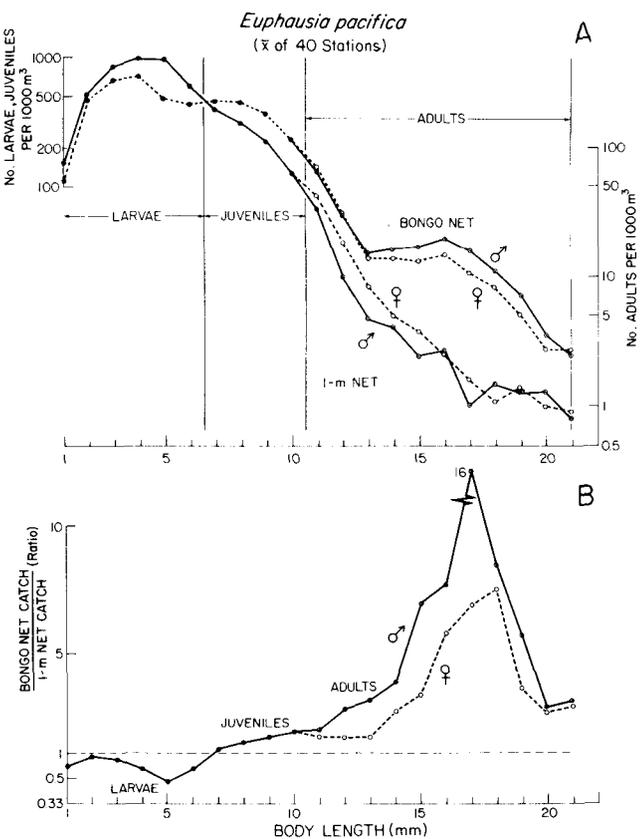


Figure 10. A. LF distributions of *Euphausia pacifica* (3-point running averages), comparing mean of all 1975-78 Bongo catches with mean of 1-m net catches. Adult males and females are separated. B. Bongo/1-m-net catch ratios for abundances shown in A.

avoidance by adult euphausiids, and it caught more females than males.

For males, the ratio of Bongo catches to 1-m net catches increases during adulthood from 11 mm to 17 mm body length (Figure 10B). For females, it increases during 13 mm to 18 mm. After 17 or 18 mm, this ratio decreases sharply, as does the number of individuals.

When the Bongo/1-m-net catch ratio is changed to a logarithm (Figure 11), straight lines may be fitted to segments of the curve representing that ratio plotted as a function of body length. The individual segments have different slopes and appear to relate to life phases.

The 1-m net is the better catcher of larvae, and the ability of *E. pacifica* to avoid the Bongo increases during larval development. This trend is reversed at the start of the postlarval period. By 7-mm body length, the Bongo has become the better catcher. There is a diminished rate of increase in catch ratio during juvenile growth from 7 to 11 mm, followed by an increased rate.

At 17-mm body length, the Bongo is catching an average of 16 times more males and eight times more females than the 1-m net. After 17-18 mm the ratios decrease. By 21 mm the Bongo catch of both sexes is only three times the greater.

A measure of the statistical significance of the larger average catches of 1-6-mm *E. pacifica* by the 1-m net (Figure 10A) is the following: 150 pairs of Bongo/1-m net abundances contributed to the mean abundances at the six 1-mm body-length increments, and in 98 (65%), abundance in the 1-m net sample was the greater.

Significance of the larger average catches of 7-21-mm *E. pacifica* by the Bongo net (Figure 10A) is seen in the same way: 407 pairs of Bongo 1-m net

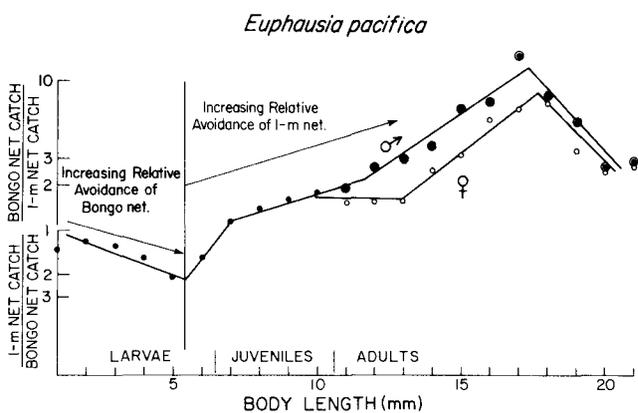


Figure 11. Catch ratios for *Euphausia pacifica*, logarithmic scale, relating 1975-78 mean distribution from Bongo catches with mean from 1-m net catches.

abundances contributed to the 15 pairs of mean abundances, and in 287 (71%), abundance in the Bongo sample was the greater.

Nematoscelis difficilis

Nematoscelis difficilis is more broadly distributed than its cool-water associate, *E. pacifica*, in the California Current (Brinton 1962b, 1967b). It was present in substantial numbers in 56 of the 90 net-comparison pairs of tows compared to 40 for *E. pacifica* but was usually at lower density when the two species co-occurred.

Larvae and small juveniles (to 6-mm length) of *N. difficilis* were better sampled by the 1-m net than by the Bongo (Figure 12 A,B). The Bongo/1-m-net catch ratio decreased somewhat during the course of the larval phase (Figure 12B), as in *E. pacifica*, before beginning an unsteady increase into the juvenile phase. The sharp decrease in abundances measured by both nets during development from 3 to 10 mm almost certainly represents a period of rapid growth associated with increasing ability to avoid the 1-m net.

Mean abundance increases with body length between 10 and 15 or 16 mm, indicating slowed growth during the late juvenile phase and the onset of maturity. Bongo catches are three times the greater during this period.

After about 16-mm body length there is a trend in both sexes toward increasing capability to avoid the

1-m net. This coincides with diminishing numbers of individuals at given body lengths due to increasing mortality, reaccelerated growth, or both. Improved ability to avoid both nets may also play a role. The smallness of numbers of individuals upon which the ratios for largest sizes are based reduces their significance.

The maximum length reached by female *N. difficilis* is known to be about 2 mm more than the male. Sampling by the 1-m net would have indicated a greater disparity, 26 mm for females and 21 mm for males. However, the Bongo caught some males as large as 24 mm.

Statistical significance of the larger average catches of 1-6-mm *N. difficilis* by the 1-m-net (Figure 12A) may be estimated from the following: 211 pairs of Bongo/1-m-net abundances contributed to the mean abundances at the six 1-mm length increments, and in 135 (65%), abundance in the 1-m-net sample was the greater.

Significance of the larger average catches of 7-25-mm *N. difficilis* by the Bongo net is seen in the same way: 464 pairs of Bongo-1-m net abundances contributed to the 26 pairs of mean abundances, and in 334 (72%), abundance in the Bongo sample was greater.

The bimodal shape of the LF curves (Figure 12A) closely agrees with the shape of an unpublished catch curve for *N. difficilis* representing an average of data from many monthly CalCOFI cruises extending from 1953 to 1958. Thus, this bimodal distribution seems to be the persisting population structure in this species. It reflects alternating phases of rapid and slowed growth.

The two modes appeared in exaggerated form in LF curves representing the 1975 winter and summer series off central California (Figure 13 A,B). The curve combining those Bongo/1-m-net catch ratios peaks particularly sharply at 8-11-mm body lengths.

As with *Euphausia pacifica*, the combined data on *N. difficilis* for all of 1977-78 (Figure 13 C,D) indicate less disparity between Bongo and 1-m-net catches than does the 1975 data. A modest mode in the catch ratio curve was nevertheless distinguishable at 8-10 mm, corresponding with the extreme mode in the 1975 data.

Euphausia eximia and *E. gibboides*

Euphausia eximia and *E. gibboides* are two large species inhabiting, respectively, more southern and more offshore waters of the California Current than do *E. pacifica* and *Nematoscelis difficilis*, while also overlapping parts of the range of those cool-water species. At night, *E. eximia* migrates up into the mixed layer, and *E. gibboides* only up into the ther-

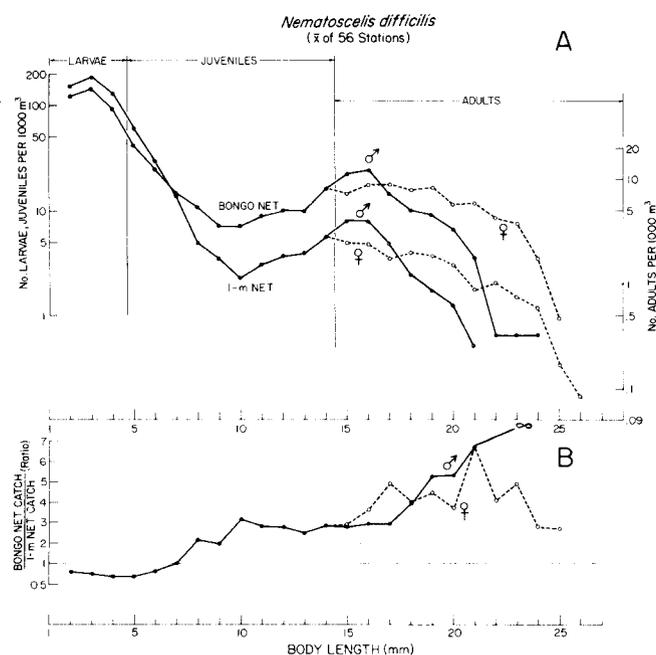


Figure 12. A. LF distributions of *Nematoscelis difficilis* (3-point running averages), comparing mean of all 1975-78 Bongo catches with mean of 1-m net catches. Adult males and females are separated. B. Bongo/1-m-net catch ratios for abundances shown in A.

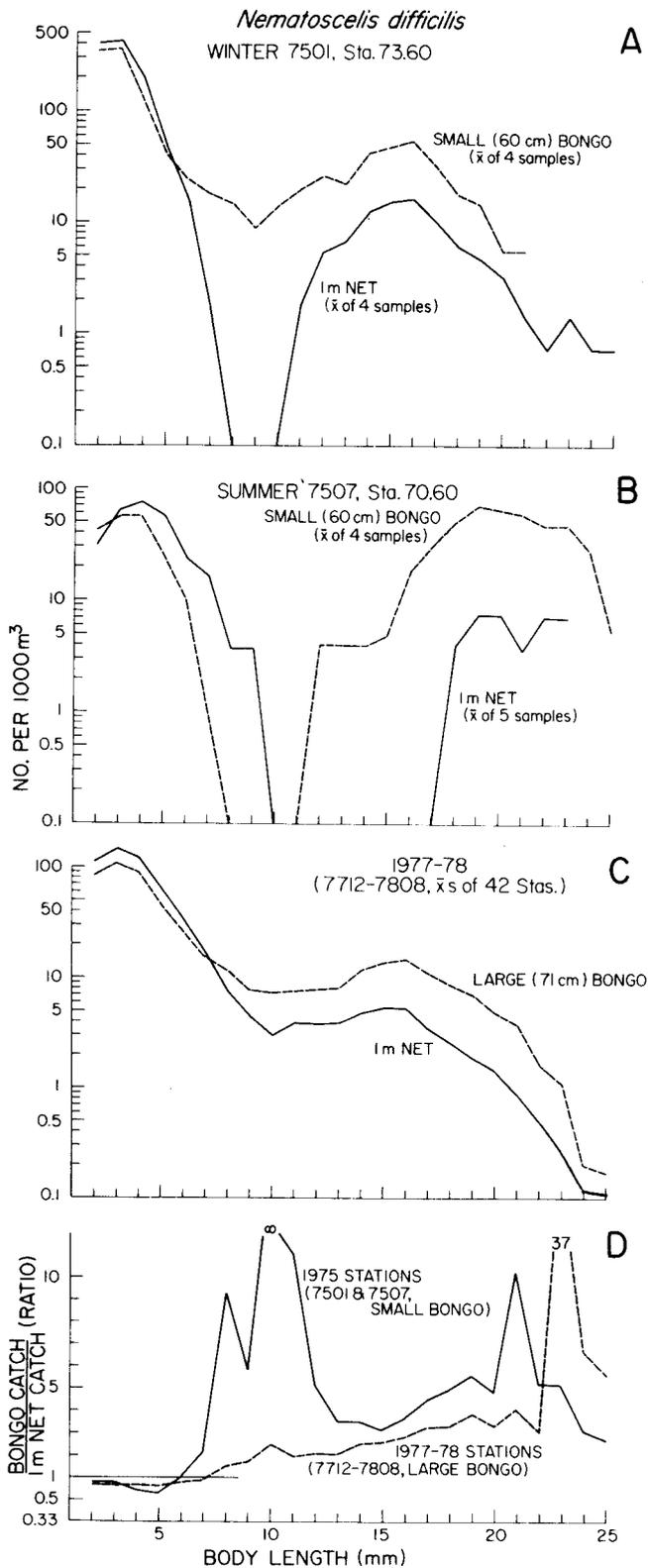


Figure 13. Mean LF distributions of *Nematoscelis difficilis* (3-point running averages): A. winter 1975 series, comparing four similar 60-cm Bongo catches with four 1-m net catches; B. summer 1975 series, also comparing 60-cm Bongo with 1-m net; C. 1977-78 tows, comparing 71-cm Bongo with 1-m net; D. Bongo/1-m net catch ratios for the combined 1975 data and the combined 1977-78 data.

mocline. The 0-210-m depth of sampling encompasses these nighttime levels.

As with *E. pacifica* and *N. difficilis*, larvae of *E. eximia* and *E. gibboides* were caught better by the 1-m net (Figure 14 A,B). The Bongo was the more effective catcher of adult *E. eximia* by as much as 3.5 times at 18-19 mm and 24-25 mm.

The Bongo was the more effective net for catching *E. gibboides* juveniles and adults. As with *E. eximia*, the body lengths at which the Bongo was relatively most effective were near 17-19 mm and again at maximum size, 24-25 mm in this species.

Euphausia hemigibba and E. recurva

These are smaller species than the above. Both are characteristic of the offshore part of the California Current, though they extended more inshore than usual during the 1977-78 period of sampling (Brinton 1981).

Euphausia hemigibba larvae were in nearly equal numbers in the Bongo and 1-m net catches, with the 1-m-net a little more effective for 3-4-mm sizes (Figure 15A). Juveniles and large adults were caught better by the Bongo by factors of 3 to 4, though mid-

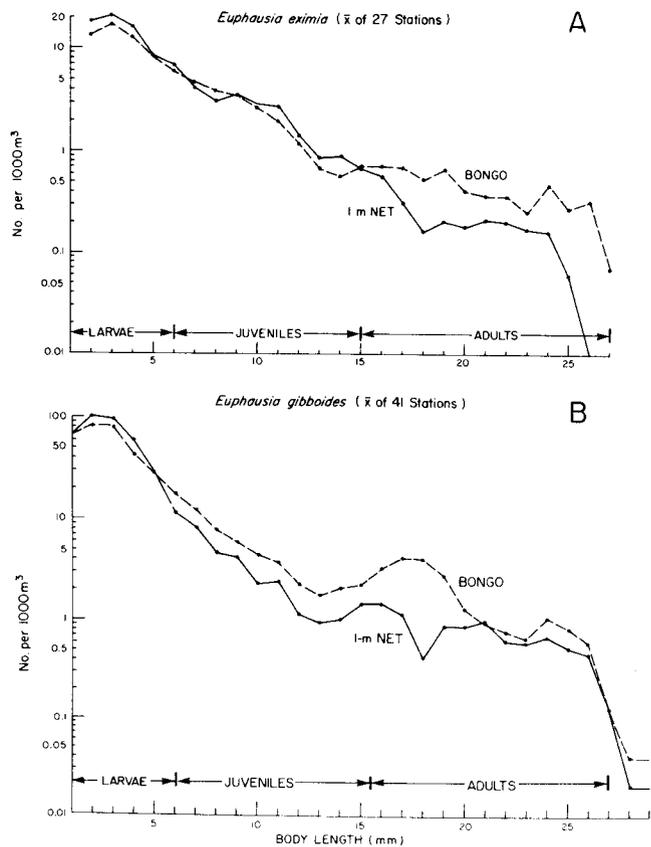


Figure 14. LF distributions comparing mean of all 1975-78 Bongo catches with mean of 1-m net catches: A. *Euphausia eximia*; B. *Euphausia gibboides*.

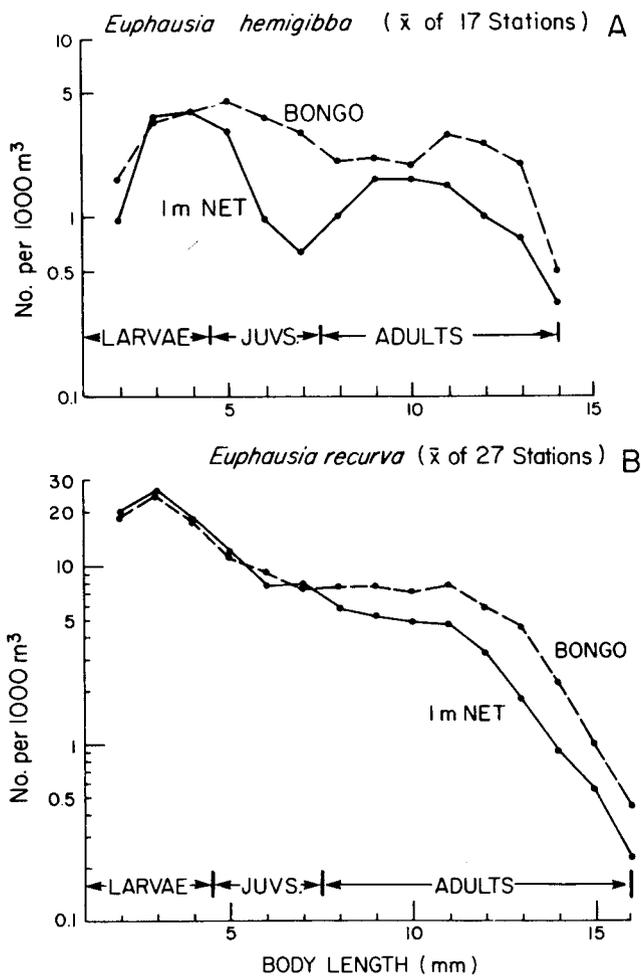


Figure 15. LF distributions comparing mean of all 1975-78 Bongo catches with mean of 1-m net catches: A. *Euphausia hemigibba*; B. *Euphausia recurva*.

adults of 9-10-mm length were almost as numerous in the 1-m net catches.

Euphausia recurva larvae were barely caught better by the 1-m net (Figure 15B). Bongo catches of adults were 1.5 times (at 8-mm length) to 2.5 times (at 13-14 mm) greater than those of the 1-m net.

Nyctiphanes simplex

N. simplex is frequently abundant in coastal waters of southern California and Baja California. Its LF distributions showed particularly clear relationships between life phase and relative retention by the two nets (Figure 16). Larvae were better sampled by the 1-m net by a factor of 2 and juveniles by a factor of 4. During the course of adulthood, the Bongo became increasingly the better collector.

Thysanoessa spinifera

Like *Nyctiphanes simplex*, *Thysanoessa spinifera* is a coastal, even neritic, species. Its range generally extends farther north than that of *N. simplex*, though

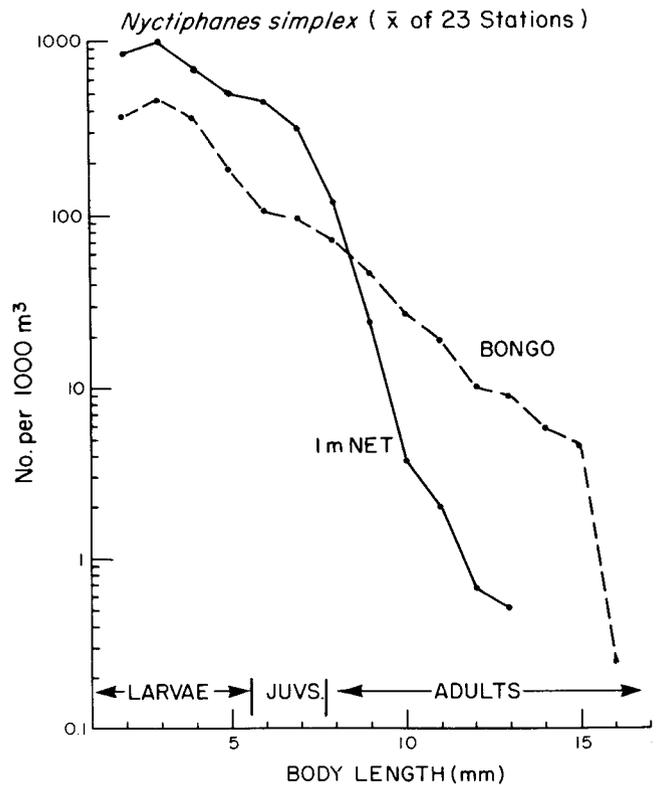


Figure 16. LF distributions of *Nyctiphanes simplex*, comparing mean of all 1975-78 Bongo catches with mean of 1-m net catches.

there is overlap, particularly along southern California.

In this large species, the larval phase, as indicated by incomplete telson development, extends to 8-mm body length, although antennae and pleopods assume the juvenile form by 6-mm length. The latter structural and functional changes also delineate the stage at which the Bongo becomes the more efficient means of capture. As a sampler of adults, the 1-m net yielded only a few specimens of 14-15-mm length, whereas the Bongo retained 13 times as many of that size, plus some as large as 21 mm.

Nematobrachion flexipes

N. flexipes is a large, sparse, widely-ranging, oceanic species having an unclear pattern of vertical migration, possibly swimming randomly through the mixed layer and thermocline, day and night (Brinton 1979). The Bongo is scarcely better than the 1-m net at capturing *N. flexipes* until this species has attained a length of 16 mm (Figure 17B). Thereafter, avoidance of the 1-m net was nearly complete, whereas the Bongo caught specimens up to 26 mm in length.

Thysanoessa gregaria, Stylocheiron affine and S. longicorne

These three small euphausiids occur throughout

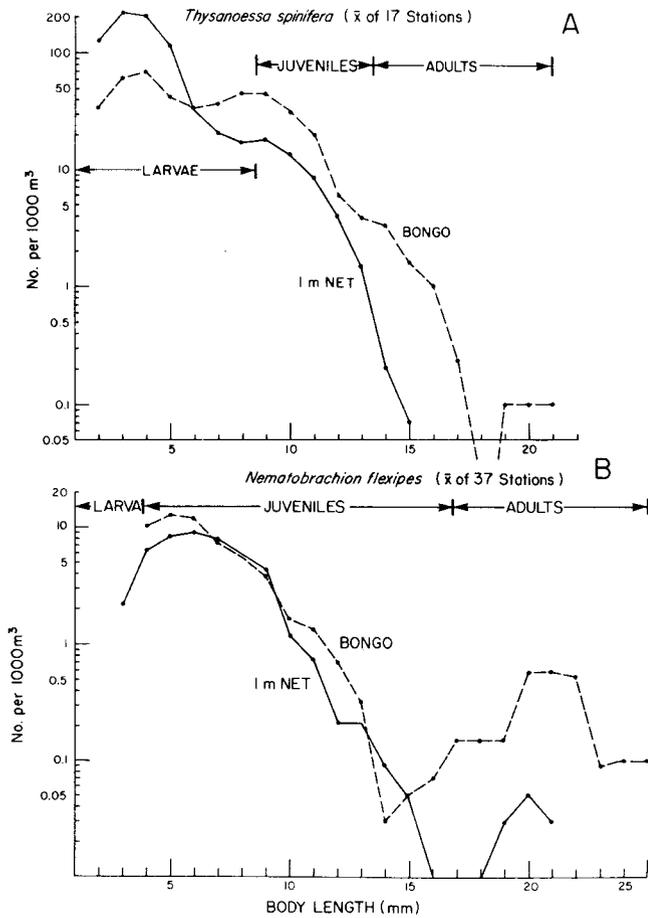


Figure 17. LF distributions comparing mean of all 1975-78 Bongo catches with mean of 1-m net catches: A. *Thysanoessa spinifera*; B. *Nematobrachion flexipes*.

much of the California Current. Unlike the other species here, all have depth ranges centered within the thermocline, day and night, in the deeper half of the 0-210-m layer sampled by our nets. The estimates of density of *Stylocheiron longicorne* may be the least accurate because this species tends to be deeper than *S. affine* and *Thysanoessa gregaria*, probably extending down to 250 or 300 m.

The three have been considered to be nonmigrators but with much stronger capacities for avoidance of nets in the daytime than at night in their mid-depth habitats (Brinton 1967a, 1979). This was construed as evidence of visual orientation to predators. During our nighttime comparative sampling, *T. gregaria* of 6-13-mm length were caught better by the Bongo net by a factor of 2. This value is much like the Bongo/1-m net-capture ratio for the approximately 6-13-mm juvenile phase of some of the larger species discussed above, e.g. *Euphausia pacifica* (Figure 10), which attained stronger avoidance capacity only beyond a length of about 13 mm, in early adulthood.

On the other hand, all sizes of the two *Stylocheiron*

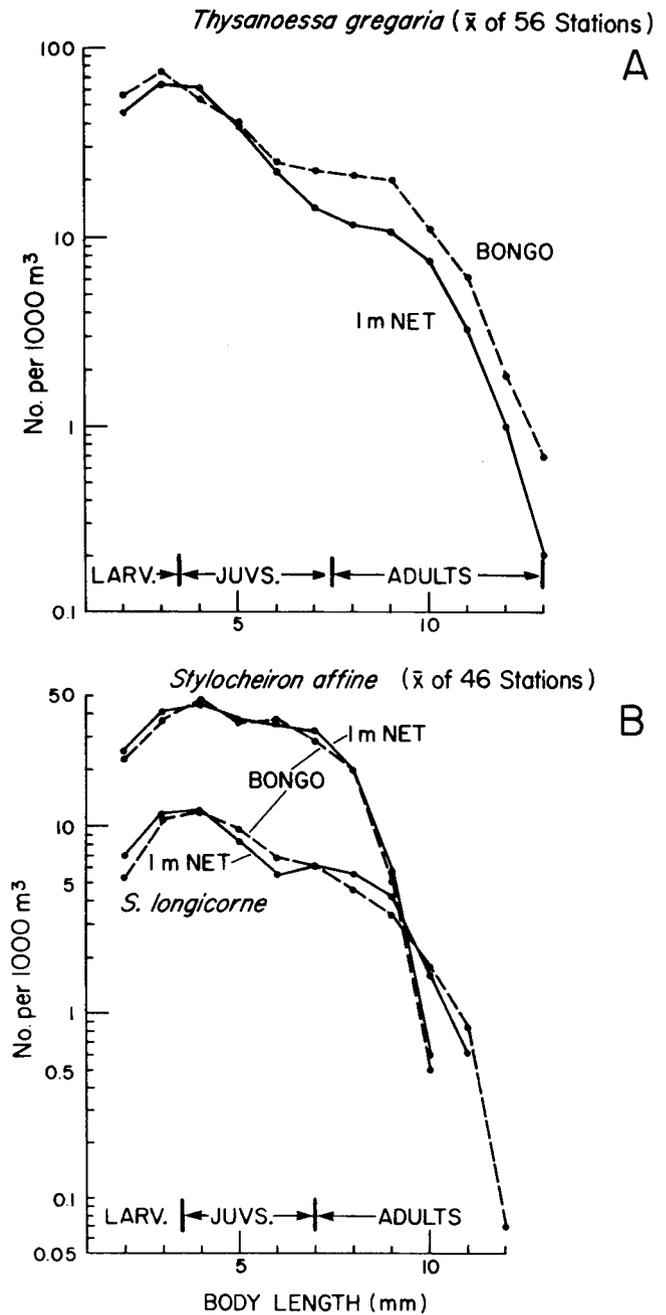


Figure 18. LF distributions comparing mean of all 1975-78 Bongo catches with mean of 1-m net catches: A. *Thysanoessa gregaria*; B. *Stylocheiron affine* and *S. longicorne*.

species were caught in near-equal numbers by the two nets. The 2-3-mm larvae were hardly more abundant in the 1-m net samples. This may indicate that these nonmigrators show little or no nighttime avoidance of either net.

SUMMARY AND DISCUSSION

Euphausiid abundances were measured by replicate tows, in which a tow with a Bongo net was followed

by a tow with a 1-m ring net. Significant characteristics of the nets are the anterior bridle on the 1-m net, compared with the bridleless Bongo, and the large mouth of the 1-m diameter ring net compared with 60-cm and 71-cm for the two types of Bongos used. However, the present set of samples are insufficient to relate differences in catching capacity to these characteristics. Comparable samples would be required from a bridleless 1-m net and from a Bongo-sized net with anterior bridle. Generalities emerging from the comparisons are the following:

1. Larval euphausiids, on the average, appear to be at higher density when sampled by the 1-m net than by the Bongo, though by a factor of less than 2 for most species.
2. Juveniles and, to a greater extent, adults of >13-mm body length are usually better sampled by the Bongo net, frequently by factors of 3 or more. Typically (Figure 19), the Bongo/1-m-net catch ratio peaks first during mid-adulthood and again at maximum size, though numbers are then becoming small.
3. Relative proportions of adult males and females differ between the Bongo and 1-m net samples.
4. Length-frequency histograms such as those averaging euphausiid population structure over a monthly period based on 1-m net tows (Brinton 1976) cannot reliably be amended by factors reflecting the greater average abundances of juveniles and adults found by Bongo sampling. However, species biomass estimates may be modified upward using Bongo/1-m-net ratios.

Larval Avoidance

The better catches of larvae by the 1-m net and of juveniles and adults by the Bongo may prove to be

related to behavior that is characteristic of particular life phases. Such behavior should be amenable to experimental study. For example, in 10 of 11 species, mean LF curves indicate that larvae with, as yet, incomplete development of pleopods (swimming legs) are somewhat better sampled by the 1-m net than by the Bongo. In *Nematobrachion flexipes*, larvae with incomplete development of pleopods are smaller than about 3.5-mm and were not present in these samples. During much of larval development, euphausiids swim by means of antennae and do not yet engage in extensive vertical migration. The proportion of larvae able to avoid the Bongo net relative to the larger 1-m net increases during the larval phase in *E. pacifica* and *N. difficilis* (Figures 10B, 12B). Larvae may be relating to the size of the approaching net and less cued directionally by the approach of a net bridle. The smallest, least active larvae were found at the same abundance by the two kinds of net. With increasing body length, fewer larvae seem able to avoid the 1-m-net than the Bongo mouth with its greater perimeter-to-area ratio. That is, if larvae of a particular size are in the path of an approaching net and are capable of an avoidance reaction of a specific distance, there will be more such larvae, relative to the mouth area, within avoiding distance of the rim of a small net compared with a larger one. As larvae grow to 2- to 5-mm length, the extent of this avoidance reaction should increase, so that progressively smaller densities will be recorded by the Bongo, relative to the 1-m net, as is observed to be the case.

A reviewer of this paper has suggested that weakly swimming larvae might cease conspicuous activity upon sensing the approach of a predator. This could have the effect of increasing numbers of larvae near the leading bridle and cause overestimation of larval abundance.

Curiously, *E. pacifica* larvae were sampled at higher density by day than by night by both the Bongo and the 1-m net (Figure 3).

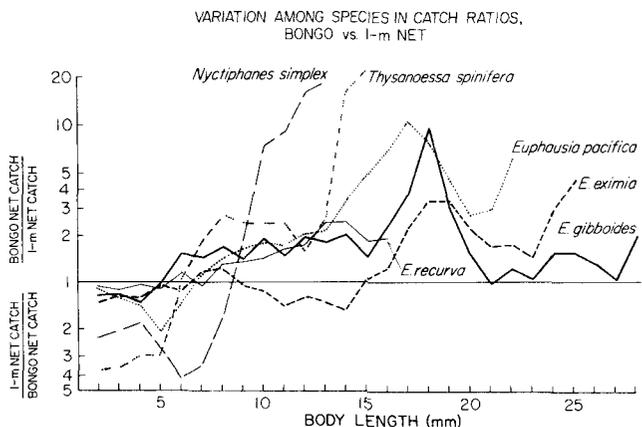


Figure 19. Catch-ratios relating mean LF distributions of all 1975-78 Bongo catches with the mean of all 1-m net catches for six representative euphausiid species. At small body lengths, ratios favor 1-m net, and at larger sizes ratios favor Bongo net, with maxima tending to fall at 13-19 mm and at >22-mm length.

Juvenile and Adult Avoidance

Toward the end of larval life, natatory function is transferred from antennae to pleopods, and antennae become sensory. These new capacities evidently better serve the animal in relation to the approach of the 1-m net than the Bongo. They increase rapidly in the postlarval period, 6-7 mm in *E. pacifica* and 6-8-mm in *N. difficilis*, followed by a diminished rate of increase through the juvenile phase. For the adult phase of most species, the rate of increase in the relative efficiency of the Bongo net is greatest.

The two *Stylocheiron* species (Figure 18B) seemed least affected by differences between the samplers.

The catches were nearly equal. The eye of these non-migrators consists of two differently oriented lobes, each with facets of a particular size. It may be rotated in the sagittal plane. *S. affine* and *S. longicorne* show strong daytime net-avoidance ability in their thermocline habitats (Brinton 1967a). They may have greater visual than tactile perception of predators, as may also be inferred in the present study from the equal abundances found by different nets during darkness. Land (1980) described function of the euphausiid bilobed eye in *Nematoscelis* in relation to daylight. He concluded that the upper lobe is designed to detect prey objects against downwelling light and the lower lobe to detect animals that reflect downwelled light against the dark background below.

On the other hand, vertically migrating round-eyed species such as comprise the genus *Euphausia*, live in near darkness day and night. They may therefore be relying more upon tactile than visual receptors in sensing the approach of predators, hence their better ability to better sense the bridled net than the 1-m net at night.

Sex Ratio, as Function of Net Type

Males of *Euphausia pacifica* outnumbered females in the Bongo samples by 1.1 to 1.0. This is construed to be a best estimate of the real sex ratio because both sexes are better sampled by the Bongo. The ratio in the 1-m net samples was 1.37:1, favoring females. A sex ratio for *E. pacifica* based on 1-m net samples from other years favored females, by 1.34:1 (Brinton 1976). The Bongo/1-m-net catch ratio was higher for males than females at all 1-mm body-length increments (Figure 10).

In *Nematoscelis difficilis*, males outnumbered females during early adulthood, 15-16 mm in Bongo samples, and 15-17 mm in 1-m net samples (Figure 12A). At greater body lengths, females outnumbered males, either due to higher mortality rates in males or to their better ability to avoid capture. An overall sex ratio favors females by 1.2:1 in the Bongo samples and by 1.1:1 in the 1-m net samples. The Bongo/1-m-net catch ratio was greater for males than for females at body lengths greater than 18 mm in this species. Thus, only these largest males of *N. difficilis* tend to avoid the 1-m net more effectively than females.

Bongo/1-m net Ratios of Abundance and Biomass

Much of the biogeographical mapping and study of euphausiid populations in the California Current has been based on CalCOFI surveys of 1950-76, during which the 1-m net was employed. The present data indicate that, for adult euphausiids at least, abundances estimated from the 1-m net catches are sub-

stantially less than those from the Bongo net. On the other hand, larvae, and in some species, juveniles, tend to be caught better by the 1-m net. Total numbers usually differed little between the two nets.

Ratios comparing Bongo and 1-m net catches of the principal life phases of the 12 euphausiid species are given in Table 1. These factors would not alter biogeographical information. An order of magnitude has commonly been used to separate intervals of total abundance (e.g. Brinton 1967b).

In the study of population dynamics, as in *Euphausia pacifica* (Brinton 1976), the larger number of juveniles and adults retained by the Bongo will significantly affect estimations of survivorship. They are already seen to clarify modes in length frequencies (e.g. Figures 5-7), the time progressions of which are used to determine growth rates. However, a danger in applying correction factors is that the factors cannot, as yet, deal with inconsistencies in catching capacity related to season or population structure. Furthermore, for large adults the factor would often be an unmanageable "infinity." Estimates of annual abundance or biomass of life phases (Table 1) rather than of 1-mm body-length increments, appear amenable to correction.

The Bongo/1-m net ratio for adult *Nematoscelis difficilis* is particularly high, 3.7, even in these nighttime samples. Strong daytime net avoidance by *N. megalops*, the Atlantic Ocean sibling of *N. difficilis*, led Wiebe and Boyd (1978) to question whether *N. megalops* engages in vertical migration at all. Adults of our two largest species, *Thysanoessa spinifera* and *Nematobrachion flexipes*, appear to be the strongest nighttime avoiders of the 1-m net, relative to the Bongo.

Biomass estimates are particularly affected by the Bongo/1-m net factors given in Table 1, because the bulk of biomass for the mean population of each species is seen to exist in juveniles and adults—for *E. pacifica*, 69% based on 1-m net sampling and 88% based on Bongo sampling, and in *Nematoscelis difficilis*, 91% and 96% respectively. For this reason, the mean biomass of the California population of *E. pacifica* is 1.7 times greater when measured by the Bongo than by the 1-m net, and of *N. difficilis*, 3.1 times greater.

Avoidance of the 1-m net has been described here only in relation to the Bongo-net catch. Bioluminescence and pressure signals are certain to be associated with any net and to prompt avoidance behavior by active plankters, as yet unmeasured in absolute terms.

ACKNOWLEDGMENTS

We are pleased to acknowledge the collaboration of

TABLE 1.
 Bongo/1-m-Net Mean Catch Ratios of Abundance and Biomass

Species	Number of Stations	Abundance (Number/1 000 m ³)				Biomass (wet cc/1000 m ³)			
		Larvae	Juveniles	Adults	Total	Larvae	Juveniles	Adults	Total
<i>Euphausia pacifica</i>	40	$\frac{1864}{2705} = 0.7$	$\frac{1028}{792} = 1.3$	$\frac{379}{149} = 2.5$	$\frac{3271}{3646} = 0.9$	$\frac{2711}{4111} = 0.7$	$\frac{9142}{6034} = 1.5$	$\frac{10290}{3223} = 3.2$	$\frac{22143}{13368} = 1.7$
<i>E. eximia</i>	27	$\frac{51}{63} = 0.8$	$\frac{25}{26} = 1.0$	$\frac{6}{3} = 2.0$	$\frac{82}{92} = 0.9$	$\frac{33}{39} = 0.8$	$\frac{174}{198} = 0.9$	$\frac{446}{184} = 2.4$	$\frac{653}{421} = 1.5$
<i>E. gibboides</i>	41	$\frac{289}{349} = 0.8$	$\frac{59}{37} = 1.6$	$\frac{20}{8} = 2.4$	$\frac{368}{394} = 0.9$	$\frac{135}{163} = 0.8$	$\frac{448}{273} = 1.6$	$\frac{1423}{723} = 2.0$	$\frac{2006}{1159} = 1.7$
<i>E. recurva</i>	27	$\frac{61}{65} = 0.9$	$\frac{28}{28} = 1.0$	$\frac{45}{28} = 1.6$	$\frac{133}{120} = 1.1$	$\frac{31}{34} = 0.9$	$\frac{65}{64} = 1.0$	$\frac{555}{319} = 1.7$	$\frac{651}{417} = 1.6$
<i>E. hemigibba</i>	17	$\frac{5}{5} = 1.0$	$\frac{15}{8} = 1.7$	$\frac{14}{8} = 1.7$	$\frac{34}{21} = 1.6$	$\frac{2}{2} = 1.0$	$\frac{28}{12} = 2.3$	$\frac{172}{95} = 1.8$	$\frac{202}{109} = 1.9$
<i>Nyctiphanes simplex</i>	23	$\frac{260}{649} = 0.4$	$\frac{298}{1242} = 0.2$	$\frac{200}{154} = 1.3$	$\frac{758}{2045} = 0.4$	$\frac{142}{418} = 0.3$	$\frac{739}{2888} = 0.3$	$\frac{1958}{946} = 2.1$	$\frac{2839}{4252} = 0.7$
<i>Nematoscelis difficilis</i>	56	$\frac{368}{479} = 0.8$	$\frac{220}{132} = 1.7$	$\frac{118}{32} = 3.7$	$\frac{706}{643} = 1.1$	$\frac{184}{246} = 0.7$	$\frac{1245}{597} = 2.1$	$\frac{6580}{1767} = 3.7$	$\frac{8009}{2610} = 3.1$
<i>Thysanoessa gregaria</i>	56	$\frac{130}{109} = 1.2$	$\frac{120}{122} = 1.0$	$\frac{83}{49} = 1.7$	$\frac{333}{280} = 1.2$	$\frac{48}{41} = 1.2$	$\frac{162}{158} = 1.0$	$\frac{582}{334} = 1.7$	$\frac{792}{533} = 1.5$
<i>T. spinifera</i>	17	$\frac{323}{734} = 0.4$	$\frac{112}{46} = 2.4$	$\frac{3}{0.1} = 30$	$\frac{438}{780} = 0.6$	$\frac{629}{718} = 0.9$	$\frac{1174}{475} = 2.4$	$\frac{130}{2} = 65$	$\frac{1933}{1195} = 1.6$
<i>Nematobrachion flexipes</i>	37	$\frac{10}{9} = 1.1$	$\frac{46}{38} = 1.2$	$\frac{2}{0.1} = 20$	$\frac{58}{47} = 1.2$	$\frac{9}{7} = 1.3$	$\frac{188}{157} = 1.2$	$\frac{221}{8} = 26.1$	$\frac{418}{172} = 2.4$
<i>Stylocheiron affine</i>	46	$\frac{58}{65} = 0.9$	$\frac{119}{118} = 1.0$	$\frac{54}{59} = 0.9$	$\frac{231}{242} = 1.0$	$\frac{22}{25} = 0.9$	$\frac{178}{176} = 1.0$	$\frac{259}{281} = 0.9$	$\frac{459}{482} = 1.0$
<i>S. longicorne</i>	46	$\frac{16}{18} = 0.9$	$\frac{29}{26} = 1.1$	$\frac{17}{18} = 0.9$	$\frac{62}{62} = 1.0$	$\frac{7}{7} = 1.0$	$\frac{40}{35} = 1.1$	$\frac{102}{108} = 0.9$	$\frac{149}{150} = 1.0$

the Instituto Nacional de Pesca of Mexico. Portions of these data were collected under authority of the Secretaría de Relaciones Exteriores and the Departamento de Pesca of Mexico.

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SEASONAL AND BATHYMETRIC DISTRIBUTION OF THECATE AND NONTHECATE DINOFLAGELLATES OFF LA JOLLA, CALIFORNIA

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ABSTRACT

A one-year study of the spatial and temporal distribution of thecate and nonthecate dinoflagellates over 50 μm in length was carried out at two stations off La Jolla, southern California.

The survey revealed larger dinoflagellate populations at the Secchi level than at the surface, composed principally of nonthecate forms. The relative contributions of thecate and nonthecate dinoflagellates at three levels within the euphotic zone are presented, with special reference to autotrophic or heterotrophic characteristics of the leading species.

RESUMEN

Se realizó durante un año un estudio de la distribución espacial y temporal de dinoflagelados tecados y atecados de más de 50 μm de longitud, en dos estaciones frente a La Jolla, en el sur de California.

El reconocimiento reveló la presencia de poblaciones más grandes de dinoflagelados en la profundidad Secchi que en la superficie, compuestas principalmente por formas atecadas. Se presentan las contribuciones relativas de dinoflagelados tecados y atecados en tres niveles dentro de la zona eufótica, con atención a las características autotróficas o heterótrofas de las especies más abundantes.

INTRODUCTION

A one-year study, December 1976–December 1977, of both thecate (armoured) and nonthecate (naked) dinoflagellates was carried out at two stations off La Jolla, California.

Although the terms thecate and nonthecate are used throughout this contribution, the author is aware of differences of opinion among various investigators regarding these terms. The existence of platelike polygonal patterns observed on some of the "naked" species may be caused by membrane-lined cavities within the outer layer of the cells as discussed by Taylor (1976), who also reviews the work of other investigators in this respect.

The primary purpose of the present study was to

assess distribution patterns and the ratio of naked to armoured dinoflagellates with particular stress on the ability of the former to use phagotrophy as one method of heterotrophic nutrition. Although phagotrophy is not limited to nonthecate dinoflagellates, this form of nutrition is more common in members of this group. Many of them are devoid of photosynthetic pigments, and they must rely entirely on heterotrophic nutrition either by ingesting or otherwise absorbing dissolved or particulate organic matter.

There was more likelihood of detecting instances of phagotrophy in the larger forms of thecate and nonthecate dinoflagellates. However, the occurrence of large numbers of dinoflagellates smaller than 50 μm was noted.

The author became aware, at an early stage of the study, of the presence of a number of fairly large naked dinoflagellates in the live samples collected qualitatively by fine-mesh nets from the same stations or from the Scripps Institution of Oceanography (SIO) pier. Many of these dinoflagellate species, belonging chiefly to the genera *Gymnodinium*, *Gyrodinium*, and *Warnowia*, showed a variety of inclusions, both as food storage bodies as well as ingested particles. However, the presence of these organisms in the preserved samples collected at the same stations was often overlooked due either to distortion resulting from fixation or to disintegration. It is proposed to discuss further these large phagotrophic dinoflagellates in a separate contribution.

LITERATURE SURVEY

There are a number of contributions dealing with the occurrence of dinoflagellates off the coast of southern California, mainly in relation to those species causing red tides. The dinoflagellates considered are a fairly limited number of autotrophic bloom-forming species such as *Prorocentrum micans*, *Gonyaulax polyedra*, *Gymnodinium splendens*, and several species of *Ceratium*. The earlier works by Allen who monitored the occurrence of red tides in La Jolla Bay between 1917 and 1945, Lackey and Clendenning (1965), and other investigators were reviewed by Holmes et al. (1967). The latter authors confirmed Allen's (1941) findings that tides caused by *Prorocentrum micans* occurred before midsummer

¹Visiting research biologist, Food Chain Research Group, Institute of Marine Resources, University of California San Diego, 1976–78.

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whereas those caused by *Gonyaulax polyedra* occurred after midsummer. An interdisciplinary approach to the plankton ecology of the area is to be found in a series of articles dealing with various aspects of this subject by members of the Food Chain Research Group in a publication edited by Strickland (1970).

The specific physiological ecology of *Gonyaulax polyedra*, among the dominant bloom-forming dinoflagellates mentioned above, has recently been analyzed by Eppley and Harrison (1974). These authors relate the local red tides caused by such organisms to nutrient enrichment via upwelling and consider the grazing by phagotrophic dinoflagellates, such as *Noctiluca miliaris*, *Polykrikos kofoidii*, and *Fragilidium heterolobum*, as one of the factors responsible for the decline of these local blooms.

Diurnal vertical migration of dinoflagellates as a function of the particular environmental conditions prevailing off La Jolla was considered by Eppley et al. (1968) in reference to *Ceratium furca* following a bloom off the California coast. This migration in some red tide dinoflagellates, particularly *Gonyaulax polyedra*, might serve as a survival mechanism enabling them to reach water depths where nutrients are available (Eppley and Harrison 1974).

The role of *Gymnodinium spendens*, an unarmoured dinoflagellate, as an important bloom-forming organism in Baja California and off the coast of California is described by Kiefer and Lasker (1975). This bloom seems to be limited to inshore waters, and the species constitutes an important food organism for anchovy larvae (Lasker 1975).

Many of the unarmoured dinoflagellates occurring off the coast of southern California may not be responsible for any of the red tides reported in the past but may well play a significant role in the food chain as active phagotrophs. The most notable contribution on this subject is in Kofoid and Swezy's (1921) monograph on unarmoured dinoflagellates. In this work, many of the large heterotrophic dinoflagellates also encountered in the present study have been described in detail, many of them showing ingested organisms. More recent references on phagotrophic nutrition by dinoflagellates are by Norris (1966), Norris (1969), Beers et al. (1975), who also review other reports of phagotrophic feeding, and by Kimor (1979) in relation to the predation of *Noctiluca miliaris* on *Acartia tonsa* eggs in the inshore waters of southern California.

MATERIALS AND METHODS

Location of the Stations (Figure 1)

Two stations, designated as 2 and 3, were occupied approximately every two to three weeks. Station 1, the

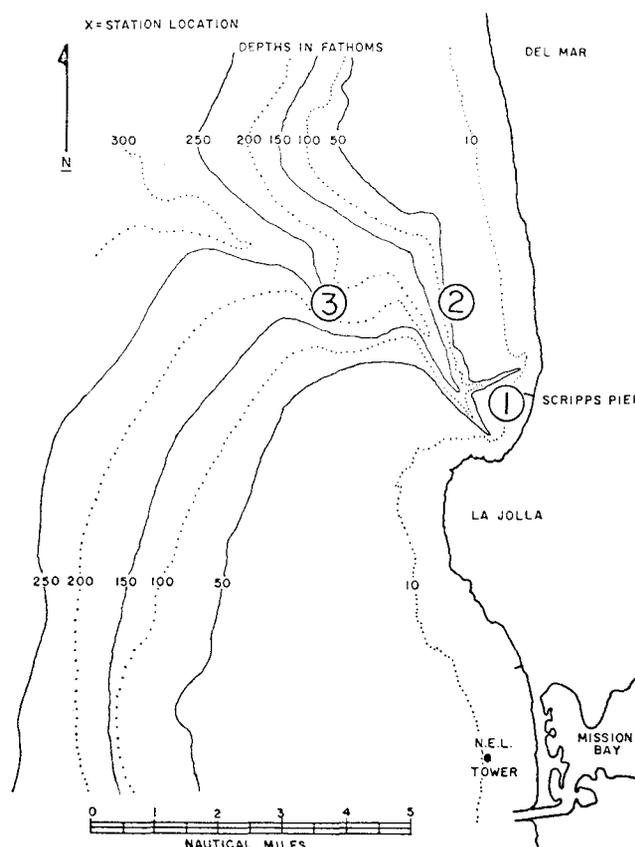


Figure 1. Location of Stations 1-3 (after Strickland 1970).

end of the SIO pier, was used extensively for the collection of living organisms and for records of temperature and salinity.

Station 2 was located at $32^{\circ}53.4'N$, $117^{\circ}16.5'W$, 1.6 km west of the coastline, in waters 72–90 m deep on a gradually sloping coastal shelf which drops rapidly to depths of over 360 m into the La Jolla Submarine Canyon to the west.

Station 3 was located at $32^{\circ}53.4'N$, $117^{\circ}18.6'W$, 5.3 km west of the coastline, in waters 470 m deep in a narrow depression in the La Jolla Submarine Canyon.

Drifting of the boats made it necessary to indicate the location of the two stations by circles, about 400 m in diameter (Figure 1). The coordinates listed above for the two stations refer to the center of the circles.

Sampling

a. Physical data. Transparency measurements (using a Secchi disk) were made routinely at the two stations (Figure 2). It is assumed that 20% of the surface illumination occurred at 1 x Secchi-disk depth (the shallowest depth at which the disk was no longer visible) and 1% at 3 x Secchi-disk depth, as outlined in Strickland et al. (1970), who also referred to the shortcomings of this method. However, technical

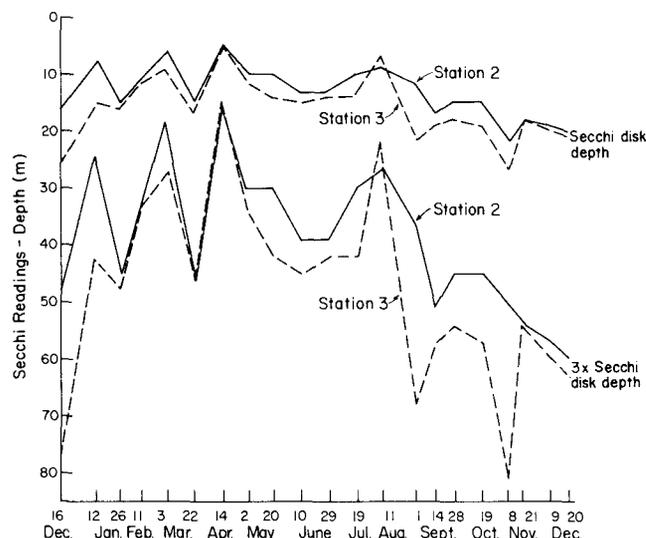


Figure 2. Secchi-disk and 3 x Secchi-disk depth readings at Stations 2 and 3 (December 1976-December 1977).

limitations in the available field work facilities of this investigation prevented the use of a more precise method for measuring the light profile. On four occasions temperature was determined at each of the three depths sampled (Figure 3). Otherwise only surface temperature was determined at both stations as measured by a bucket thermometer (Figure 3). Surface and bottom temperatures and salinities at the end of the SIO pier (Anonymous 1978) during the sampling days are also referred to in this report (Figure 4).

b. Niskin bottles (5 liters) were used to collect water for the preserved material and the chlorophyll samples. Bottles were deployed at the surface, the Secchi disk depth, and 3 x the Secchi-disk depth.

c. The plankton net used to collect live material was a ¼-m open-mouth net of 35- μ m mesh. The materials for live examination were stored in a styrofoam insulated box immediately after sampling.

Sample Analysis

a. Chlorophyll *a* and phaeophytin. Seawater samples (250 ml) were filtered onto Whatman GF/C filters, placed in 90% acetone, extracted for 24 hours at 8–10°C in the dark, and read on a Turner model 110 Fluorometer according to the Strickland and Parsons (1968) method.

b. Preserved microplankton samples. To preserved samples, reagent grade formaldehyde was added to 1-quart prescription bottles so as to produce a final 5% concentration after the addition of the sample. A subsample (100 ml) was removed for subsequent reference if necessary, and the remainder was allowed to settle for about 48 hours. The supernatant fluid was removed by vacuum aspiration. The resulting con-

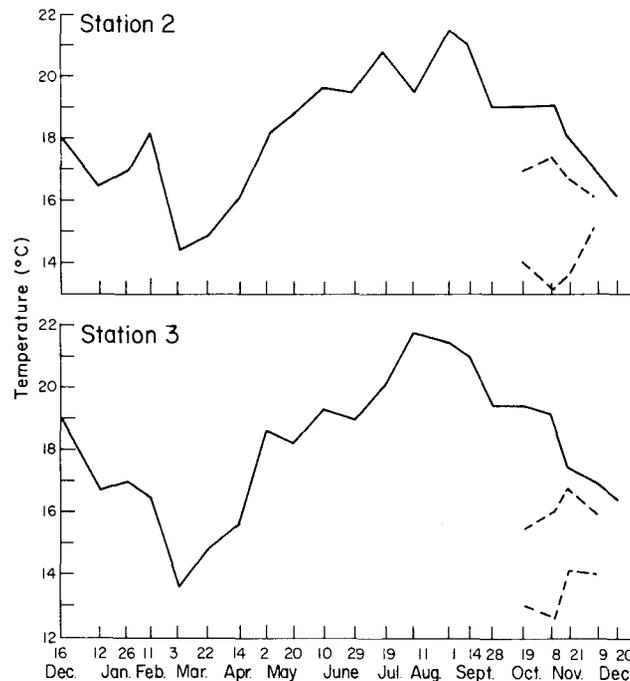


Figure 3. Temperatures at Stations 2 and 3 (December 1976-December 1977).

centrated sample had a known volume between 75–100 ml.

Aliquots (25-50 ml) from the concentrated sample were allowed to settle for at least 24 hours in 9.2-cm-tall cylinders, after which the numerical abundance of the dinoflagellates larger than 50 μ m in length was determined. An inverted microscope at 100 and 200 magnification was used for the counts by the Utermöhl (1932) method. The thecate and nonthecate dinoflagellate species were counted, and instances of inclusions were recorded. The results are expressed as numbers per liter at the species and group level.

The live samples collected from net hauls were examined within an hour of their collection. Photo-

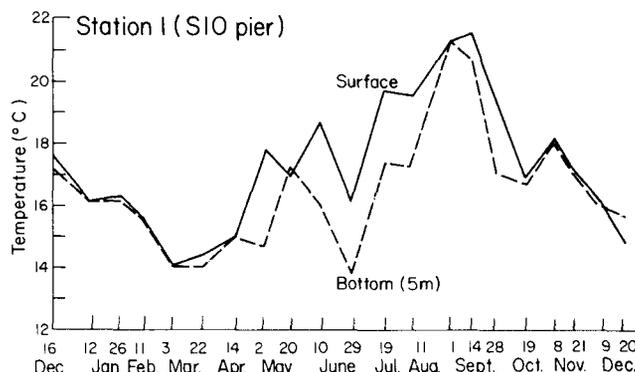


Figure 4. Surface and bottom temperatures at SIO pier (December 1976-December 1977).

graphic records were made, particularly of those forms that showed easily identifiable ingested organisms.

RESULTS AND DISCUSSION

The Environment

The area chosen for investigation is known for its highly variable hydrographic and biological properties (Strickland et al. 1970). The environmental data taken during the present study tended to confirm this variability, with the exception of salinity. The fluctuations of surface salinity recorded at the end of the SIO pier were small, with a minimum of 33.37‰ in August and a maximum of 34.15‰ in July. The differences in the data recorded at the same station at 5-m depth were insignificant (Anonymous 1978).

Temperature records (Figure 4) for the SIO pier (Anonymous 1978) at surface and bottom (5 m) levels indicated a minimum of 14°C in March and a maximum of 21.5°C in September at the surface for the year of this study. Bottom temperatures were roughly 2°C lower during the period April to August 1977, approaching the surface values during the following months.

Surface temperatures at the study sites (Figure 3) showed the same general pattern at both stations.

Temperature records for Secchi and 3 x Secchi depths at Stations 2 and 3, taken during four consecutive cruises between October 19 and December 9, 1977, indicate a decrease in temperature with depth, which might impact on the spatial distribution of the dinoflagellates (Figure 3).

Transparency measurements as indicated by Secchi depth showed strong temporal fluctuations at both stations throughout the year with higher transparencies reported for the outward station during most of the cruises. This trend proved particularly obvious during the latter part of 1977 (Figure 2).

The chlorophyll data for the total phytoplankton population at the two stations cannot be directly related to the standing crop of the portion of the dinoflagellate population considered here (Figure 5). This may be attributed to the difficulty in determining the contribution of photosynthetic dinoflagellate species relative to other autotrophs, notably diatoms, present in the plankton at the same time, location, and depth. For this reason we cannot be sure whether the fairly prominent peak in chlorophyll *a* values recorded at Station 3 in April 1977 was caused mainly or solely by the photosynthetic dinoflagellate *Peridinium trochoideum*. This species was noted as abundant at that time, although it was not counted in the samples since it is smaller than 50 μm . Similarly, the abundance of *Prorocentrum micans*, also a photosynthetic, bloom-forming thecate dinoflagellate, was over 1,400

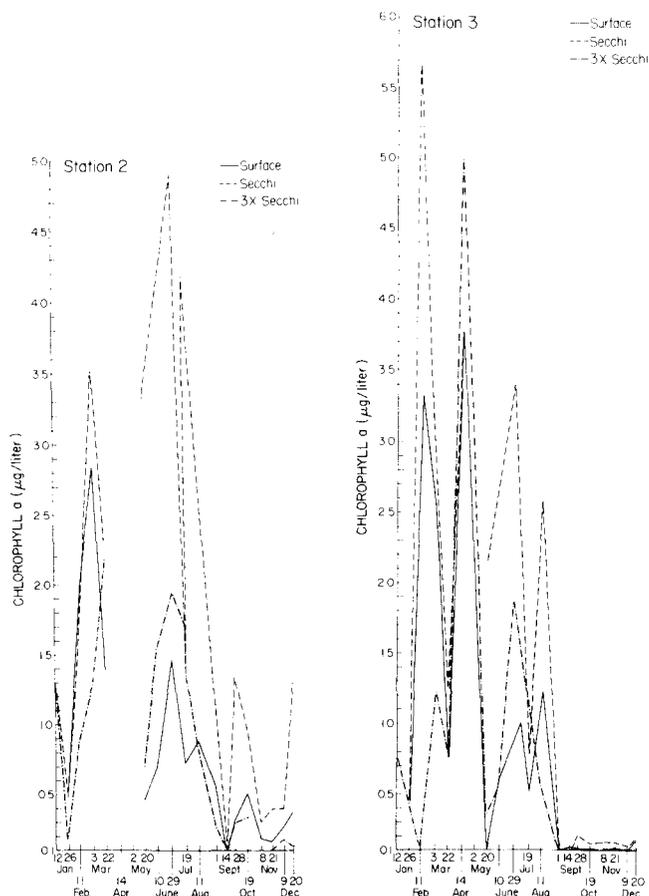


Figure 5. Chlorophyll *a* concentrations (surface, Secchi, and 3 x Secchi) at Stations 2 and 3 (December 1976-December 1977).

cells/liter in the surface layer. This species, together with *Ceratium dens* listed in Table 1, may have contributed to the 29 June 1977 peak at Station 2 (Figure 6).

In general, with the exception of the March peak in surface and Secchi-depth chlorophyll concentrations at both stations, the chlorophyll fluctuations during the latter months did not seem to coincide at the two sites either in time or in depth, suggesting the existence of significant differences in the environment even over this comparatively short distance.

Species composition

Sixty-three taxa of thecate and twenty-eight taxa of nonthecate dinoflagellates were encountered in the course of this investigation. However, in the following sections, reference will only be made to those taxa considered most important on the basis of their numerical abundance or their possible significance as ecological indicators.

Table 1 summarizes for each station and depth the abundances of six dominant thecate species and three dominant nonthecate species recorded in the study. Heterotrophic species are indicated.

TABLE 1
 Dominant Thecate and Nonthecate Dinoflagellates¹ at Stations 2 and 3, December 1976-December 1977.

Species	Depth	Dec 16	Jan 12	Jan 26	Feb 11	Mar 3	Mar 22	Apr 14	May 2	May 20	Jun 10	Jun 29	Jul 19	Aug 11	Sep 1	Sep 14	Sep 28	Oct 19	Nov 8	Nov 21	Dec 9	Dec 20
Station 2.																						
A. Dominant thecate dinoflagellates																						
<i>Ceratium cf. dens</i>	surface				13			96			29	1379	1012	271	27			22				
	Secchi				2			258	13					342			25					
	3 x Secchi							1570														
<i>Ceratium furca</i>	surface	34		24	245	62	1722	2765	57		12	819		1671	22		456	1490	180		166	67
	Secchi					32	51	3914	31				18	949	46	227	628				13	27
<i>Ceratium fusus</i>	3 x Secchi				6			2667														
	surface				27		15	16					200	13	38	38	41	50	222	51	52	18
<i>Dinophysis fortii</i>	Secchi						77							13			13		11			
	3 x Secchi																					
<i>Peridinium depressum</i> ²	surface						95					331	43		22							
	Secchi								31				282	760		38			11			13
<i>Peridinium divergens</i> ²	3 x Secchi								32		13											
	surface						382						115	13								6
<i>Peridinium depressum</i> ²	Secchi					13	109	67					28	24	23	24	21					
	3 x Secchi						13															
<i>Peridinium divergens</i> ²	surface	17			13						12	51	964	23	92	89			222	48		
	Secchi	30		16							11		94	253			25	61	86			
<i>Peridinium divergens</i> ²	3 x Secchi			2	14			126														
	surface																					
<i>Cochlodinium catenatum</i> ²	Secchi					3209	131	21						101		6	264	110				
	3 x Secchi					4119	3388							51	1116	5877	1500				179	
<i>Gyrodinium spp. >65µm</i> ³	surface							21					21									
	Secchi				21		57	43			830	89	94	25	59	10	63					
<i>Torodinium robustum</i> ²	3 x Secchi				12		60				103	21	44					10	10			
	surface											17	12			38	41	44		18		
<i>Torodinium robustum</i> ²	Secchi							56					447	114	42	13			11	13	10	
	3 x Secchi							32							26							
Station 3.																						
C. Dominant thecate dinoflagellates																						
<i>Ceratium cf. dens</i>	surface						41	409						311	27			6				
	Secchi							244						292								
	3 x Secchi							45						11								
<i>Ceratium furca</i>	surface				21	80	937	3117						85	11		45	24		43	23	43
	Secchi					118		2438	6				11		15		124	23				12
<i>Ceratium furca</i>	3 x Secchi							1796														
	surface			21	21		26							29	27	28	10	98	17			8
<i>Ceratium fusus</i>	Secchi													146	5		12		6	37		
	3 x Secchi																					
<i>Dinophysis fortii</i>	surface						118	142						11	5			5		7		
	Secchi					7		105	6				90	785	49			6	8		14	
<i>Peridinium depressum</i> ²	3 x Secchi							60														
	surface						134			6												
<i>Peridinium depressum</i> ²	Secchi						28							11								9
	3 x Secchi																		3			
<i>Peridinium divergens</i> ²	surface				21			53						187	141	5	33	18				10
	Secchi							122						146				12	7			8
<i>Peridinium divergens</i> ²	3 x Secchi	13						30						6		16						3
	surface																					
<i>Peridinium divergens</i> ²	Secchi																					
	3 x Secchi	28	10									5		6								
D. Dominant nonthecate dinoflagellates																						
<i>Cochlodinium catenatum</i> ²	surface					1340		18									22	335	110		106	40
	Secchi					3397		35									67	1990	9444	65	88	22
<i>Gyrodinium spp. >65µm</i> ³	3 x Secchi																33					
	surface																					
<i>Gyrodinium spp. >65µm</i> ³	Secchi														27		5	6				
	3 x Secchi											164			29	20	61				10	21
<i>Torodinium robustum</i> ²	surface																					
	Secchi																					
<i>Torodinium robustum</i> ²	3 x Secchi																					
	surface																					
<i>Torodinium robustum</i> ²	Secchi																					
	3 x Secchi																					
<i>Torodinium robustum</i> ²	surface																					
	Secchi																					
<i>Torodinium robustum</i> ²	3 x Secchi																					
	surface																					
<i>Torodinium robustum</i> ²	Secchi																					
	3 x Secchi																					
<i>Torodinium robustum</i> ²	surface																					
	Secchi																					
<i>Torodinium robustum</i> ²	3 x Secchi																					
	surface																					
<i>Torodinium robustum</i> ²	Secchi																					
	3 x Secchi																					

¹In cells/liter. ²Heterotrophic. ³Mostly heterotrophic.

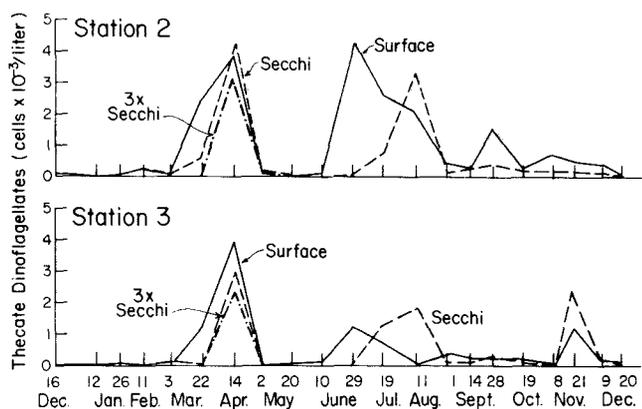


Figure 6. Spatial and temporal abundances (cells $\times 10^{-3}$ liter) of thecate dinoflagellates (December 1976-December 1977).

Spatial and Seasonal Distribution of the Dinoflagellates in the Study Area

The seasonal progression of thecate and nonthecate dinoflagellates at both stations consisted of alternating peaks composed of species belonging to either of the two groups. This pattern, although similar in its general trends at both stations, varied in intensity and species composition (Figures 6 and 7).

For a better assessment of the contribution of the leading species to the total standing crop of dinoflagellates larger than $50 \mu\text{m}$ at any time and depth, as presented in Figures 6 and 7, the abundances of six dominant thecate species and of three nonthecate species are listed in Table 1 by station and depth. One criterion for selecting these species was their general perennial distribution at the two sampling stations. However, other species, such as the photosynthetic *Gonyaulax polyedra*, produced a short-lived peak in November 1977 at Station 3 with 960 cells/liter in the surface sample and 2377 cells/liter at the Secchi-disk depth. At Station 2, it showed more moderate abundances, with 317 cells/liter at surface and 158 cells/liter at Secchi-disk depth (Figure 6).

Additional species of *Peridinium* occurring in low concentrations, such as *P. conicum*, *P. oceanicum*, and *P. steinii*, considered to be heterotrophic (Reid et al. 1970) would add to the heterotrophic component of the dinoflagellate populations if included with the *Peridinium* species listed in Table 1. *Peridinium trochoideum*, recorded as very abundant at both stations in the April 1977 samples and known as one of the few photosynthetic species belonging to this genus, is excluded here as it is less than $50 \mu\text{m}$.

Among the nonthecate dinoflagellates, a number of species of known phagotrophic capability were recorded sporadically in the samples, generally in low numbers. Of these, most common were *Achradina sulcata*, *Erythroopsis minor*, *Kofoidinium* sp., *Noc-*

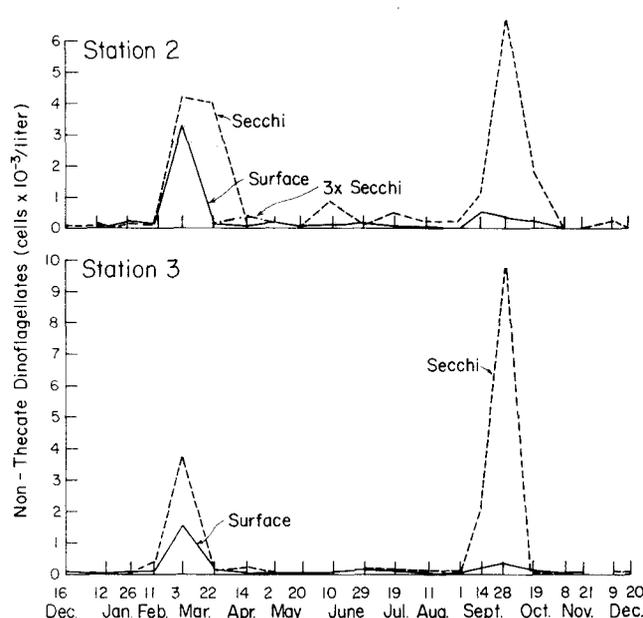


Figure 7. Spatial and temporal abundances (cells $\times 10^{-3}$ liter) of nonthecate dinoflagellates (December 1976-December 1977).

tiluca miliaris, *Polykrikos kofoidii*, *Pronoctiluca pelagica*, and *P. spinifera*. These species were generally preserved in adequate condition to be enumerated. Other species among the nonthecates devoid of photosynthetic pigments, belonging to the genera *Balechina*, *Gymnodinium*, *Gyrodinium*, and *Warnowia*, were recorded principally in live samples collected at Stations 2 and 3 and off the SIO pier and examined soon after being brought to the laboratory. As these species disintegrated completely or lost their shape beyond recognition soon after fixation, they could not be included in the counts.

In some species, such as *Balechina coerulea*, both chromatophores as well as ingested food bodies were detected, suggesting myxotrophic nutrition.

The data, as summarized in Table 2 and Figure 8 on a cruise-by-cruise basis, clearly indicate that the total

TABLE 2
 Yearly Averages¹ of Total, Thecate and Nonthecate
 Dinoflagellates at the Two Stations

Depth	Total	Thecate	Non-thecate	% thecate	% Non-thecate	Whole euphotic zone
<i>Station 2</i>						
Surface	1253	993	260	79	21	
Secchi	1512	542	970	36	64	1100
3 x Secchi	227	176	51	35	65	
<i>Station 3</i>						
Surface	688	529	159	77	23	
Secchi	1601	508	1093	32	68	980
3 x Secchi	187	125	62	67	33	

¹in cells/liter.

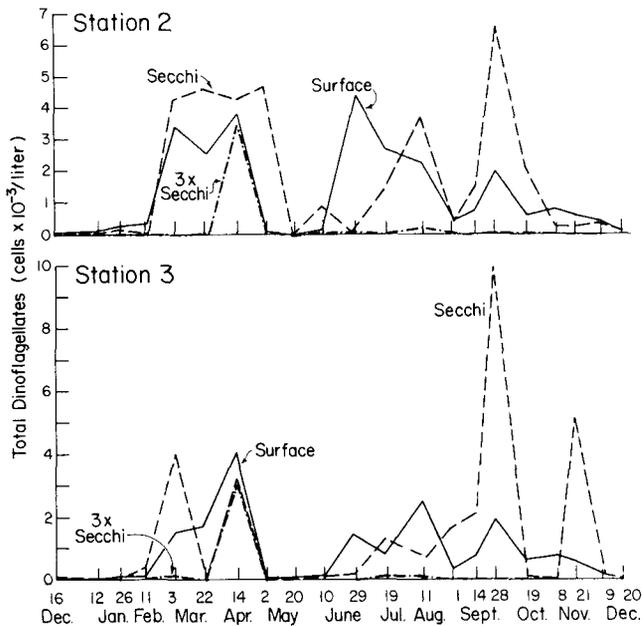


Figure 8. Abundances (cells $\times 10^{-3}$ liter) of total dinoflagellates (December 1976-December 1977).

dinoflagellates showed the highest numerical abundance at the Secchi-disk level. This depth is at about 20% of the surface radiation (Lorenzen 1970) and it often coincided with the chlorophyll maximum within the euphotic zone. However, at both stations the thecate dinoflagellates showed a decrease in numbers with depth, which was more abrupt at Station 2, wherever the nonthecates considerably increased in numbers at the Secchi level relative to the surface values (Figures 6 and 7). This is also reflected in the ratio of thecate to nonthecate dinoflagellates at the three levels (Table 2). In the surface layer at both stations, the thecates predominated (79% and 77% of the total population at Stations 2 and 3, respectively; Table 2 and Figure 9). At the Secchi-disk depth, the ratio was reversed with the nonthecates prevailing at both stations (64% and 68% at Stations 2 and 3, respectively). At both stations there was a marked decrease in numerical abundance at 3 x Secchi, suggesting that light may be a limiting factor, at least for autotrophs, except for a few dark-adapted species. Among the species currently recorded at this depth level, generally in low numbers (with the exception of *Ceratium furca* in April 1977), were species of *Ceratium* and *Peridinium*, *Pyrophacus horologicum* and *Gyrodinium* spp., *Noctiluca miliaris*, *Polykrikos kofoidii*, *Torodinium robustum*, and occasionally *Cochlodinium catenatum*. Many of these species are either facultative or obligate heterotrophs, and some are proven phagotrophs (Steidinger and Williams 1970). On the whole it seems evident that the non-

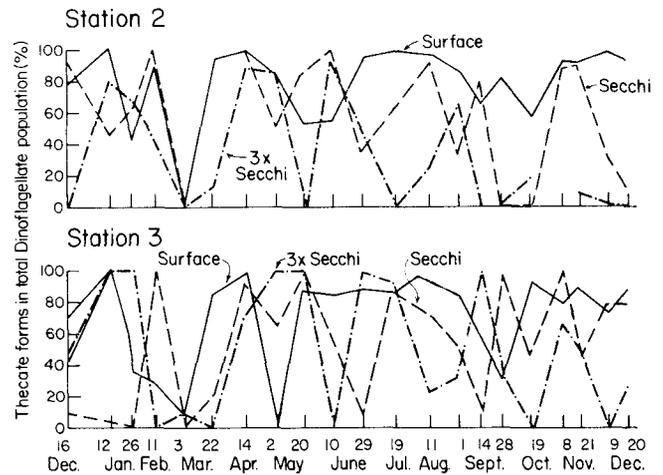


Figure 9. Percentages of thecate forms in total dinoflagellate population (%) (December 1976-December 1977).

thecate dinoflagellates, which include many heterotrophic forms, are better adapted to "shade conditions" as prevailing at and below the Secchi-depth zone.

Characteristics of the Dinoflagellate Community off La Jolla

In this study, 91 taxonomic categories were recorded, most of them identified to the species level. Of the 91 taxa, 63 were thecate forms. The most abundant among these species proved to be *Ceratium furca*, recorded as perennial at Station 2 and particularly common in the upper water layers of both stations. This is in agreement with the biogeography of this euryhaline species, which is considered to be neritic and epipelagic in other parts of the world (Kimor 1972, 1975). Of the 63 thecate taxa, about 20% are considered nonphotosynthetic on the basis of data from literature (Steidinger and Williams 1970) and from personal observations. These supposedly nonphotosynthetic thecate dinoflagellates include among others most of the *Peridinium* forms, with the exception of *P. trochoideum* (F.J.R. Taylor, personal communication). These *Peridinium* species, although present at most times, were not abundant constituents of the plankton during this period. On the other hand, although the genus *Ceratium* as a whole is considered photosynthetic, some of the species, particularly those occurring at the base of the euphotic zone such as *C. setaceum*, seem devoid of photosynthetic pigments and may thus add to the heterotrophic component.

Of the 28 nonthecate taxa within the size class being considered, about 50% are nonphotosynthetic. Some genera, such as *Noctiluca*, *Polykrikos*, *Gyrodinium*, *Warnowia*, and some species of the genus *Cochlodinium*, are typical phagotrophs. Their presence in the

plankton, often in high numbers relative to other members of the dinoflagellate community, makes them an important factor in the structure of the food web.

A survey of the organisms with visible inclusions (whether as accumulation bodies or phagocytized organisms) showed that most were nonthecate species. Among the thecate dinoflagellates, such inclusions were seen in several *Ceratium* species, notably *C. cf. dens* and *C. massiliense*, both with a *Gymnodinium*-like cell inside, *C. pentagonum*, *Dinophysis fortii*, and *D. caudata*. Among the nonthecate dinoflagellates, evidence of phagotrophy was clearly recorded in *Noctiluca miliaris*, *Polykrikos kofoidii*, *Cochlodinium* spp., *Gyrodinium* spp., *Gymnodinium* sp., and *Balechina coerulea*. Dinoflagellate species bearing such inclusions were recorded at all three depths sampled, at both stations. However, most of the species showing accumulation bodies (whether thecate or nonthecate species) were recorded in the surface layer, whereas those species (mostly nonthecate) with phagocytized cells were recorded at the Secchi and 3 x Secchi levels, i.e. toward the base of the euphotic zone.

SUMMARY

1. The seasonal and bathymetric distribution of thecate and nonthecate dinoflagellates greater than 50 μm in length at the surface, Secchi depth, and 3-x-Secchi depth has been described over a one-year period at two stations off La Jolla, southern California.

2. In general, thecate dinoflagellates showed a decrease in abundance with depth, whereas the nonthecates showed a marked increase at the Secchi-disk level.

3. The seasonal peaks in numerical abundance showed an alternation between species belonging to thecate and nonthecate forms, although the occurrence of such peaks did not always coincide for both stations at a given time and depth.

4. Most of the nonthecate heterotrophic dinoflagellates (in the size class considered) were recorded at the Secchi depth during the 3 May 1977 peak, with the partial exception of *Cochlodinium catenatum*.

5. Phagotrophic inclusions, as distinct from food storage bodies, were noted in a few thecate species of the genus *Ceratium* and in a number of the larger nonthecates such as *Noctiluca miliaris*, *Polykrikos kofoidii*, and *Gyrodinium* spp.

6. Examination of live samples collected from different depths at the survey site and at the end of the SIO pier revealed the presence of a number of non-preserved fragile dinoflagellates, most of which contained phagocytized inclusions. Among the species

noted were *Balechina coerulea*, *Warnowia cf. purpurata*, *W. maxima*, and *Gymnodinium* spp.

ACKNOWLEDGMENTS

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EUPHAUSIID DISTRIBUTIONS IN THE CALIFORNIA CURRENT DURING THE WARM WINTER-SPRING OF 1977-78, IN THE CONTEXT OF A 1949-1966 TIME SERIES

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ABSTRACT

Euphausiid species having affinities with warm offshore and southerly waters of the California Current extensively penetrated the region of the southern California eddy during the winter of 1977-78. Coastal *Nyctiphanes simplex* was then more strongly displaced than had previously been observed for that season.

During 1949-1960, three two-year cool periods were interrupted by warm periods of differing duration, timing, and intensity. Euphausiid biogeography off southern California during December 1977 to August 1978 developed much as during November 1959 to April 1960—the wane of the longest warm period, 1957-60. Those three years were uninterrupted by marked spring-summer upwelling and strong southerly flow.

By June-July 1978, as in January-March 1960, water temperatures and species distributions returned to average. The cool-water euphausiids *Euphausia pacifica* and *Nematoscelis difficilis* again were predominant from central California to northern Baja California.

RESUMEN

Especies de eufáusidos con afinidades a las cálidas aguas sureñas y de afuera de la Corriente de California penetraron extensivamente en la región del giro del sur de California durante el invierno de 1977-78. La especie costera *Nyctiphanes simplex* estuvo entonces más fuertemente desplazada de lo que se había observado previamente para aquella estación.

Durante 1949-1960, tres períodos frescos de dos años cada uno fueron interrumpidos por períodos cálidos de duración, tiempo, e intensidad diferentes. La biogeografía de eufáusidos frente al sur de California, desde diciembre de 1977 hasta agosto de 1978, se desarrolló de una manera muy parecida a la del período entre noviembre de 1959 y abril de 1960—a fines del período cálido más largo, desde 1957 hasta 1960. Esos tres años siguieron ininterrumpidos por las surgencias marcadas de primavera-verano y el fuerte flujo hacia el sur.

Ya por junio y julio de 1978, las temperaturas del agua y las distribuciones de especies regresaron al

promedio, tal como había sucedido en enero-marzo de 1960. Los eufáusidos de aguas frescas, *Euphausia pacifica* y *Nematoscelis difficilis*, volvieron a ser predominantes desde California central hasta la parte norte de Baja California.

INTRODUCTION

Ocean temperatures were 1-2°C above average, and salinities were below average along the California coast during the stormy winter of 1977-78. Northwest winds were unusually strong for that season. Extensive zooplankton collections were obtained during the CalCOFI surveys of December 1977 to August 1978, permitting comparisons with earlier surveys.

Changes in distributions of plankton species generally suggest roles of interactions among species and of changing environment. When changes appear to be particularly related to the environment, they can be aids in understanding variability in climate and circulation, provided that the broad geographical affinities of the species are understood.

Geographical associations of species within the California Current have been variously described (Bieri 1959; Brinton 1962; Johnson and Brinton 1963; McGowan 1968, 1971). If these are presumed to be functional assemblages, they have been documented with less certainty than the distributions of individual constituent species (e.g. Fleminger 1964; Alvariño 1965; Brinton 1967a, 1973; Brinton and Wyllie 1976; McGowan 1967; Berner 1967; Bowman and Johnson 1973; Reid et al. 1978).

Species of Chaetognatha (e.g. *Sagitta hexaptera*), Pteropoda (*Limacina inflata*), and Euphausiacea (*Euphausia hemigibba*) occurring in westerly and southwesterly California Current areas have been shown to be associated with North Pacific Central Water (Fager and McGowan 1963). Other subtropical euphausiids, also occupying offshore parts of the California Current (*Euphausia recurva*, *E. mutica*), now appear to be particularly adapted to margins of the Central Gyre, when abundance as well as range is a criterion. *Euphausia eximia* was thought to indicate northerly intrusions of Equatorial Water into the California Current (Brinton 1962). *E. eximia* is now understood to be a species that proliferates at cool margins of the eastern tropical Pacific, including Baja

Californian waters (Brinton 1979; Brinton and Townsend 1980). Even the subarctic affinity of the much studied Californian population of *Euphausia pacifica* (Lasker 1964, 1966; Brinton 1976) is uncertain because this species is strongly reproductive all along the California coast.

The California Current system is a zone of hydrographic transition extending from the southern edge of the cool-temperate, Subarctic Water mass of the Gulf of Alaska (ca. 42°N) to equatorial water at the Tropic of Cancer, and from coastal upwelling centers westward toward or into the Central Water mass. A species tends to be most abundant in, or restricted to, a particular sector of the current system: northern, southern, coastal, or offshore. More species overlap off southern California and northern Baja California, 30-35°N, than elsewhere.

Comparisons of 1977-78 distributions with those in a 1949-1966 time series will be made using only the data from a designated area extending westward from southern California. The inshore part of this area includes the Southern California Bight, in which coastal upwelling develops particularly well to the south of promontories, notably Point Conception, in response to northerly winds (Reid et al. 1958; Reid 1960). The offshore part frequently includes a southerly component of the California Current which, on the average, lies 240 km off northern Baja California where it bends shoreward (Hickey 1979). The southern California eddy is formed from the easterly edge of this flow, together with northwesterly flow in the Bight (Figure 1). This eddy supports dense reproductive populations of California Current euphausiids (Brinton 1976).

The distributions of euphausiids show that those species with distinct affinities for Subarctic, Central, or Equatorial Water masses, as defined by Sverdrup et al. (1942), have not massively intruded into the California Current system during the past 30 years of CalCOFI observations. Subarctic *Thysanoessa longipes* and *Tessarabrachion oculatus* have often occurred southward to about 38°N, to the west of San Francisco, but individuals reaching farther south are rare (Brinton 1973). Occurrences off southern California during the cold spring of 1956 will be referred to, below, when the more coastal northern species *Thysanoessa spinifera* is discussed.

Four euphausiids that are numerically important within the current from central California southward (*Nematoscelis difficilis*, *Euphausia gibboides*, *E. recurva*, *Thysanoessa gregaria*) also extend northward into the North Pacific Drift (38-45°N), evidently a biogeographical extension of the California Current Transition Zone. The North Pacific Drift is in the zone

40-45°N. According to Dodimead et al. (1963) the Drift is a part of the Subarctic Zone, though they consider it to be transitional with Central Water. Species of other taxa which appear to be endemic to the North Pacific Drift—California Current Transition Zone are the chaetognath *Sagitta scrippsae* (Alvarino 1962) and the copepod *Eucalanus californicus* (Johnson 1938; Fleminger 1973). California Current endemics include the copepods *Calanus pacificus californicus* (Brodsky 1965) and two species of *Labidocera*, *L. jollae* and *L. trispinosa* (Fleminger 1978). Newman (1979) summarizes evidence for a Californian Transition Zone.

California Current euphausiids have not been observed to extend into the tropical waters, excepting *Euphausia eximia* mentioned above. Tropical species have sometimes ranged northward into Baja Californian waters, particularly during the "warm years," 1957-59 (e.g. *Nematoscelis gracilis*, Brinton 1967a), when central species were also particularly strong in easterly range extensions.

Thus, the more abundant euphausiids occurring off California and Baja California may be considered to be of a Transition Zone Fauna. Based on the period 1949-1966, these species may be further grouped as follows.

- 1) Northern, including North Pacific Drift, 35-45°N (with reproductive areas along coastal California):
Euphausia pacifica (having both transition zone and subarctic populations), and
Nematoscelis difficilis.
- 2) Intermediate or Subtropical, including North Pacific Drift (with offshore reproductive tendencies):
Euphausia gibboides,
E. recurva, and
Thysanoessa gregaria.
- 3) Baja Californian:
Euphausia eximia, *Stylocheiron affine* (California Current Form, Brinton 1962)

In addition, there are nearshore euphausiids:

- 1) the Gulf of Alaska to California species *Thysanoessa spinifera*, and
- 2) the Baja Californian *Nyctiphanes simplex*.

In mid-year, the two coastal species have shown strongest overlap, particularly off southern California during May-July when *T. spinifera* is reproductive.

The distributions of these euphausiids will be shown for the 1977-78 period. Extents of range and abundance (ubiquitous species) within the southern California area will be compared with earlier CalCOFI collections. Limitations in the data are obvious. Sur-

GESTROPHIC FLOW AT THE SURFACE

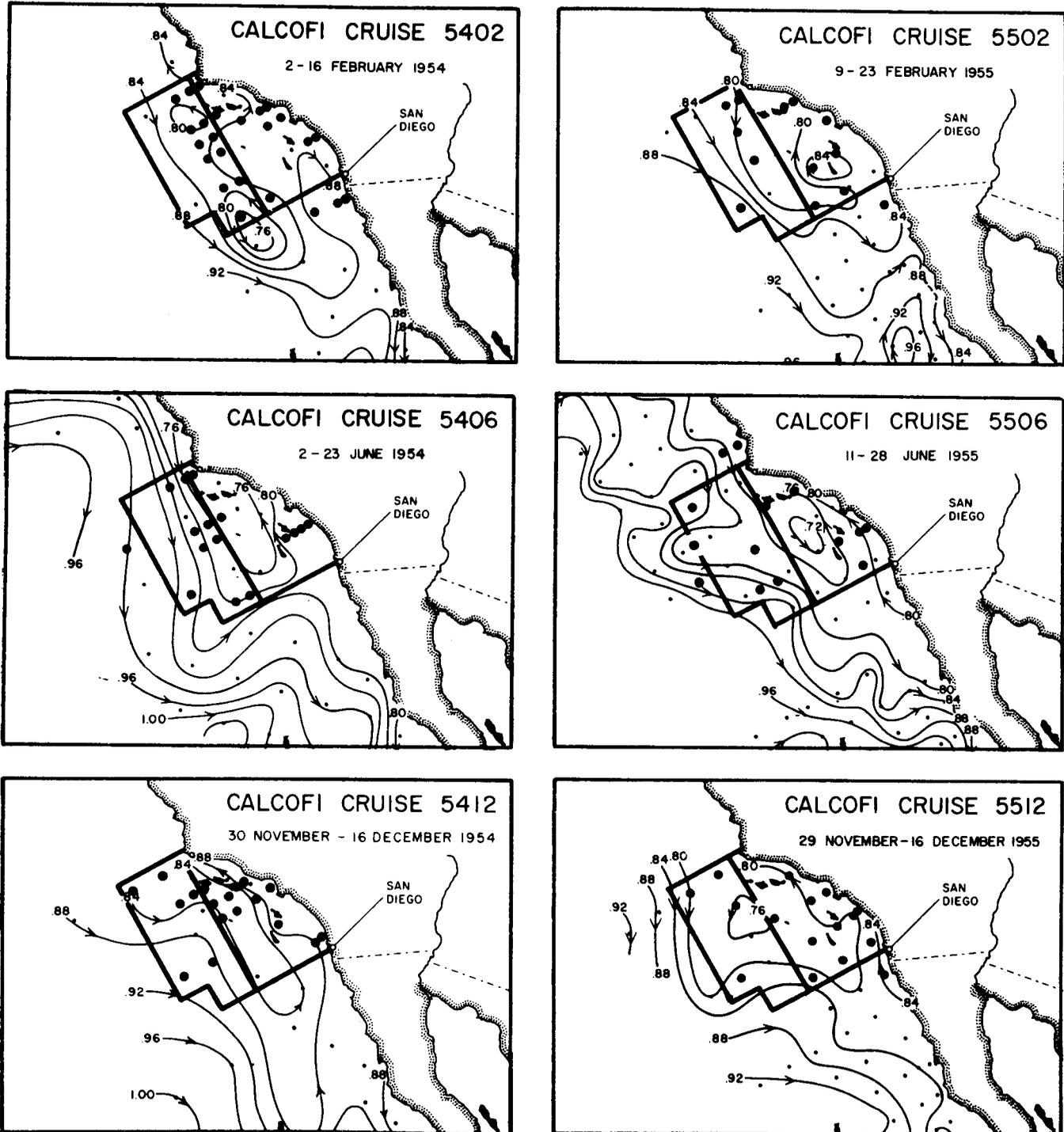


Figure 1. Geostrophic flow at the surface relative to 500 decibars in the southern California region for three months of the warm year 1954 and cool 1955, from Wyllie (1966). The area treated in time series of euphausiid distributions is outlined. Characteristics of inshore and offshore halves are described in text.

veys from the period 1967 to 1977 have yet to be analysed for the distribution of zooplankton species. Cruises differ greatly in the number of samples examined, and the time series does not make adequate

use of our information on areal abundances of the species. Nevertheless, it was deemed appropriate to present the more timely and available data as a supplement to a symposium on climatology and biology

of the California Current appearing in this volume, particularly Bernal (1981), Chelton (1981), and Eber (1981).

MATERIALS AND METHODS

Sampling during 1949 to 1966 was by means of a CalCOFI 1-m-diameter ring net towed obliquely from 70-m depth during 1949 and 1950, and from 140 m after 1950. Field and laboratory procedures follow those described by Kramer et al. (1972). The 1977-78 samples were obtained by use of 0.71-m-diameter Bongo nets, towed obliquely from 210 m. Brinton and Townsend (1981) show that abundances of given species of euphausiids are not significantly different from replicate Bongo and 1-m net tows. Bongos catch the larger sized animals better, whereas the 1-m net provides the better estimates of larvae, to about 6 mm in length. Subsampling and counting procedures are described in Brinton (1979).

All samples of the 1977-78 cruises were counted. Many of the 1949-1966 cruises were analysed in their entirety. However, only those samples from a southern California study area (Figure 1) are used in the time series upon which this report will focus. In the many cases in which cruises were examined only from the standpoint of the southern California area, only nighttime samples were studied. Such samples provide best estimates of both abundance and presence or absence of rare species. By reducing the number of samples to be studied, it has been possible to obtain data from many more months than would otherwise have been possible. As few as ten samples in a given month and as many as 47 were used to describe distributions in the southern California area.

Much of the data in the time series is presented as the percentage of the southern California area occupied by each species during each month. When only presence or absence is considered, as with six of the eight species in the time series, basic principles of contouring are used in assessing the areas occupied. In the other two species, areas of high abundance are determined in the same way.

Mean temperatures and salinities for the area were obtained by weighting each temperature or salinity increment by the amount of area closer to that isotherm than to any other isotherm, as plotted in CalCOFI Atlas I (Anonymous 1963) and Wyllie and Lynn (1971).

RESULTS

The Temperature and Salinity Environment

The distributions of temperature at 10-m depth reflect states of the California Current during December

1977 to July 1978 (Figure 2). The position of the 15°C isotherm varied little during these seven months of above-average temperatures. The western half of the southern California area was <15°C, and the eastern was >15°C during December-January when temperatures were 2°C warmer than average.

Water having a temperature of 13-14°C was to the north and offshore of Point Conception until early March. It extended into the Santa Barbara Channel in April, as upwelling developed along all of the coast, excepting Los Angeles to San Diego. Coastal cooling continued during May-June. A plume of <14°C water extending well to the west of southern California continued to develop into June-July. East-west temperature gradients indicate that this prominent westerly meander of the cool coastal stream extended 200-300 km southwestward from near Morro Bay (35°N) before returning shoreward into the southern part of the Southern California Bight. Eastward development of 15-16°C temperatures along 35°N, just to the north of this meander, indicate an easterly intrusion of the offshore environment, usually encountered only off northern Baja California.

The 17°C water reached northward well into southern Californian waters in December, complementing the southeasterly penetration of cooler offshore waters. The opposing parallel tongues were associated with intense unseasonal storms from the northwest. The 17°C temperatures retreated to the latitude of Vizcaino Bay (29°N) by February-March. The 17-18°C water returned to the southern California area during May-July as a northeasterly tongue. This lay inshore of the cool-water tongue described above as part of the westerly, then easterly meander of central California coastal waters.

Within the region designated the southern California area (Figure 1), mean temperature at 10-m depth (Figure 3) and ranges of temperature and salinity values across the area (Figure 4) help to describe events of 1977-78 in relation to certain other years. Mean temperature minima were during February-March in the inshore half of the region and during March to May in the offshore half (except 1951). Maxima were in July to October in both places, the values being higher inshore of the prevailing southerly flow.

During December 1977 to May 1978, the mean temperatures were like those of the warm years 1958-59, both offshore and inshore (Figure 3). The offshore means for December 1977 to January 1978 were the highest recorded. Inshore, they were in line with those of the winters of 1957-58 and 1958-59. Only the 1959-60 winter was warmer, after which the 1957-60 warm period lost its extreme characteristics. The similarity of 1977-78 to the warm years disap-

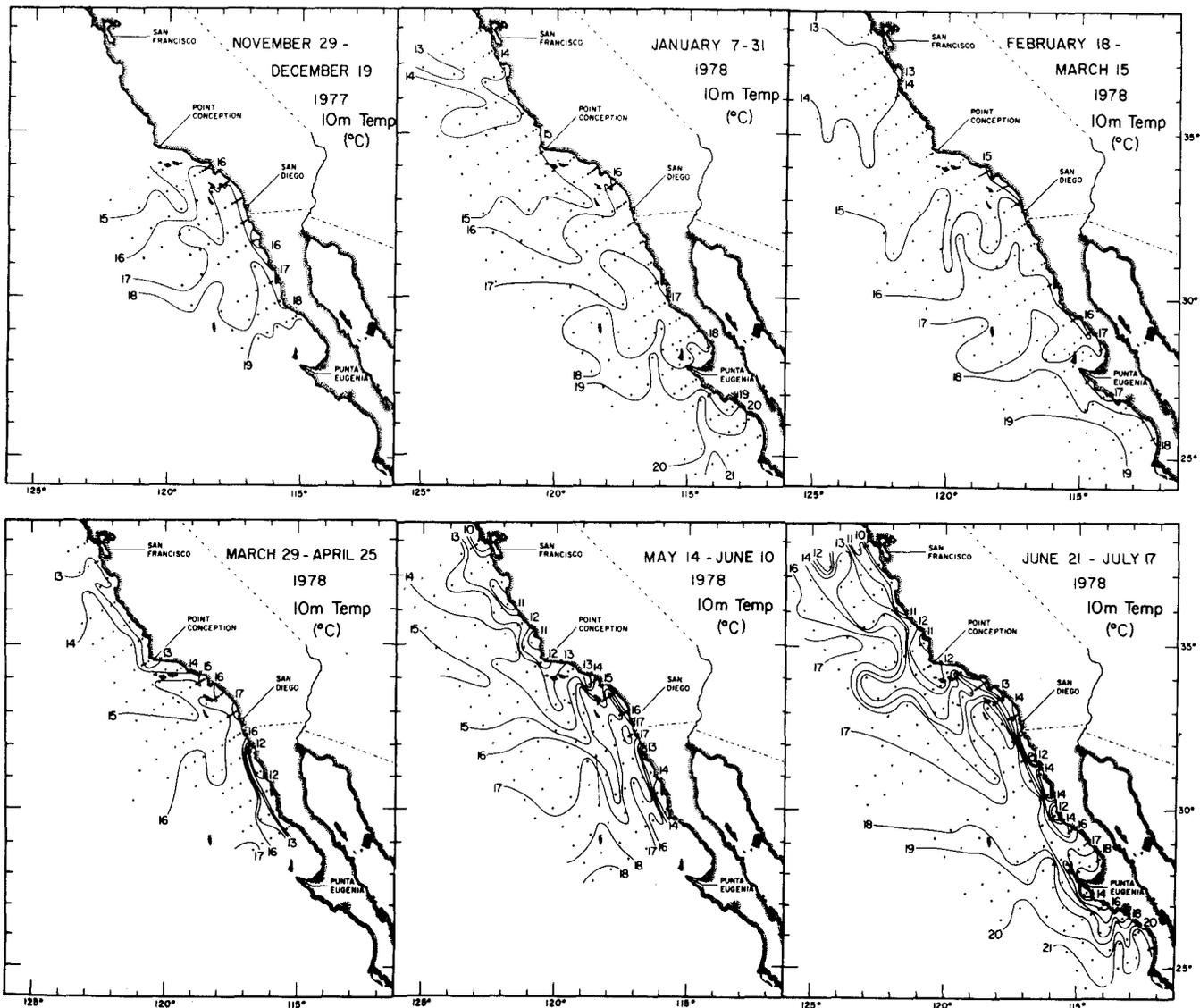


Figure 2. Distributions of temperature (10 m) in the California Current during December 1977 to July 1978.

peared by July 1978.

Three two-year periods stand out in the 1949-1960 temperature distributions plotted in CalCOFI Atlas I as being consistently cooler than average in the southern California area: September 1949 to September 1951, January 1952 to December 1953, and April 1955 to March 1957. During 1953 and 1956, the monthly mean temperatures (Figure 3) were 1-3°C lower than during warm 1958 and 1959 and the warm winter-spring of 1977-78. The year 1951 differed from 1953 and 1956 in being (1) intermediate in temperature in the offshore region during February-May, and (2) like the warm years during October-December, offshore, and September-December, inshore.

Mechanisms behind these variations in mean temperatures are expected to relate to plankton dis-

tributions. They may be further inferred through examination of the ranges of temperature and salinity in the offshore and inshore southern Californian regions (Figure 4). For example, spring temperature minima offshore reflect southerly flow from the central California coast, whereas inshore minima reflect local upwelling.

The year 1952-53 was cool, 1958-59 a warm year, 1959-60 a warm December-January followed by a cool February and a near normal spring-summer, and 1977-78 a warm December-May followed by a moderate June-July. The year 1977-78 differed from the other three years in the following ways:

1) During December-March 1977-78, temperature minima (ca. 14.5°C) and maxima (16-17°C) were relatively constant, both onshore and offshore.

AVERAGE TEMPERATURES IN SOUTHERN CALIFORNIA EDDY

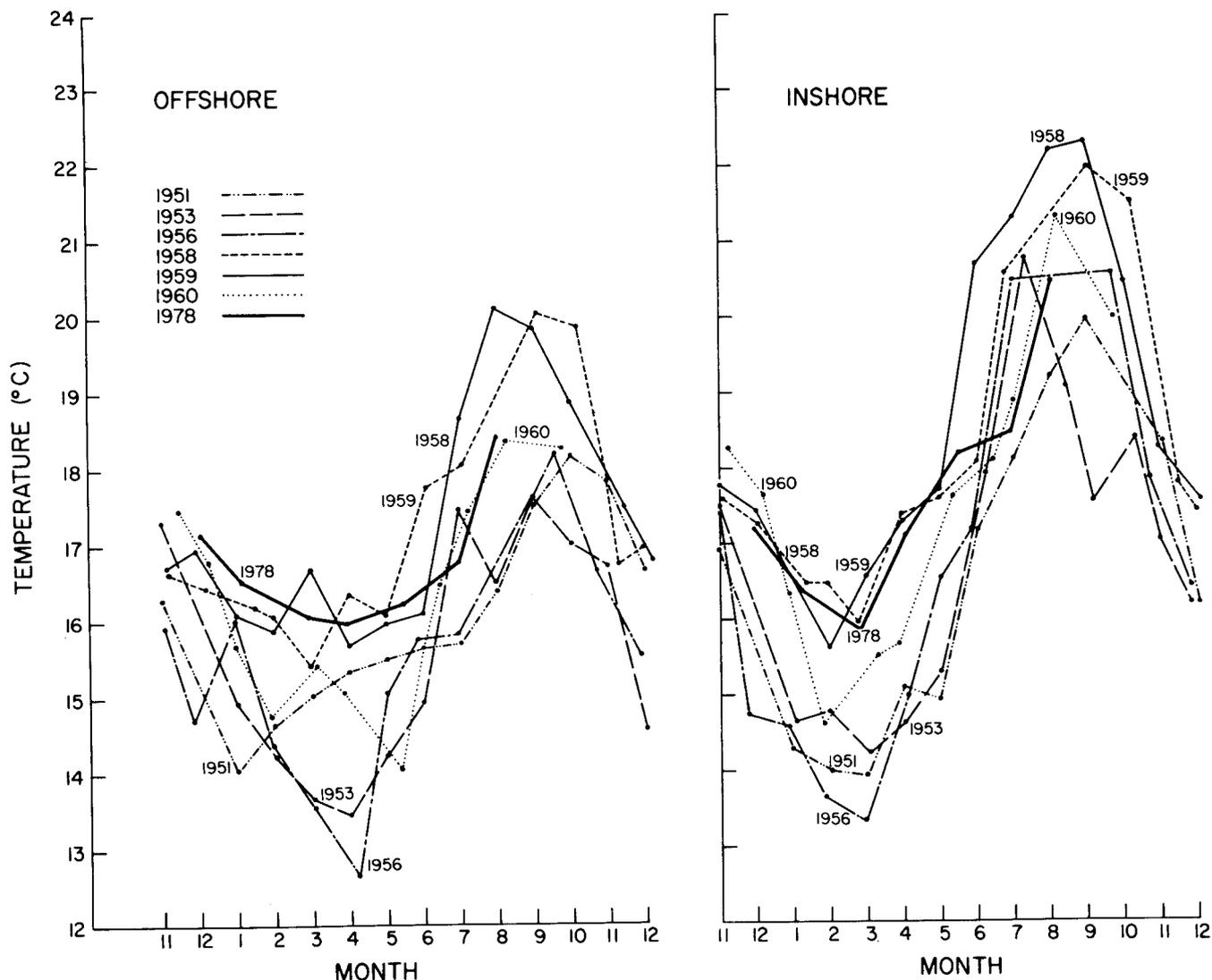


Figure 3. Monthly mean temperatures (10 m) in offshore and inshore parts of the southern California area during years of temperature extremes. Temperature values are from Oceanic Observations of the Pacific (1949-1960) and Wyllie and Lynn (1971).

2) In late 1977, water with salinity as low as 32.9‰ appeared in the offshore region and as low as 33.0‰ in the inshore region. Much of this water of low salinity and high temperature appears to have penetrated well into the Bight.

3) The highest salinities of January-February 1978 were like those of the cool 1952-53 winter, that is, 0.3‰ less than in the warm years 1958-60 when southerly flow and coastal upwelling were depressed.

In the inshore area during May-July 1978, temperature minima of $<12^{\circ}\text{C}$ were associated with salinity maxima to 33.9‰ inshore, indicating the resumption of upwelling. In the offshore area, temperature minima were then $<13^{\circ}\text{C}$ and the salinity range was

broad, 33.0-33.8‰, indicating continuing southerly flow, but now of both northern offshore water and of central Californian upwelled water.

In general, inshore temperature ranges were similar to offshore ranges during winter months. Winter temperatures of 1977-78 differed from other years by decreasing little as the season progressed from December to February. Later in 1978, the inshore range of temperature became broader than the offshore range and encompassed it. Upwelling and northerly flow into the Bight appear as causes. Inshore salinities are generally higher than offshore, for the same reasons. But during December 1977 to April 1978, inshore-offshore differences were little.

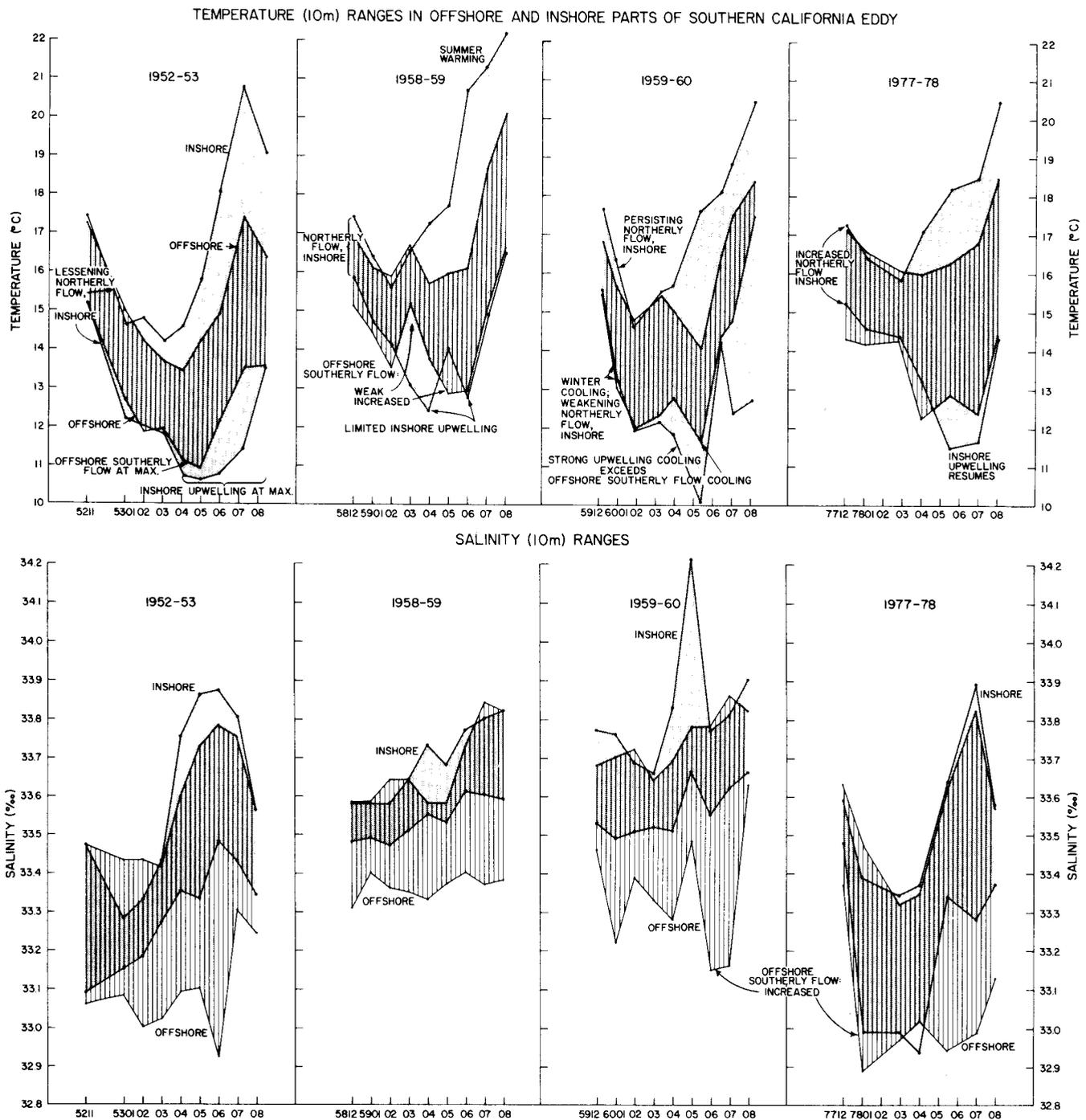


Figure 4. Ranges of temperature and salinity values (10 m) in offshore and inshore parts of the southern California area during cool 1952-53, warm 1958-59, warm 1959-60 and cool 1977-78.

Distributions of the Species during December 1977- July 1978

***Euphausia pacifica* (Figure 5)**

During December-January, high densities of *Euphausia pacifica* (>500/1000 m³) in the southern California area were restricted to a narrow tongue extending southward from the Channel Islands. This was

associated with the southwesterly extension of the 15°C isotherm at 10 m. The population was extraordinarily weak to the south, scarcely extending into Baja California waters. Some larvae were nevertheless produced.

As in January, the substantial parts of the February-April distributions were conspicuously coastal along central California. However, they now extended

Euphausia pacifica (Calif. Current, Northern)

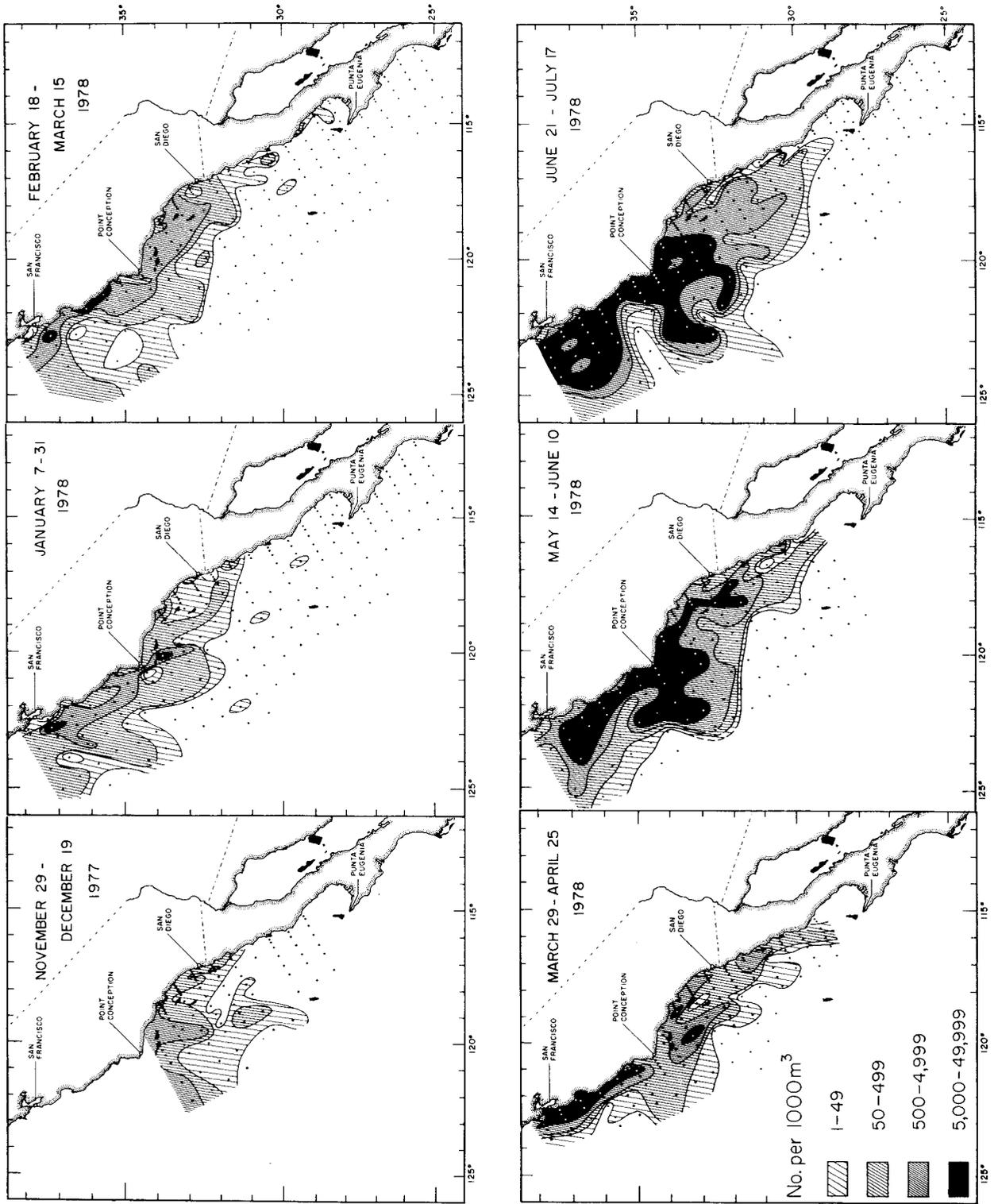


Figure 5. Distributions of the northerly California Current species *Euphausia pacifica* during 1977-78.

well into the Bight. The nearshore Baja California population developed progressively.

The increasingly dense population of May-July appears to be a reproductive response to the development of coastal upwelling. It extended well into Baja California waters and some 250 km seaward of Point Conception. The extensive meanders of isotherms are associated with the contours of abundance. The easterly intrusion of warm water to the north of Point Conception and the reduction of *E. pacifica* there appears more extreme than that observed during April of 1962 and 1963 (Brinton 1967a). It becomes the second aberrant event of this year, following the winter warming and its effects.

Euphausia gibboides (Figure 6)

A Transition Zone species usually centered well offshore, *E. gibboides* ranged far into waters of central California and the Southern California Bight during December 1977 to March 1978. Incursions into the Bight appear to be both from the west and from the south. Coastal occurrences to the north of Point Conception and the generally shoreward displacement of the distributions are reminiscent of 1958 (Brinton 1967a). Retraction from coastal waters appears to have commenced in April as cooling developed. The May-July easterly incursions off central California are complementary to the easterly retraction of the distribution of *E. pacifica* (Figure 5).

Maximum production of larvae by this species is typically well offshore. It has been maximal during spring and summer (Brinton 1967a), as was the case in 1978.

Euphausia eximia (Figure 7)

The extensive occurrences of *E. eximia* along southern California and extending to the north of Point Conception in early 1978 reinforce the significance of a climatological feature of that period already stressed. The offshore and southerly environment of the California Current Transition Zone shifted to the east and somewhat to the north. To a degree, it displaced *E. pacifica* and, as will be seen, the northerly Transition Zone species *Nematoscelis difficilis* and coastal *Nyctiphanes simplex*.

The northerly spread of *E. eximia* from its Baja California center diminished after March. Substantial production of larvae in the southern California and northern Baja California areas stopped at the same time, evidently due to coastal cooling.

Nyctiphanes simplex and *Thysanoessa spinifera* (Figure 8)

Nyctiphanes simplex is a southerly coastal species usually having a northern limit near Point Conception. As in the warm year 1958, *N. simplex* ranged to north-

ern California during the winter and spring of 1977-78. The winter distribution along California was particularly bound to the coast. By June the central California distribution had retracted and the southern California population became dense, extending westward into the region of southerly flow.

Thysanoessa spinifera is northerly and coastal. Its range is clearly complementary to that of *N. simplex*, though its April to June or July peaks in abundance are more seasonal than in *N. simplex*. Winter occurrences off southern California and Baja California were sparse during 1977-78, as is regularly the case. The May-August distribution off southern California, comprised mainly of spring larvae, was the most extensive that has been observed. It was associated with the massive meander of cool water to the west and south of Point Conception.

Springtime expansion of the range of *T. spinifera* off southern California will be shown to have regularly occurred during both warm and cold years. The exception was the particularly cold spring of 1956. Then, two subarctic species having relatively offshore affinities, *Tessarabrachion oculatus* and *Thysanoessa longipes* made rare appearances 90 km south-southwest of Point Conception (Station 83.60) during both April and June.

The Central Pacific Species (Figure 9)

These species have highest densities and reproductive areas in the Central Pacific Gyre, to the west of the California Current. Low densities drift westward into the Transition Zone, particularly during winter when southerly flow is weakest. Composite range and abundance of these nine species varied little during December 1977-July 1978. As with the Transition-Zone species having warm-water affinities (*Euphausia gibboides* and *E. eximia*), the central species were patchily present in the southern California area during December to March, after which they were almost absent. Their association with the easterly incursions of warm water to the north of Point Conception and off northern Baja California are striking (Figure 2).

These species include *Thysanopoda astylata*, *T. obtusifrons*, *Euphausia brevis*, *E. hemigibba*, *Nematoscelis atlantica*, *N. tenella*, *Stylocheiron affine* (Central Form), *S. carinatum*, and *S. suhmii*. Only one of these, *E. hemigibba*, will be plotted in the time series to be described.

A 1949-66 and 1977-78 Time Series of Species Ranges off Southern California

Examples of species distributions in the southern California area are shown in Figure 10. The 1949-1960 period produced three cool episodes and three

Euphausia gibboides (Transition Zone, Offshore)

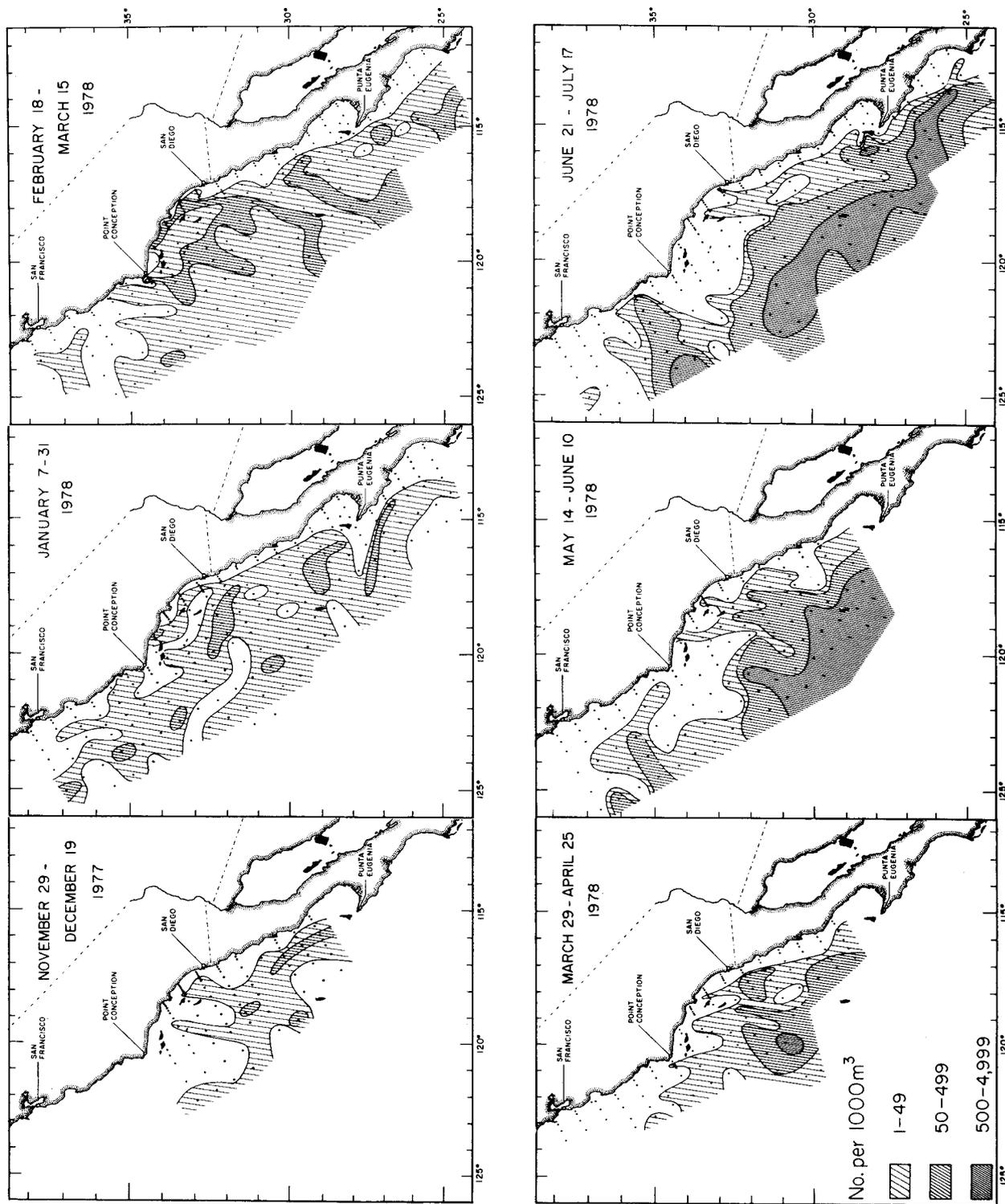


Figure 6. Distributions of the Transition Zone species *Euphausia gibboides* in the California Current during 1977-78.

Euphausia eximia (Transition Zone, Southern)

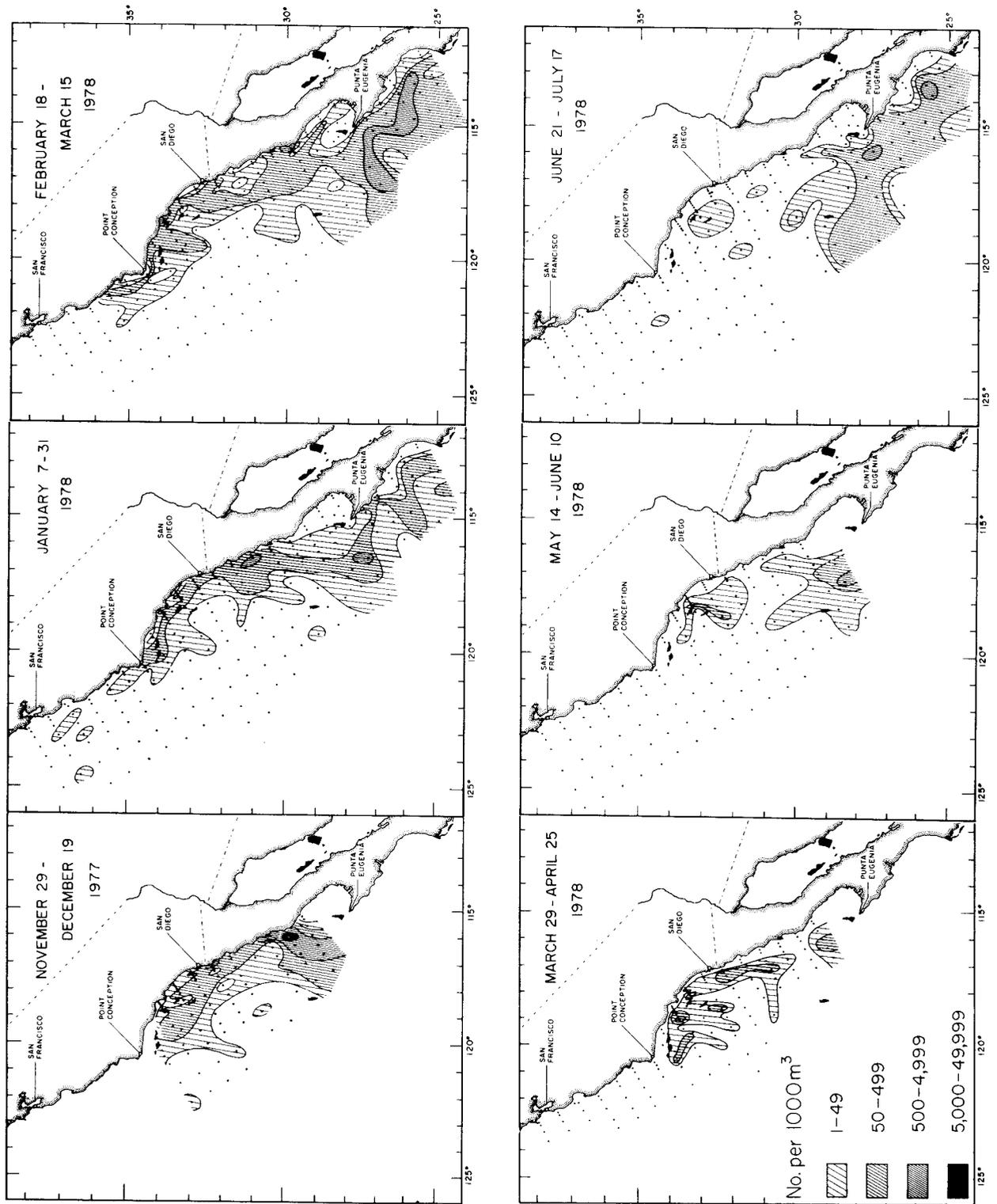
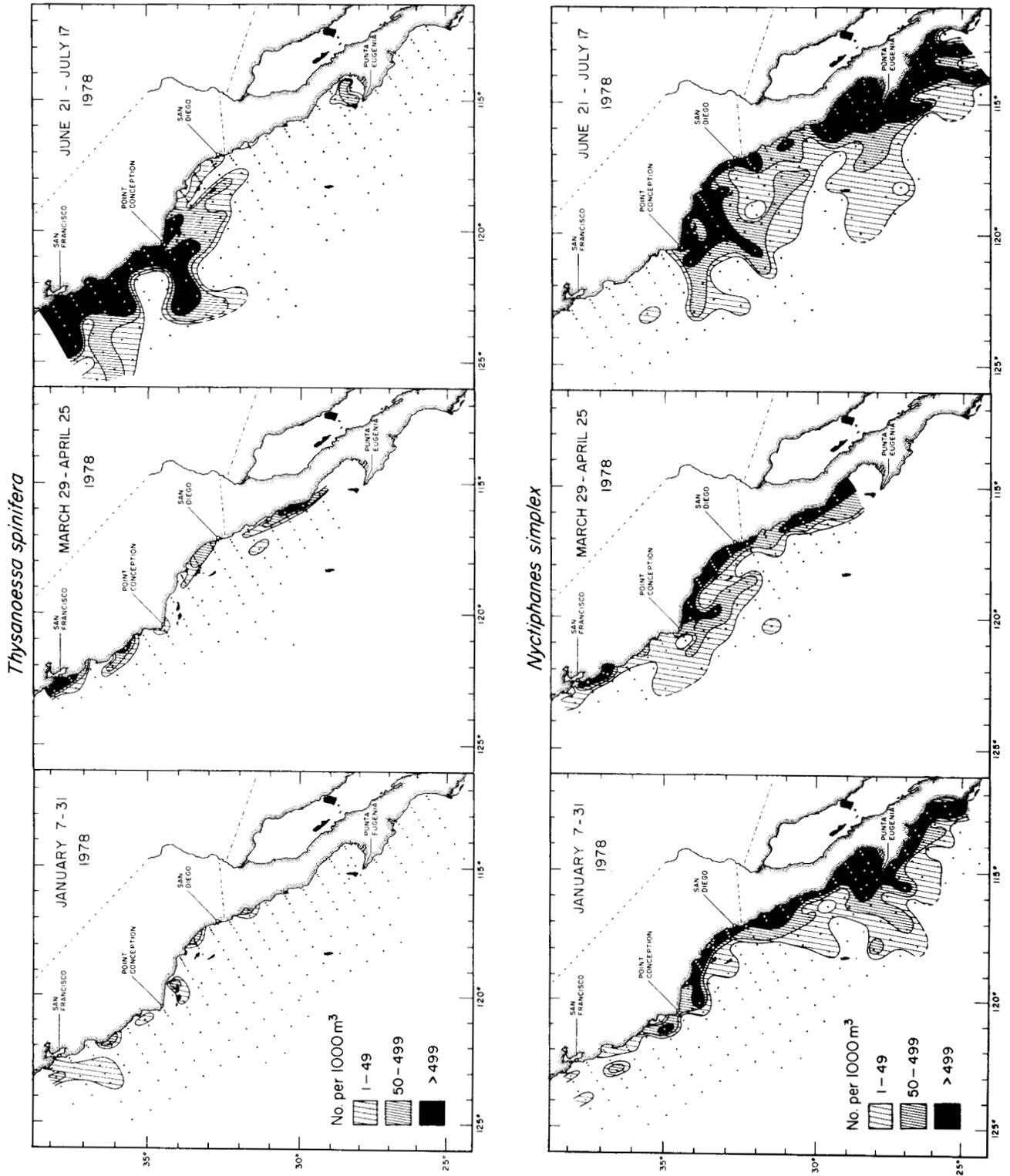


Figure 7. Distributions of the southerly Transition Zone species *Euphausia eximia* in the California Current during 1977-78.



Central Pacific Group, 9 species combined

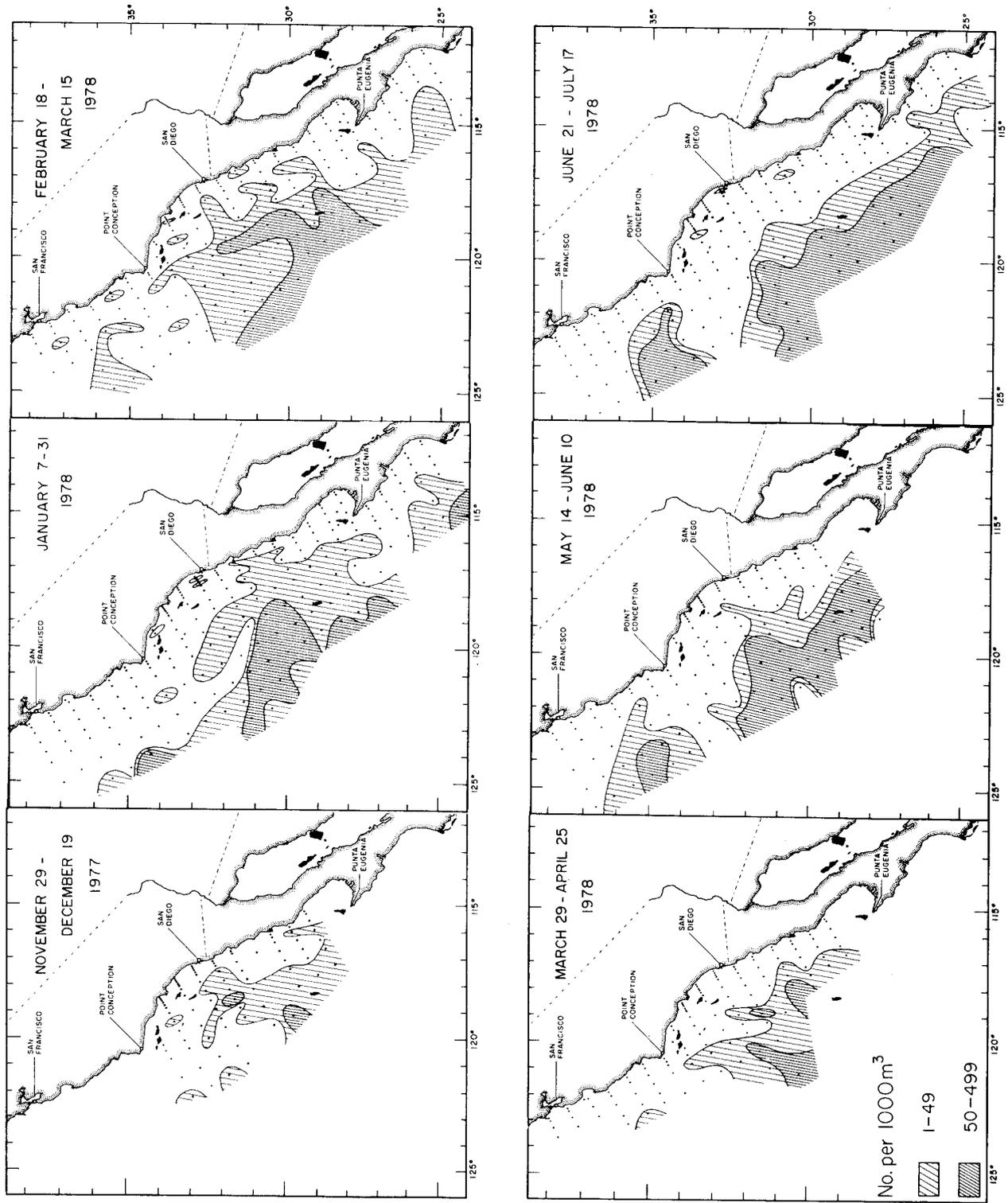


Figure 9. Combined distributions in the California Current of a group of nine Pacific Central Water species, 1977-78.

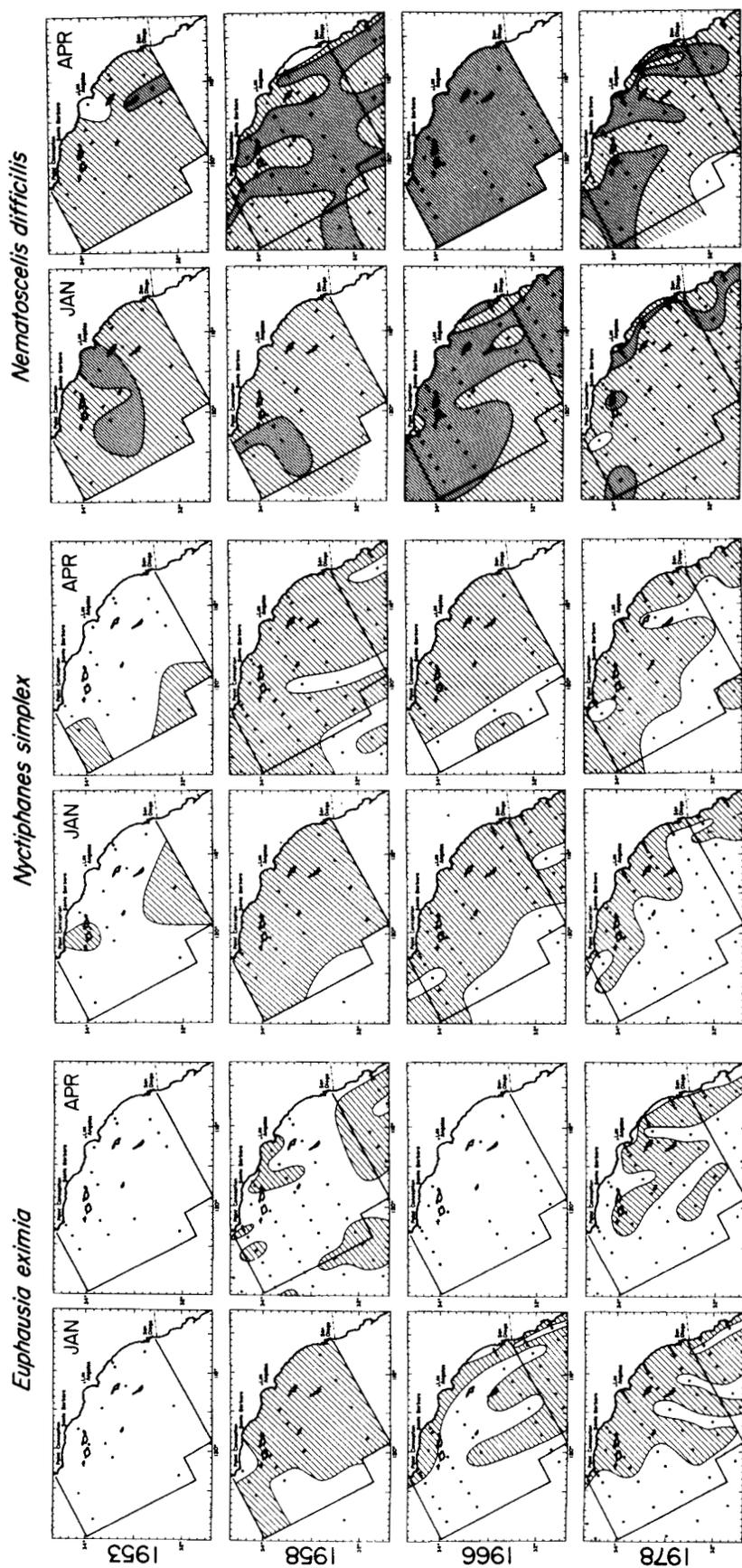


Figure 10. Examples of distribution in the southern California area of species representing the southerly part of the Transition Zone (*Euphausia eximia*), the coastal part (*Nyctiphanes simplex*) and the northerly part (*Nematoscelis difficilis*), for which abundances $>500/1,000 \text{ m}^3$ are also shown, as plotted in Figure 11).

warm ones in this area (Figure 11). The standard against which a given month has been measured is the 10-year (1949-1959) monthly mean for that month, determined from data in CalCOFI Atlas I.

The three cool episodes are each of two years' duration: September 1949 to September 1951, January 1952 to December 1955, and April 1955 to March 1957. Late 1955 to mid-1956 was the coldest period.

The first warm episode was brief—October to December 1951, although during April-September 1951, monthly mean temperatures had alternated between normal and subnormal. The second was from February to August 1954, with aftershocks in December 1954 and March 1955. The third lasted 2½ years, from May 1957 to January 1960. Our analysis of the plankton from the 1960s and 1970s is very incomplete. The years 1962 and 1963 were cool and 1966 was near normal, judging by January and April data from those years. Monthly surveys were replaced by quarterly surveys during most of 1961-1977. The reader is referred to Eber (1981) for North Pacific temperature records for those decades. Summers of 1971, 1972, and 1976 were warmest.

The year 1977-78 appears to have been the time of strongest wintertime development of warm water off California subsequent to 1957-60.

The percentage of area off southern California occupied by each euphausiid species was determined as described in MATERIALS AND METHODS. Flow from the east and the south contribute warm-water plankton to this area. The cool-water species *Euphausia pacifica*, *Thysanoessa gregaria* and *Nematoscelis difficilis* have persistent reproductive populations in the eddy, apparently receiving most infusions from the northwest. Coastal *Nyctiphanes simplex* is usually present, pulsing northward from Baja California centers.

Distributions of northerly *Nematoscelis difficilis*, southerly *Euphausia eximia*, and coastal *Nyctiphanes simplex* (Figure 10) will provide examples of values plotted in Figure 11. Extents of occupancy of the southern California area during January and April in years of contrasting temperature characteristics are shown. Ubiquitous *N. difficilis* is measured in terms of the area in which >500 individuals per 1000 m³ were present.

During the cool year 1953, *E. eximia* was absent, *N. simplex* occupied <25% of the area, and high abundances of *N. difficilis* were in <25% of the area.

In a warm year, 1958, *E. eximia* was significantly present during January but less so in April. *N. simplex* occurred at nearly all stations both months. *N. difficilis* increased its spread of high abundance from January to April.

Temperatures during 1966 were more nearly normal

than in 1953 and 1958. *E. eximia* was present in the winter period of northerly flow but was lacking during April upwelling. *N. simplex* and high abundances of *N. difficilis* were widely present during both months.

During the warm winter of 1977-78, *E. eximia* was present throughout the inshore half of the area. As the system reverted toward normal in April, *E. eximia* began its retreat southward. Over the same period, coastal *N. simplex* increased its range from <40% to >60% of the area. Similarly, *N. difficilis* increased its area of abundance from 5% to 35%.

Before summarizing the warm and cool periods in terms of the eight euphausiids plotted in Figure 11, the general responses of the separate species to the changing temperature regime will be considered.

Euphausia hemigibba, representing the central Pacific group, was present in 20% or less of the area until the period of particularly variable temperature of April 1951 to February 1952. It was then scarce until 1958. Warming in 1954 appears not to have involved central incursions. Only during 1958 and in early and late 1959 was *E. hemigibba* present in much of the area. In 1978 its area increased to 35% by March, before declining to zero by July.

Three species of the warmer offshore waters of the Transition Zone reacted similarly. Occurrences of southern *Euphausia eximia* and offshore *E. gibboides* and *Stylocheiron affine* increased during or following times of average or above-average temperature: July-September 1949, October-December 1951, November 1952 (*E. eximia*'s peak preceded that of *E. gibboides* and *S. affine*), November 1954, January-May 1954 (not *E. gibboides*) and, more significantly, July-November 1954. All three occupied much of the area during July 1957 to January 1960, and again during December 1977 to March 1978.

The typically southern inshore species *Nyctiphanes simplex* closely followed the pattern of the Transition Zone species mentioned above. It differed in showing (1) no significant occurrences during late 1952, when the mean temperatures showed only weak warming, and (2) increased occurrences during December 1977 to July 1978 when *E. eximia* and *S. affine*, and to some extent, *E. gibboides* decreased.

The cold-water nearshore species *Thysanoessa spinifera* seems to have been relatively indifferent to year-to-year changes in ocean climate, because its occurrences were always few during winter, when annual temperature variations were most notable. It became prominent each mid-year as larvae dispersed. The April-July peaks in *T. spinifera* tended to be during or near times of moderate depressions in occurrences of *N. simplex*. This is expected in view of the complementary distributions of these nearshore

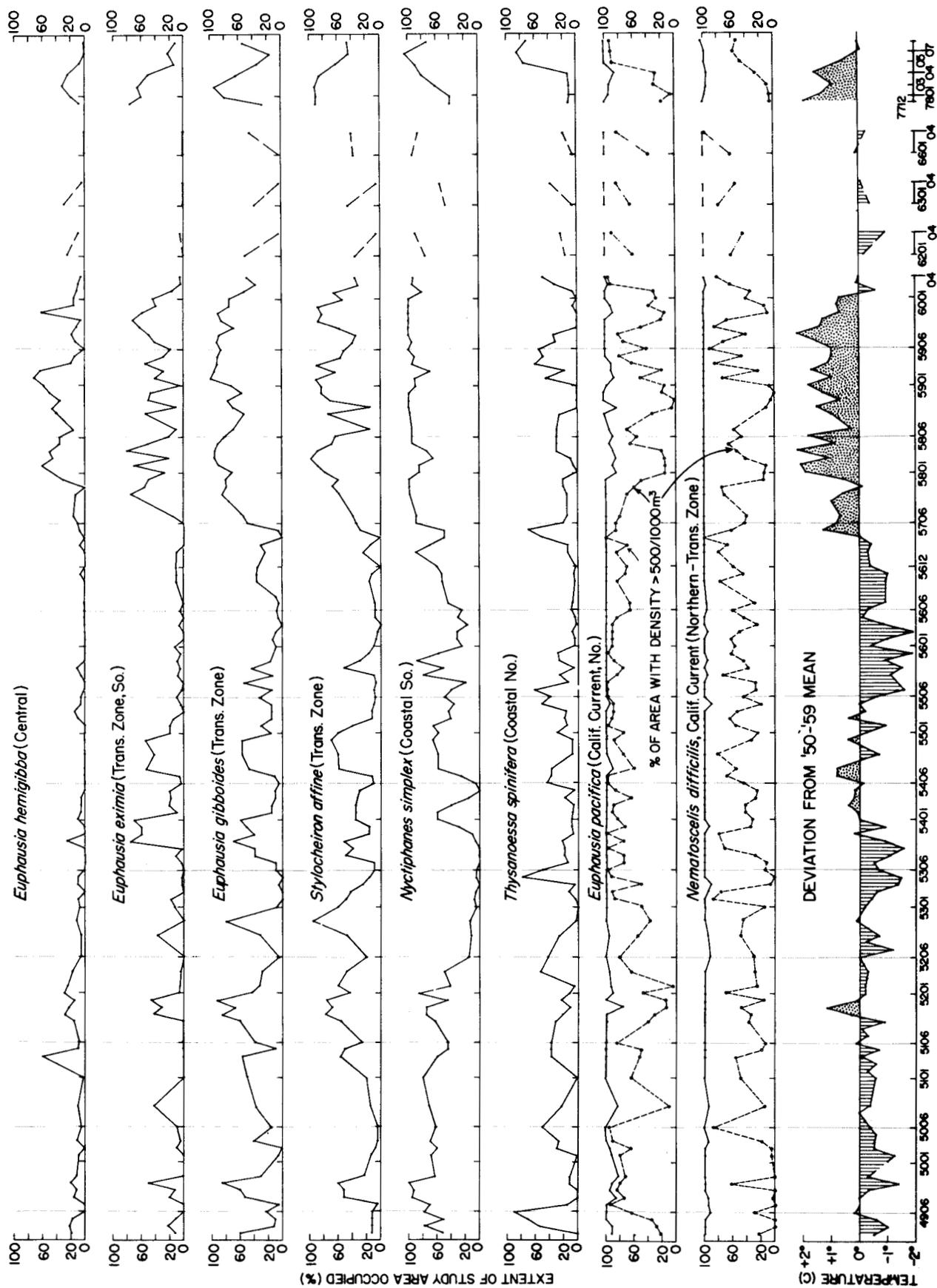


Figure 11. Percentages of the southern California area occupied by species having principal affinities with different parts of the Current are plotted for 1949-1966 and 1977-78. For the two ubiquitous species, the percentage of area with densities > 500/1,000 m³ are plotted. Deviations from 10-year monthly means of the mean monthly temperatures for the area are shown.

species, outside of the southern California area of overlap.

Euphausia pacifica has been the dominant euphausiid in the California Current from central California northward during all years of observations. *Nematoscelis difficilis* is predominant somewhat seaward and to the south of *E. pacifica*. Both are usually present throughout the southern California area. Times during which either species is consistently (1) absent from any part of the area or (2) at low density, are considered noteworthy. The 1949-50 sampling, which extended only to 70-m depth, is probably unreliable for these two species (Brinton 1967b), particularly for estimating abundance of *N. difficilis* and daytime presence of *E. pacifica* (Figure 11).

E. pacifica was absent from part of the area during the warm periods of October-December 1951, January 1958-April 1959, November-December 1959, and December 1977-May 1978. These are also times when high densities of *E. pacifica* ($>500/1000^3$ m) were most restricted, approaching 0% of the area during each of the four periods.

N. difficilis appeared to be consistently lacking from part of the area only during 1977-78. This may have been due to particularly thorough sampling of the area (Figures 5-10). The percentage of area occupied by high abundance of *N. difficilis* was generally equal to or greater than for *E. pacifica* during warm periods and less during cool periods. However, the ups and downs of the high abundance curves for the two species agree more often than not.

SUMMARY

During December 1977 to May 1978 there were higher than average ocean temperatures in the California Current. Offshore zooplankton species then reached shoreward, and southerly species ranged far to the north along the coast, much as during the warm year of 1958 (Ahlstrom 1960; Berner 1960; Brinton 1960). In 1978, however, temperatures in the Current returned to average by July-August.

In southern Californian waters, where emphasis has centered in this description, the distributions of euphausiids showed that Transition Zone species having northern affinities were at much reduced abundances during the 1977-78 winter period of temperatures 1-2°C above average. Some easterly incursions of offshore Transition Zone species (e.g. *Euphausia gibboides*) and stronger northerly incursions of southerly *Euphausia eximia* were associated with shoreward and northerly retraction of the usually dominant cool-water *Euphausia pacifica* and *Nematoscelis difficilis*. This also happened during the three winters of the best documented and most pronounced warm-

water period of 1957-60. For example, high densities of *N. difficilis* ($>500/1000$ m³) occupied <18% of the southern California area during December 1957 to February 1958 and during November 1958 to January 1959, comparing with 5-11% during December 1977 to March 1978.

The 1977-78 winter differed from warm winters during 1957-60 in that even the southerly coastal species *Nyctiphanes simplex* was much compressed shoreward. About half of the southern California area became occupied by this species, compared with 70-80% of the area during winters of 1957-60.

The salinities as low as 32‰ off southern California during 1977-78 (Figure 4) were also anomalous. Such values normally indicate water of northern origin. The high temperatures make this improbable. Substantial precipitation along all of the California coast during December-January certainly contributed. The euphausiid distributions along central and southern California did not then indicate substantial transport from the northwest. The more extensive occurrences in the southern California eddy of *Euphausia eximia* and *Stylocheiron affine*, as compared with *Nyctiphanes simplex*, are evidence of northerly development of the southern part of the Transition Zone, rather than of the southern coastal environment.

Another feature of 1977-78 was the distinct development during spring months of tongue-like extensions of offshore Transition Zone species (Figure 6) and central Pacific species (Figure 9) into the California Current to the north of Point Conception, as well as toward northern Baja California as commonly occurs. This took place as warming tendencies subsided. Easterly incursions of offshore species toward central California have been observed during spring months (Brinton 1967a). However, they were particularly pronounced in 1978, appearing to be associated with extensive springtime meanders in the Current. The cool-water component of the meander brought *Euphausia pacifica* and *Thysanoessa spinifera* far to the west of Point Conception. The dispersion there of *T. spinifera* (Figure 8) was the most extensive yet seen.

The 1949-1966 time series (Figure 11) of euphausiids in southern California waters, against which the events of 1977-78 have been measured, indicated three warm periods separated by two-year cool periods. Only the warm period of 1957-60 was of substantial duration. Nevertheless, April-December 1951 and January-August 1954 permitted local spreading of species with warm-water affinities (e.g. *E. eximia*, *E. gibboides*, and *Nyctiphanes simplex*).

January, when northerly coastal flow is usually maximal, and April, when southerly, offshore flow and upwelling often develop strongly, are ecologically

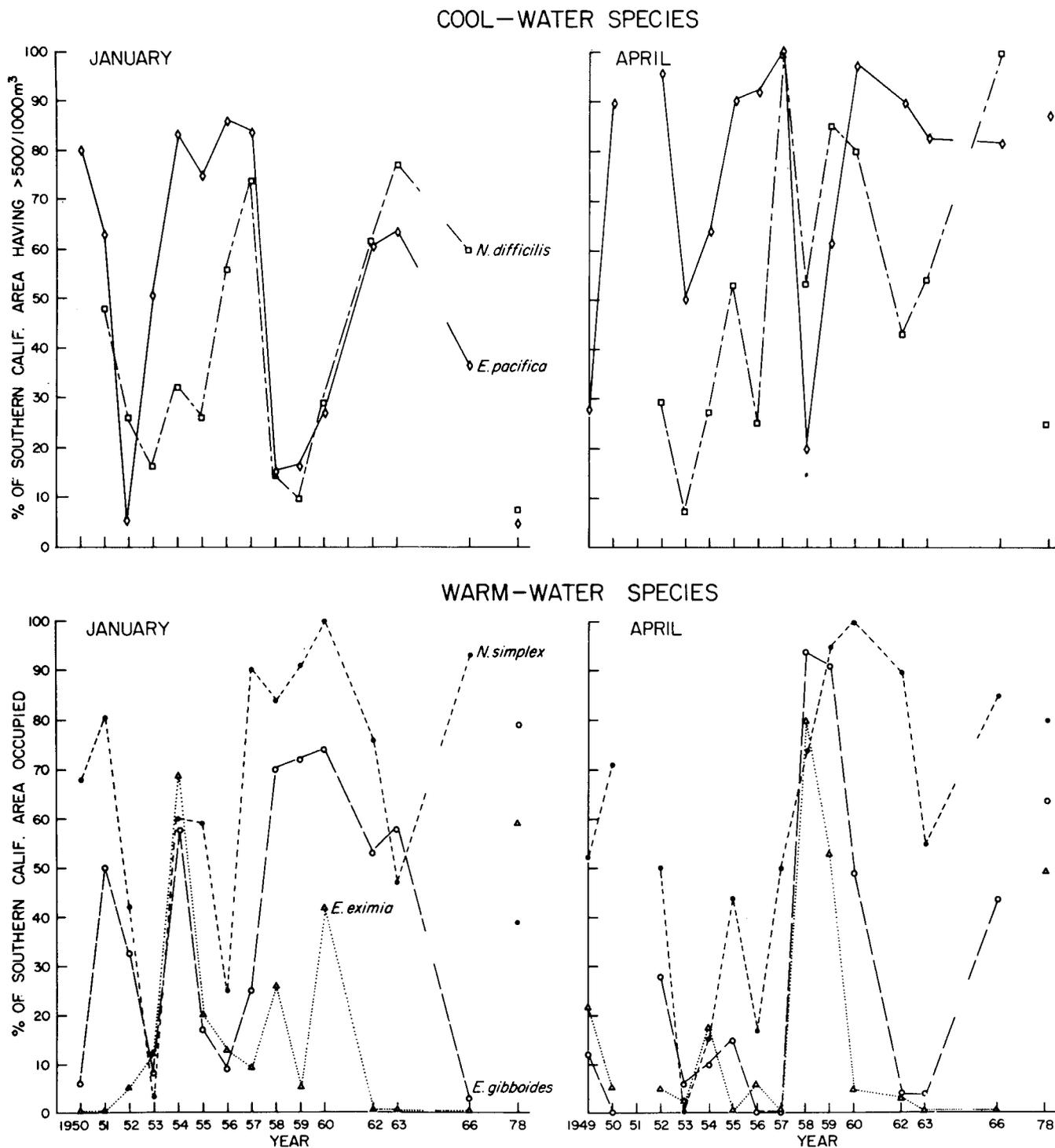


Figure 12. Percentage of southern California area occupied during January and April of 1950-66 and 1978 by the cool-water species *Euphausia pacifica* and *Nematoscelis difficilis* compared with the warm-water species *Euphausia gibboides* (offshore), *E. eximia* (inshore), and *Nyctiphanes simplex* (inshore).

critical times in the annual cycle of climate. Distributions during these months may be used as measures of presence of cool-water and warm-water euphausiids in the southern California area during 1950 to 1978. The generally complementary tendencies of the two groups are evident (Figure 12).

However, there are also some dissimilarities between northern *Euphausia pacifica* and more offshore *Nematoscelis difficilis*. Both show broader though generally parallel distributions of high densities in April compared with February. This is to be expected with the development of upwelling. *E. pacifica* was

particularly diminished during January 1952 following warm conditions in late 1951 and was also sparse during warm 1958-59 and January 1978. *N. difficilis* reached a minimum in cool January 1953, as did the several warm-water species, while *E. pacifica* was somewhat less affected. During Januarys of the extended warm period 1958-60, the warm-water species were broadly distributed while the cool-water species were reduced. This was true of April distributions during 1958-59 but not of 1960 by which time cooling had commenced.

Figure 12 also suggests that *Nyctiphanes simplex* persisted widely along California following its northerly proliferation during 1958-60, and that it did not retract southward thereafter to the extent seen during 1953-56. However, in January, 1978, *N. simplex* was more restricted than during Januarys of 1957-60 as well as of 1962, 1963, and 1966.

Diminution in the area of abundances of *E. pacifica* and *N. difficilis* in January 1958 contrasts with the concurrent northerly spread of *E. eximia* and the shoreward spread of *E. gibboides*, as has been emphasized. By April 1958, *E. pacifica* had returned to its normally high density for that season. *N. difficilis* was still much reduced, while April occurrences of the warm-water species (excepting *N. simplex*) were intermediate between the January maxima and mid-1978 minima.

The distributions of temperature and of euphausiids during 1977-78 indicate much zonal transport within the prevailing meridional flow. Clearly, adjacent eddies serve in such transport (e.g. Brinton and Wyllie 1976). Understanding of eddy structure off southern California and in neighboring waters is developing through satellite imagery (e.g. Bernstein et al. 1977; Owen 1980). This will importantly complement conventional means of describing complex coastal environments, in which details of flow are proving to be as important as mean components.

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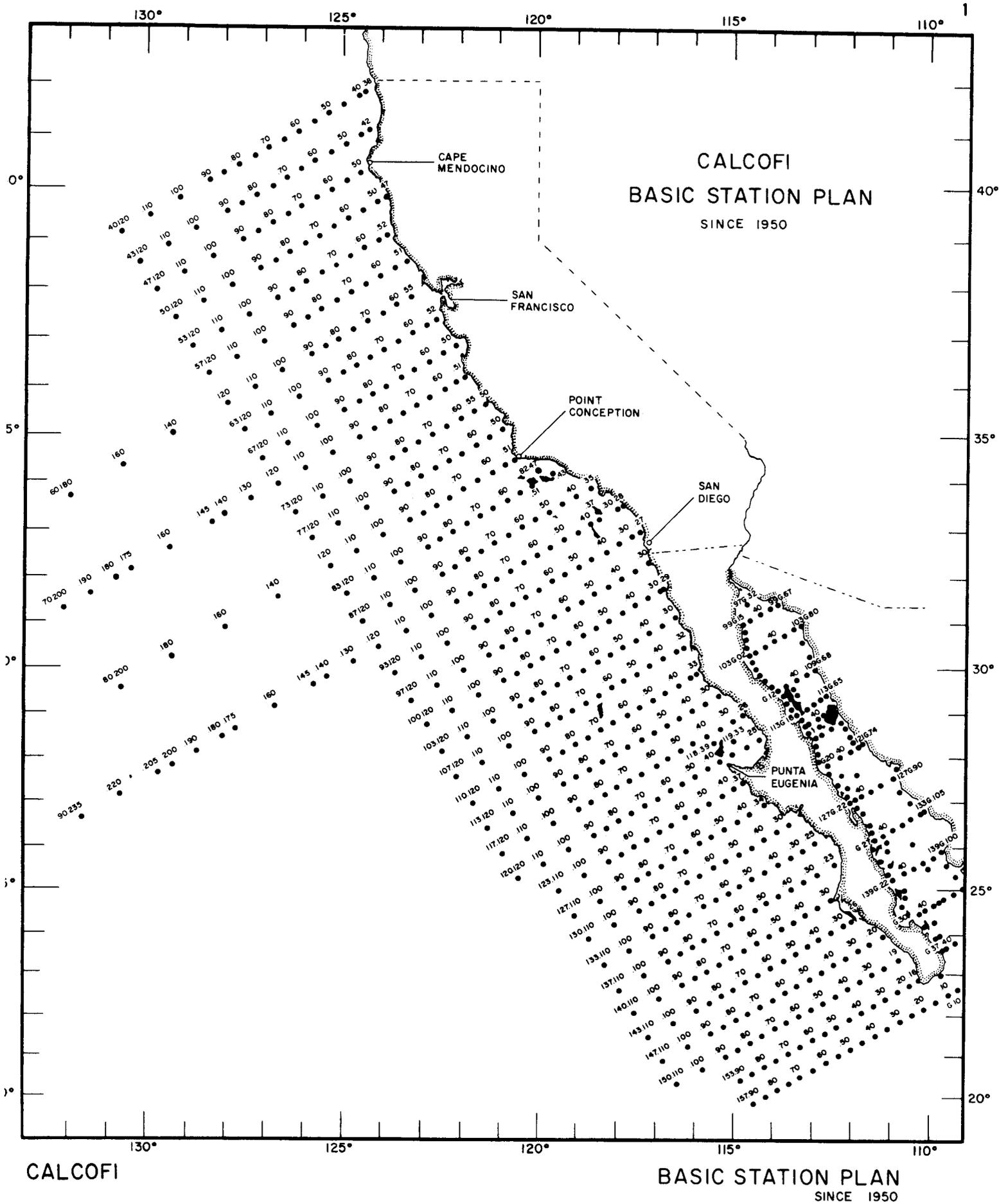
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