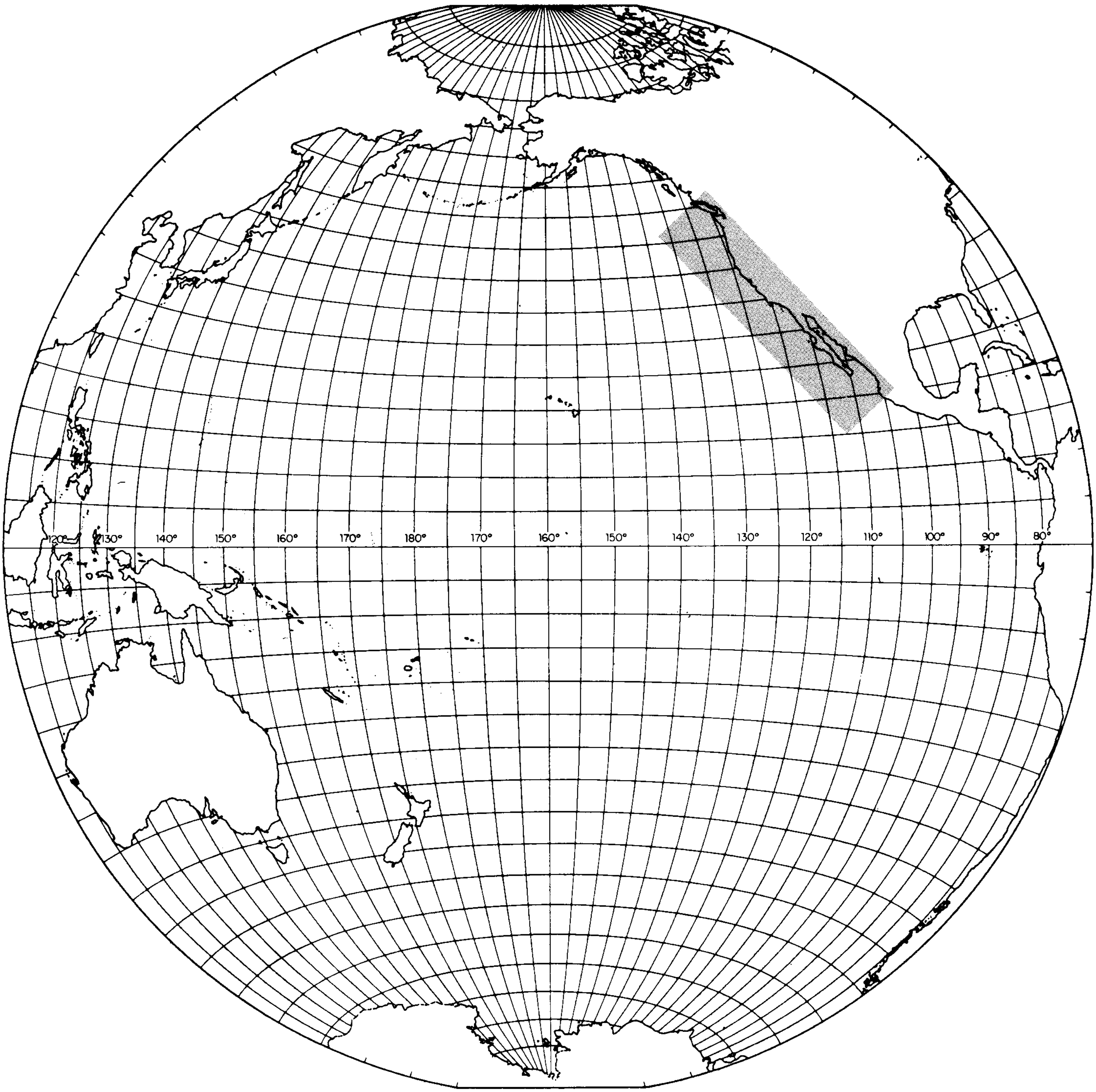

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

INCLUDES INDEX
FOR 1950–1982

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CALIFORNIA
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UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL MARINE FISHERIES SERVICE

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE FOR 1982

This year the egg production method was improved for anchovy biomass assessment, and the anchovy management plan was rewritten based on this newly instituted procedure. Adoption by the Pacific Fishery Management Council is scheduled for 1983.

Warm-water conditions typical of an El Niño event were detected in July 1982 off the coast of South America, and off Mexico and California in November. The last major warm-water event off California took place in 1957-58 and was documented in *CalCOFI Reports,* Volume VII, 1960. In February 1983, scientists aboard R/V *Townsend Cromwell* measured the physical, chemical, and biological parameters associated with this event on a transect from Hawaii to California, following CalCOFI line 90 to the coast.

CalCOFI has committed its resources for 1984, including R/V *New Horizon* and R/V *David Starr Jordan,* to a full-scale 7-cruise survey of the California Current. In 1983, the Marine Life Research Group will use R/V *Ellen B. Scripps* to make monthly transects across the Southern California Bight; weekly measurements of sea level, salinity, temperature, and phytoplankton are to be made from the Scripps Pier. These activities are intended to fully document the biological effects of the current El Niño condition.

In October 1982 the CalCOFI Conference was held once again in Idyllwild, California, at the University of Southern California's conference center in the San Bernardino mountains. A symposium entitled "The Larger Pelagic Fishes of the California Current" was convened by Alec MacCall. The symposium papers, reprinted in this volume, make a valuable, up-to-date record of fishes rarely discussed in a conference of this kind. The CalCOFI Committee was pleased to provide the forum for presenting much new information. Forty-three research papers and nine posters were presented at the conference and were highlighted by a special Peruvian section on anchovy, sardine, and hake. Peruvian scientists are applying the egg production method for anchovy biomass assessment to the Peruvian anchoveta, chiefly with the help of Paul E. Smith of the Southwest Fisheries Center.

The CalCOFI Committee continued to solicit new ideas and directions for the CalCOFI program. Scientists participating in a September 1982 workshop on "Future Directions for CalCOFI" included John McGowan, Scripps Institution of Oceanography; Dudley Chelton, Jet Propulsion Laboratory; Edmund Hobson, National Marine Fisheries Service (NMFS); Richard Klingbeil, California Department of Fish and Game; Barbara Hickey, University of Washington; Alec MacCall, NMFS; Richard Methot, NMFS; Willard Bascom, Southern California Coastal Water Research Project; Gregor Cailliet, Moss Landing Marine Laboratory; and Robin LeBrasseur, Pacific Biological Laboratory, Nanaimo, Canada. Douglas DeMaster of NMFS led the discussion.

In 1982 we published *CalCOFI Atlas No. 30: Vertical and Horizontal Distributions of Seasonal Mean Temperature, Salinity, Sigma-t, Stability, Dynamic Height, Oxygen and Oxygen Saturation in the California Current, 1950-1978,* by Ronald Lynn, Kenneth Bliss, and Lawrence Eber.

We regretfully report the death in 1982 of John Fitch. John was a scientist for the California Department of Fish and Game and contributed greatly to our understanding of California fishes. He was known best for his pioneering work on the otoliths of fishes and for his editorial excellence on the journal *California Fish and Game* during the 1960s. We will all miss him.

As this volume was going to press we learned of the death of Julian C. Burnette on January 28, 1983. Mr. Burnette was the first chairman of the Marine Research Committee (MRC), the state agency governing CalCOFI. Mr. Burnette also was spokesman for the entire sardine industry at a time when the sardine fishery was a major business in California. In his longtime capacity as MRC chairman, Mr. Burnette helped guide and support the research for which CalCOFI is now noted. Although he retired from MRC in 1967, his efforts have left their mark and are reflected in the approach CalCOFI takes today.

This is the last of two issues of *CalCOFI Reports* (Volumes XXIII and XXIV) for which Reuben Lasker, as CalCOFI Coordinator, had responsibility. We would like to thank him and Julie Olfe, who edited this volume, for their excellent work.

The CalCOFI Committee:
Izadore Barrett
Herbert Frey
Joseph Reid

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1982[1]

Total California landings for the pelagic wet fisheries decreased slightly during 1982 (Table 1). While landings of anchovy, Pacific mackerel, and market squid declined, jack mackerel and Pacific herring landings almost doubled. Pacific sardine landings, incidental to catches of mackerel, were the highest since the moratorium on their commercial take was established in 1973.

Pacific Sardine

The moratorium on the commercial take of sardines remained in place during 1982, amidst rumors that the resource was resurging. These rumors arose, in part, because Pacific sardines were being seen and taken more frequently during 1982 than in any other year since the moratorium took effect in 1973.

Live-bait fishermen from most southern California ports reported encountering pure schools, and frequently logged incidental catches of sardines while targeting on anchovies. Mackerel fishermen also reported sightings of sardine schools, and the incidental catches of sardines rose to 144 short tons in 1982. Although most of the sightings of sardines were unconfirmed, the California Department of Fish and Game's young-fish, midwater-trawl survey provided additional information regarding the relative abundance of this resource.

The 1982 survey captured sardines in 14 of 152 midwater-trawl tows. Although the total catch of 145 fish was minor compared to the catch of other species (primarily anchovies), this was the best showing of sardines in 17 years of survey trawling in California waters. Another encouraging sign was that nearly two-thirds of the trawl catches consisted of young sardines spawned during 1982.

Northern Anchovy

The year began with 6,795 tons and 135,336 tons remaining to be harvested against the 1981-82 season quotas for the northern (10,000-ton quota) and southern (140,000-ton quota) permit areas, respectively.

In the northern permit area, there were no landings during January, as most fishermen were participating in the highly lucrative herring roe fishery. After the interseason closure (February-March) fishing success remained at a low level, with only a few scattered weeks of sizable landings during April and May. Substantial numbers of fish under the 5-inch size limit began to show up in May's landings and caused one vessel to be cited. By mid-June most of the local fishermen had shifted their efforts to squid or salmon. The season closed on June 30, with total landings of 4,953 tons for the northern permit area (Table 2).

In the southern permit area, a continuing dispute over price and unloading rules between unions, boat owners, and canneries kept most of San Pedro's fleet from fishing for anchovy during January. Only four San Pedro boats fishing for the smaller Terminal Island processor, and

TABLE 1
Landings of Pelagic Wet Fishes in California in Short Tons in 1964-82

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1964	6,569	2,488	13,414	44,846	175	8,217	75,709
1965	962	2,866	3,525	33,333	258	9,310	50,254
1966	439	31,140	2,315	20,431	121	9,512	63,958
1967	74	34,805	583	19,090	136	9,801	64,489
1968	62	15,538	1,567	27,834	179	12,466	57,646
1969	53	67,639	1,179	26,961	85	10,390	105,307
1970	221	96,243	311	23,873	158	12,295	133,101
1971	149	44,853	78	29,941	120	15,756	90,947
1972	186	69,101	54	25,559	63	10,303	104,993
1973	76	132,636	28	10,308	1,410	6,031	150,489
1974	7	82,691	67	12,729	2,630	14,452	112,576
1975	3	158,510	144	18,390	1,217	11,811	190,075
1976	27	124,919	328	22,274	2,410	10,153	160,115
1977	6	111,477	5,975	50,163	5,827	14,122	187,570
1978*	5	12,607	12,540	34,456	4,930	18,898	83,436
1979*	17	52,768	29,392	17,562	4,651	18,954	123,434
1980*	38	46,873	32,349	22.225	7,109	16,021	124,615
1981*	31	57,355	42,477	15,513	6,444	24,840	146,660
1982*	144	46,352	31,057	28,908	11,075	17,901	135,437

*Preliminary

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[1] Includes review of the pelagic wet fisheries.

TABLE 2

Anchovy Landings for Reduction in the Southern and Northern Areas from 1966 to 1982, in Short Tons

Season	Southern Area	Northern Area	Total
1966-67	29,589	8,021	37,610
1967-68	852	5,651	6,503
1968-69	25,314	2,736	28,050
1969-70	81,453	2,020	83,473
1970-71	80,095	657	80,752
1971-72	52,052	1,314	53,426
1972-73	73,167	2,352	75,519
1973-74	109,207	11,380	120,587
1974-75	109,918	6,669	116,587
1975-76	135,619	5,291	140,906
1976-77	101,434	5,007	106,441
1977-78	68,476	7,212	75,688
1978-79	52,696	1,174	53,870
1979-80*	33,383	2,365	35,748
1980-81*	62,161	4,736	66,897
1981-82*	45,149	4,953	50,102

*Preliminary

the Port Hueneme fleet of four seiners were able to maintain landings through the end of January.

When the season reopened on April 1, no fishing occurred, because negotiations ensued over a new price formula and port rules. Fishing didn't begin until late April, at a price reduced from $46.00 to $41.50 per ton. The fishermen's interest in anchovy steadily increased, and on May 22 they voted to suspend port rules and fish every day (except Memorial Day weekend) until the end of the season. Commercial-size schools of anchovies were found close to San Pedro, and the fleet was able to fish "round-the-clock" until the June 30 season closure. Total landings in the southern area for the 1981-82 season were 45,149 tons, with over 38,000 tons landed from April through June.

Sampling indicated the southern area spring fishery landings comprised 17% 1981 year-class fish, 30% 1980 year-class fish, 42% 1979 year-class fish, with 11% older fish. The contribution of the incoming year class (1981) was less than half that of the previous two seasons' incoming year class during the months of May and June.

On July 1, the U.S. Department of Commerce announced reduction quotas for the 1982-83 season. An egg production estimate of 425,000 tons spawning biomass was calibrated to an "equivalent" larval census estimate of 2,060,000 tons. This resulted in federal reduction quotas of 10,000 tons and 224,000 tons for the northern and southern permit areas, respectively.

The Fish and Game Commission chose to retain the same processing quotas as in the previous reduction season: 10,000 tons for the northern permit area and 140,000 tons for the southern permit area.

The 1982-83 season opened in the northern permit area on August 1, with only two boats fishing for anchovy at a modest pace through October. No landings were made during November because of a lack of commercial-size schools in Monterey Bay. By December most of the local fishermen had left for the lucrative herring roe fishery in San Francisco Bay. A single seiner made one landing of anchovies in mid-December. Total landings for the northern area through December stood at only 1,210 tons, down considerably from the 3,500 tons landed during the same period in 1981.

In the southern permit area, the 1982-83 season opened on September 15, but fishermen showed little interest in fishing for anchovy. The San Pedro fleet concentrated its efforts on mackerel and bonito. The smaller Terminal Island processor did place a "no-limit" order for anchovies with its boats in early November, but the larger processor decided not to place an order, At mid-month a scouting trip by four seiners found commercial-size schools; however, the fish were judged to be too small. No loads of anchovies for reduction were landed at Terminal Island through the end of December.

Seiners based at Port Hueneme began fishing in their local waters for anchovy in mid-October. The sporadic appearance of commercial-size schools, and intermittent storms held down the landings to a total of 1,960 tons through the end of December; these were the only landings for reduction delivered in the southern area.

The total reduction landings for 1982 statewide were 45,109 tons. Additionally, 5,300 tons were landed for live bait and an additional 1,300 tons for other nonreduction purposes. During 1982 the price of anchovy for reduction ranged from $46.00 to $41.50 per ton, much lower than the 1981 price.

Jack Mackerel

After contributing only 27% of combined mackerel landings in 1981, jack mackerel was the dominant species in 1982 landings until late in the year. From January through October jack mackerel accounted for 55% of mackerel landings. However, in November the major cannery at Terminal Island expressed a preference for Pacific mackerel, and jack mackerel landings slackened dramatically. The 1982 total landings of 28,908 tons represent 48% of the total mackerel landings.

The ex-vessel price for both mackerels dropped from $190 per ton to $174 per ton during October. The decrease resulted from negotiations between fishermen and canneries for the purpose of increasing production.

Pacific Mackerel

The year began with approximately 4,000 tons remaining on the 1981-82 season (July 1-June 30) quota of

33,000 tons. On January 31 the allowable catch for the season was increased to 38,000 tons after a reevaluation of the 1981 total biomass estimate. Fishing success was excellent during both January and February, and on March 6 the quota season was closed. Interseason restrictions allowed for a 50% incidental catch with jack mackerel and 3-ton pure loads. The 12-month catch (July 1981-June 1982) of 42,100 tons was the highest "seasonal" catch since 1940-41.

The 1982-83 season opened on July 1, 1982, with a quota of 29,000 tons. This was based on a total biomass estimate of 165,000 tons, which was lower than the previous year's assessment. The reduced biomass level resulted from lower levels of recruitment by the 1979 and 1980 year classes and the projected moderate recruitment of the 1981 year class.

Although mackerel fishing was good during most of the summer and fall, the better availability of jack mackerel and possibly a smaller biomass of Pacific mackerel combined to hold down landings of the latter. It wasn't until November that Pacific mackerel began to predominate in catches, but this appeared to be a direct result of marketing considerations. During the last two months of the year, one cannery at Terminal Island established higher daily boat limits for deliveries that contained 100% Pacific mackerel. This was the first time since the 1950s that a sustained preference for Pacific mackerel had been exhibited by a major buyer.

Landings of Pacific mackerel, against the season quota, reached 19,000 tons at year's end. The age composition of these landings supported conclusions regarding weak recruitment in recent years. Four-year-olds (1978 year class) and older fish accounted for approximately 70% of the tonnage landed between July 1 and December 31, 1982. The 1982 total landings of 31,057 tons represents the first decline in annual landings since the resurgence of the fishery (Table 1).

Market Squid

California's total harvest of market squid continues to result from the operations of two separate fisheries: the late-spring-summer-early-fall fishery of Monterey Bay and the late-fall-winter-early-spring fishery off southern California.

The southern California market squid fishery declined during 1982, with total landings estimated at 6,275 tons, down considerably from the over 10,000 tons landed in 1981. The normal late-fall appearance of schools of squid in southern California waters failed to occur in any numbers comparable to recent years. San Pedro markets received over 90% of their landings of squid during the first 5 months of the year. During December these markets were offering $300-400 per ton for squid because of the market demand, which could not be supplied. The major squid canneries, located at Port Hueneme and Terminal Island, received all of their landings during the first 3 months of 1982.

Purse seine and scoop/dip-net-rigged vessels brought in over 95% of the catch. As in previous years, the greatest amount of squid was taken from waters around Santa Catalina Island and in Santa Monica Bay. The average price paid for squid during 1982 was $110.90 per ton, up about $25 from that paid in 1981.

The 1982 Monterey squid catch was 11,626 tons, and the catch has averaged 11,000 tons over the past 5 seasons. This represents the longest sustained period of high catches since the fishery began, and is only approached by the good catches made during the mid-1940s. The 1982 fishery peaked in May and October, with over half the catch taken in the early part of the season. The ex-vessel price was not increased this season and remained $285 per ton and $115 per ton for freezing and canning, respectively.

Despite the good catches and high prices paid in 1982, all is not well with the Monterey fishery. The bulk of the early season catches comprised either very small squid or squid of poor quality not suitable to be frozen for human consumption. For a short time in August the price was actually lowered to $256 per ton because of this condition. In 1981 the fall squid fishery was the best in recent years, and it is possible that good survival from a "late" 1981 spawn resulted in greater availability of small squid the following spring.

Frozen squid for human consumption has become a major part of the market, along with frozen squid for bait. When inventories of frozen squid were exhausted midway through the season, the fishery could not supply enough quality squid to meet the demand, even though catches were good. Local squid dealers considered 1982 a poor season.

Another problem during 1982 was that the size of the lampara fleet at Monterey increased to over 40 boats. Many of the new boats do not belong to the local fishermen's union, and they fish as they please on weekends and during the light of the moon. The increased fleet size also means smaller daily catch limits per boat, because catches are limited by the capacity of freezing plants.

Finally, unseasonably warm ocean temperatures during the winter of 1982-83 in central California may have a serious impact on the Monterey fishery in 1983. These same conditions prevailed in 1961 and 1973, two of the worst squid seasons on record.

Pacific Herring

The 1982 annual herring catch was 11,075 tons (Table 1). The major component of the catch is from the seasonal herring roe fishery in Tomales and San Francisco bays. The herring roe fishery season extends from December through March, and the 1981-82 seasonal catch was 11,321 tons. Catches are controlled by a quota system based on annual population estimates. The San Francisco Bay quotas were increased to 10,000 tons in 1981 and resulted in record high catches during the 1981-82 herring roe fishery.

The herring roe fishery is limited to gill nets in all areas except San Francisco Bay, where purse seines and lamparas are also used for herring. The quotas are allocated by gear in order to reduce competition between different gear. Gill net boats were divided into three platoons: the "XH" or December platoon, and the odd and even platoons that fish alternate weeks the remainder of the season. As a result of higher population estimates the San Francisco Bay quota was increased, while all other area quotas remained the same (Table 3). Quotas were taken in all areas except Tomales Bay and Crescent City Harbor. In Tomales Bay the quota was not taken because of the platoon system, which allows only half the fleet to fish each major spawning run. Regulation changes after the 1981-82 season eliminated the platoon system in Tomales Bay and combined the fleet into one group for the 1982-83 season.

The 1982 Tomales Bay herring spawning biomass was estimated to be 7,150 tons; this is the highest estimate in 4 years and reverses a declining trend. The 1982 San Francisco Bay herring spawning biomass was estimated to be 99,500 tons, a 50% increase over 1981, which represents the highest biomass estimate for the bay. These population increases are due to better than average recruitment of the 1978, 1979, and 1980 year classes.

The base price paid for herring catches with 10% roe recovery was $800 per ton for gill net and $400 per ton for round haul. The gill net catch commanded a higher price because it is selective for large herring, which have a higher quality roe. The season's average price, which is dependent on roe content, was $1,200 per ton for the gill net catch and $600 per ton for the round haul catch. The ex-vessel value of the 1981-82 herring roe fishery was over $11 million, and with the stabilization of the Japanese herring market, prices are expected to increase gradually in coming years.

TABLE 3
Permits Issued and Quotas by Area and Gear for the 1981-82 Herring Roe Fishery

Area	Gear	Permits	Quota (short tons)
San Francisco Bay	Gill net (X)	100	1,725
	Gill net (odd)	116	2,070
	Gill net (even)	116	2,070
	Purse seine	24	1,875
	Lampara	27	2,260
Tomales and Bodega Bays	Gill net (odd)	28	600
	Gill net (even)	28	600
	Beach seine	1	—
Humboldt Bay	Gill net	4	50
Crescent City	Gill net	3	30
Total		447	11,280

Groundfish

Groundfish landings continued to increase in 1982, a trend that began in the early 1970s. A new high of 61,440 tons of groundfish was landed. The commercial catch totalled 57,858 tons, and 3,582 tons were taken by recreational fishermen.

The commercial catch was dominated by rockfish, sablefish, and Dover sole. Rockfish was a combination of many species: widow rockfish, bocaccio, and chilipepper rockfish were the most important. Sablefish landings by all gears increased to 10,458 tons. Dover sole landings in 1980 were 10,990 tons, a slight increase over catches of recent years. The most important group in the recreational catch was also rockfish.

In 1982, 177 trawlers participated in the fishery. The majority of the catch, 47,755 tons, was landed by trawlers. The midwater trawl fishery continued to expand; in 1982, midwater trawlers landed 7,735 tons of widow rockfish and 965 tons of Pacific whiting. Trap, line, and gill net fishermen were also active in the groundfish fishery.

The Pacific Fishery Management Council's Groundfish Management Plan was approved and implemented in late 1982. Management actions were taken to curtail widow rockfish and sablefish catches as coastwide, optimum yield levels in the plan were exceeded.

Dungeness Crab

California Dungeness crab landings totaled 10.5 million pounds for the 1981-82 season, a drop of 1.5 million pounds from the previous season.

Landings for Crescent City, Trinidad, Eureka, and Fort Bragg were 6.9, 0.7, 2.5, and 0.2 million pounds, respectively. The northern California season commenced December 1 with intense effort generated by large vessels, many from out of state. Crab condition was good, and by the end of December, 74% of the season's catch had come across the docks. Many vessels quit fishing by mid-January because of low catch rates. Accelerated landings prompted many small vessel owners to petition for trap limits and a ban on night fishing. A total of 432 vessels engaged in the fishery, and the opening price of $.79 per pound quickly jumped to $.89, then progressed to a high of $1.40 by the end of the season.

San Francisco area Dungeness crab landings totaled just 199,548 pounds, the lowest catch on the record, which dates back to 1916. The previous low was the 1974-75 season when 231,000 pounds were landed. Approximately 100 vessels participated in the fishery. Opening price was $1.25 per pound; it dropped to $.95 in December and climbed steadily to $1.80 by the end of the season.

Pelagic Shark and Swordfish

During the first half of the 1982-83 season, 184 permits were issued to fishermen to take sharks with gill nets. A total of 330 permits were issued to swordfish harpoon fishermen.

In September the passage of SB 1573 (Beverly) voided all previously issued drift gill net permits. Subsequently, the number of new drift gill net permits has reached 183. Under this new permit, swordfish as well as sharks may be targeted by drift gill net fishermen.

The 1982 season has been another poor one for swordfish harpoon fishermen. Just over 1,000 swordfish were taken by the harpoon fleet, compared to the historic average of about 6,000 fish. Despite the poor showing by harpooners, drift gill net fishermen enjoyed a successful late season, accounting for over 12,000 swordfish for the period from July through January, and indicating the presence of large numbers of subsurface fish in southern California waters.

Ex-vessel prices for swordfish during 1982 ranged from $4.00 per pound in July down to $2.50 per pound during the peak month, November.

This year, for the first time, drift gill net vessels have ventured north of Point Conception. A group of drift gill netters working the Morro Bay area produced substantial landings of thresher sharks. During October several vessels were reported fishing as far north as Monterey.

Thresher shark landings have been good this year, dispelling fears that fish stocks might immediately suffer as a result of current levels of fishing pressure. Thus far, there is no evidence of overfishing, indicating that the thresher stock may be quite large and that the drift gill net fleet does not have access to major portions of it.

The price of thresher shark fluctuated throughout the season between $.70 and $1.00 per pound.

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CALIBRATION OF NORTHERN ANCHOVY SPAWNING BIOMASS ESTIMATES DERIVED BY EGG PRODUCTION AND LARVAL CENSUS METHODS

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ABSTRACT

A mathematical procedure is developed for converting estimates of northern anchovy spawning biomass derived by egg production methods to values equivalent to those derived by larval census methods. This calibration is based on the results of concurrent spawning biomass surveys conducted for both methods in 1980 and 1981. Two egg production surveys were made in 1981. The coefficient of proportionality for the two biomass estimators is not a simple constant but a function of egg survival, daily population fecundity, and larval mortality rate—all of which may vary from year to year. The common link between these two biomass estimators is the daily production of larvae at the time of hatching. The coefficient of proportionality between the hatching rates derived from the two estimators is relatively constant for the three test cases. The proposed equation for converting egg production estimates of spawning biomass to equivalent larval census estimates may result in a bias of 3.1% in the equivalent larval census estimate.

RESUMEN

Se desarrolla un procedimiento matemático para convertir estimaciones de la biomasa de la puesta de *Engraulis mordax* (anchoa), derivado de los métodos equivalentes para la producción de huevos y del censo larval. Esta calibración está basada en los resultados obtenidos sobre la biomasa de la puesta utilizando ambos métodos, durante exploraciones en 1980 y 1981. En 1981 se efectuaron dos exploraciones para determinar la producción de huevos. El coeficiente de proporcionalidad para los dos valores en la estimación de la biomasa, no es una constante simple, sino una función de la supervivencia de huevos, fecundidad diaria de la población y valor de la mortalidad larval, factores que varían de un año para otro. El eslabón común entre estas dos estimaciones de la biomasa es la eclosión diaria de larvas. El coeficiente de proporcionalidad entre los valores de eclosión derivados de los dos valores estimados resultó relativamente constante para las tres pruebas efectuadas. La ecuación que se propone para convertir la estimación de la producción de huevos en la estimación de la biomasa de la puesta y la estimación equivalente del censo de larvas, puede resultar con una desviación del 3.1% en la estimación equivalente del censo de larvas.

INTRODUCTION

The Fishery Management Plan (FMP) for northern anchovy specifies the seasonal catch quota for the U.S. fishery off California based on an annual estimate of anchovy spawning biomass. The quota formula options presented in the original FMP were evaluated using an anchovy population model developed from the 1951-75 time series of larval census estimates (Smith 1972; Huppert et al. 1980). The La Jolla laboratory of the Southwest Fisheries Center (SWFC), National Marine Fisheries Service, is responsible for making these annual estimates. Parker (1980) described and demonstrated the feasibility of a new method of estimating anchovy spawning biomass referred to as the egg production method. In 1980 the SWFC conducted concurrent surveys to estimate spawning biomass by both methods (Stauffer and Picquelle 1981; and MS[2]). The results indicated that the value of the egg production estimate may be 50% to 60% of the corresponding larval census estimate. Because of the advantages of the egg production method[2]—particularly fewer vessel days at sea—the SWFC decided to convert the annual surveys to the egg production method by 1982 and to conduct concurrent surveys by the two methods in 1981.

The Pacific Council instructed the anchovy plan development team to modify the FMP and to fit the anchovy population model to a time series of spawning biomass estimates equivalent to the egg production method. The council also requested that the SWFC convert the egg production estimates to equivalent larval census estimates in the intervening years until the new plan is implemented. The purpose of this report is to document the procedure for converting egg production estimates to equivalent larval census estimates beginning in 1982, based on the concurrent surveys of 1980 and 1981.

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[1] Present address: Northwest and Alaska Fisheries Center, 2725 Montlake Boulevard East, Seattle, Washington 98112.

[Manuscript received February 14, 1983.]

[2] Stauffer, G. D., and S. J. Picquelle. MS. Egg production estimates of spawning biomass of the northern anchovy, *Engraulis mordax*, for 1980 and 1981. Southwest Fisheries Center, La Jolla, California.

DERIVATION OF CALIBRATION

Simple Case of Proportionality

The basis for the calibration between the two spawning biomass estimators is that the larval census estimate, B_l, is proportional to the egg production estimate, B_e, for any year in which concurrent surveys have been conducted. This can be described by

$$B_l = c\, B_e, \tag{1}$$

where c is a coefficient of proportionality. If c is constant from year to year then the larval census estimate in year j can be derived from an egg production estimate from equation (1) where c is estimated for the calibration years. This conversion equation becomes more complex if c is quite variable from year to year, violating the assumption of constant proportionality.

Complex Case of Variable Proportionality

The calibration in the case when c is not equal from year to year can be derived from the relationship of the larval census estimate, B_l, to the daily production of newly hatched larvae, L_h, and from the relationship of the egg production estimate, B_e, to daily rate of hatching eggs, P_h. A common link between these two biomass estimators is the daily production of larvae at the time of hatching. The production of larvae estimated from the plankton data collected on the larval census survey should be proportional to the daily rate of hatching eggs estimated from the plankton data collected on the egg production survey. This says that

$$L_h = b\, P_h, \tag{2}$$

where b is a constant of proportionality. The value of b would be 1.0 if the two survey methods give equivalent estimates of L_h and P_h. The conversion from one biomass estimator to the other can be specified by expressing L_h and P_h as functions of B_l and B_e, respectively.

Daily production of larvae. Lo[3] has found that the survival of anchovy larvae increases with age such that the instantaneous rate of mortality is not constant, as previously considered (Hewitt 1982). She modeled the decay in a daily cohort of larvae, $L'(a)$ as:

$$\frac{dL'(a)}{da} = -\frac{\beta}{a} L'(a) \tag{3}$$

where a is age of larvae with time zero at fertilization, and β is the mortality coefficient. The number of larvae within a cohort at age a is the intregral of (3)

$$L'(a) = L'_h \left(\frac{a}{a_h}\right)^{-\beta} \tag{4}$$

where L'_h is the number of larvae hatched, and a_h is their age at hatching.

For the larval census estimate of spawning biomass, Smith (1972) derived B_l proportional to the census of larvae, L, for the year, that is,

$$B_l = 8.9 \times 10^{-8} L, \tag{5}$$

where B_l is in units of metric tons. The computation of the larval census, L, can be modeled as the quarterly sum of the integral of the larval mortality function (5), that is,

$$L = \sum_{i=1}^{4} L_i = \sum_{i=1}^{4} \int_{a_h}^{A} L_{hi}(t) \left(\frac{a}{a_h}\right)^{-\beta_i(t)} da$$

where $L_{hi}(t)$ is the daily production of newly hatched larvae on day t, quarter i, $\beta_i(t)$ is the mortality coefficient on day t, quarter i, and A is the maximum age larvae are effectively sampled by plankton net (505-micrometer-mesh bongo).

Solving this integral, the quarterly larval census, L_i, is equivalent to

$$L_i = \frac{L_{hi}\, a_h}{\beta_i - 1}\left(1 - \left(\frac{a_h}{A}\right)^{\beta_i - 1}\right),$$

assuming $L_{hi}(t)$ and $\beta_i(t)$ are constant for quarter i. Since the sum of the larval census for the summer and fall quarters is about 6% of the sum for the winter and spring quarters (Stauffer and Parker 1980), the annual larval census can be approximated by a function of winter-spring average production of larvae, L_h, and larval mortality rate, β, that is,

$$L = 2.12 \frac{L_h a_h}{\beta - 1}\left(1 - \left(\frac{a_h}{A}\right)^{\beta - 1}\right).$$

Substituting for L into (5) and solving for L_h gives

$$L_h = \frac{B_l}{18.9 \times 10^{-8}} \left(\frac{\beta - 1}{a_h}\right)\left(1 - \left(\frac{a_h}{A}\right)^{\beta - 1}\right)^{-1} \tag{6}$$

Daily rate of hatching eggs. The egg production estimator, B_e, from Parker (1980) and Stauffer and Picquelle[4] is

$$B_e = \frac{k_1 k_2\ PW}{R\,F\,S}, \tag{7}$$

where k_1 is the geographic area for the stock, k_2 is conversion from grams to metric tons, P is daily rate of egg production in the sea per 0.05 m^2 surface area, W is average weight of female anchovies, R is fraction

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[3] Lo, N.C.H. MS. Egg production of the central stock of northern anchovy, 1951-1982. NMFS, Southwest Fisheries Center, La Jolla, California.

[4] See footnote 2.

of females in the stock, F is batch fecundity per fish, and S is fraction of female fish spawning per day.

By combining parameters so that the daily egg production in the sea for the anchovy stock is

$$P' = k_1 P .$$

and the daily production of eggs per ton of adult fish or daily population fecundity is

$$p = RFS/WK_2,$$

equation (7) simplifies to

$$B_e = P'/p. \tag{8}$$

The daily rate of hatching eggs, P_h, can be estimated from the exponential egg mortality model,

$$P_h = P'e^{-Za_h} = P's$$

where Z is egg mortality rate, and s is total egg survival over the incubation period.

Substituting into (8) and solving for P_h gives

$$P_h = B_e\, p\, s. \tag{9}$$

Calibration equation. The equation for converting from the egg production biomass estimate to the larval census estimate is obtained by substituting L_h from (6) and P_h from (9) into (2) and solving for B_l. This gives

$$B_l = b(18.9 \times 10^{-8}) \; B_e \left(\frac{a_h}{\beta - 1}\right)\left(-1\left(\frac{a_h}{A}\right)^{\beta - 1}\right)^{ps} . \tag{10}$$

The coefficient of proportionality, c, from equation (1) is now

$$c = b(18.9 \times 10^{-8}) \left(\frac{a_h}{\beta - 1}\right)\left(-1\left(\frac{a_h}{A}\right)^{\beta - 1}\right)^{ps} . \tag{11}$$

The source of any variability in the coefficient c from year to year, other than sampling error, should be due to changes in larval mortality rate, egg survival rate, the production of eggs per unit weight of adult fish, or departures from the assumed egg and larval mortality functions.

In any year with an egg production survey, an equivalent larval census estimate of spawning biomass can be derived from equation (10) using a value of b estimated from the calibration years 1980 and 1981. If an estimate of larval mortality rate, β, equivalent to estimates derived from the analysis of larval data is not available, then a value of β must be assumed. In addition, simplification of equation (10) is possible by substituting P' for pB_e from equation (8), giving

$$B_l = b(18.9 \times 10^{-8}) \; P's \left(\frac{a_h}{\beta - 1}\right)\left(-1\left(\frac{a_h}{A}\right)^{\beta - 1}\right) . \tag{12}$$

This says that the larval census estimate can be estimated from just an ichthyoplankton survey of anchovy eggs and an assumption of larval mortality. A survey of adult fish, then, is only necessary if an egg production estimate of biomass is also desired.

ESTIMATION OF CALIBRATION COEFFICIENTS

The calibration between the two anchovy biomass estimation methods can be evaluated from the paired surveys of 1980 and 1981. The estimates of the biomass and related parameters for the larval census and egg production methods are reported by Stauffer and Picquelle (1981; also footnote 2), Stauffer and Charter (1982), and Picquelle and Hewitt (1983). These estimates are summarized in Table 1. The larval census estimates of biomass are 1,611,000 metric tons (MT) and 2,544,000 MT for 1980 and 1981, respectively. The egg production estimates of biomass are 782,000 MT in 1980, 585,000 MT for the February 1981 survey, and 343,000 MT for the second 1981 survey (April). The coefficient of proportionality, c, from equation (1) is 2.06, 4.35, and 7.42 for the three surveys, respectively. The changes in c for the two

TABLE 1

Estimates of Parameters, Spawning Biomass, and Coefficients of Proportionality for Three Calibration Surveys

Parameter estimates	Units	March 1980	February 1981	April 1981
P	$\frac{\text{egg}}{\text{tow day}}$	10.09	7.961	4.936
P'	$\frac{10^{12}\text{ eggs}}{\text{day}}$	23.97	19.01	11.46
p	$\frac{10^{6}\text{ eggs}}{\text{ton day}}$	30.65	32.60	33.46
Z		0.453	0.138	0
a_h	Days	2.71	2.75	2.75
s		0.293	0.684	1.000
β[1]		1.7999	1.7056	1.7085
B_e	Metric tons	782,000	585,000	343,000
B	Metric tons	1,611,000	2,544,000	2,544,000
c		2.06	4.35	7.42
b		0.4195	0.3249	0.3699

$\bar{b} = 0.3835$

[1] Parameter values for β are taken from Picquelle and Hewitt (1983).

1981 surveys with respect to the 1980 calibration amount to a 111% and a 260% increase. This variation in *c* is primarily due to the large differences in egg survival, since the other parameters in (11) are relatively constant (Table 1). These large differences in *c* suggest that the calibration between the two biomass methods using equation (1), which assumes *c* is constant year to year, is rather poor.

Analysis of the calibration based on equation (10) provides relatively consistent values of the constant of proportionality, *b*. The values of *b* for the three comparisons are 0.4195 for 1980, 0.3249 for February 1981, and 0.3699 for April 1981—a maximum decrease of 23% relative to the 1980 value. These values of *b* are much lower than 1.0. Based on equation (2) this implies that larval production estimated from the larval data is about 38% of the value derived from the egg data. The differences between L_h (production of larvae) and P_h (rate of hatching eggs) for 1980 surveys are illustrated in Figure 1. The daily rate of hatching eggs was approximately 3.7 eggs/tow (0.05 m^2 of sea-surface area). The daily production of larvae is about 42% of the value P_h. Possible explanations for this consistent empirical value of *b* less than 1.0 are that the estimate of L_h is averaged over winter and spring months, whereas P_h is the average of one month during the peak of the spawning season, and that the larval census estimate has not been adjusted upward for the extrusion of larvae through the meshes of the plankton net. The scalor difference between the egg production and the larval census estimators probably results from inaccuracies in the coefficient of proportionality, 8.9×10^{-8}, of the larval census estimate (5) derived by Smith (1972).

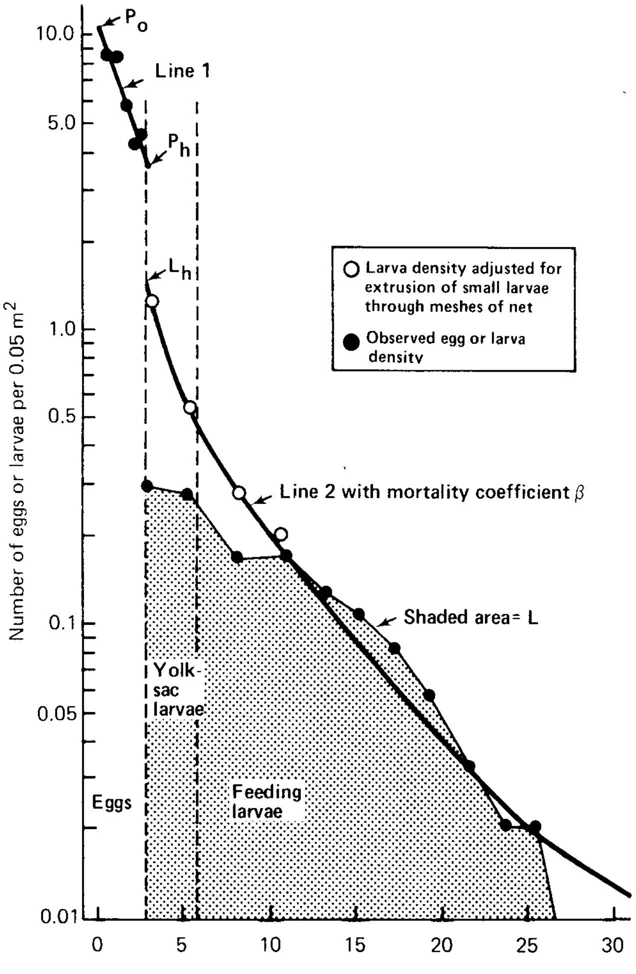

Figure 1. Conceptual basis for the calibration between the egg production and larval census estimators of anchovy spawning biomass. Lines 1 and 2 represent the mortality models for eggs and larvae, respectively.

CALIBRATION FOR AN EQUIVALENT LARVAL CENSUS ESTIMATE IN FUTURE YEARS

For years in which only an egg production survey is conducted, the optimum yield for the U.S. fishing season can be based on an equivalent larval census estimate of anchovy spawning biomass using the calibration equations (10) or (12). Estimates of egg parameters *s*, *P′* or *p*, and B_e can be derived from the egg production survey data. A weighted average of *b* for the surveys is 0.3835, given weights of ½ to the 1980 survey and ¼ to the two 1981 surveys. If a sufficient number of bongo plankton samples are collected during the egg production survey, a value of β can be estimated for the survey. Another alternative is to use the average value for 1980 and 1981 of 1.753.

A comparison of equivalent values versus the actual biomass estimates derived by larval census methods suggests that equations (10) or (12) overestimate the biomass by 3.1% using 0.3835 for *b* and yearly estimates of β. Procedures for estimating the precision of the predicting equations (10) or (12) have not been developed, primarily because of the unknown precision of the original biomass estimates for the larval census method.

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THE NORTHERN ANCHOVY SPAWNING BIOMASS FOR THE 1982-83 CALIFORNIA FISHING SEASON

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ABSTRACT

The 1982 equivalent larval census estimate of the spawning biomass of the northern anchovy (*Engraulis mordax*) central subpopulation is 1,866,000 MT (2,060,000 short tons). This estimate is based on data gathered by an egg production survey conducted from January 18 to March 9, 1982. The abundance of larvae is projected from the daily production of eggs and the subsequent mortality of eggs and larvae. This equivalent larval census estimate will be the basis of the anchovy fishery optimum yield (OY) for 1982-83.

The egg production method estimate of anchovy spawning biomass is 378,000 MT (417,000 short tons). This is based on a production of 12.30×10^{12} eggs/day and a population (males and females) fecundity of 3.253×10^7 eggs/day/MT. The standard error of the egg production method estimate is 97,200 MT, for a coefficient of variation of 25.7%.

In 1982 the central subpopulation of northern anchovy was geographically distributed in the inshore portion of the Southern California Bight, from the Santa Barbara Channel Islands to northern Baja California. A smaller group was detected between Monterey and San Francisco Bays.

RESUMEN

La biomasa de la puesta en la población de *Engraulis mordax* de la zona central de California, fué de 1.866,000 Toneladas métricas durante 1982, estimación basada en la equivalencia del censo larval. Esta estimación está basada en los datos correspondientes a las exploraciones que desde el 18 de Enero al 9 de Marzo de 1982 se llevaron a cabo para determinar la producción de huevos en la región. La abundancia de larvas se calcula considerando la producción diaria de huevos y la mortalidad de huevos y larvas. Estas estimaciones equivalentes del censo larval serán la base para determinar el rendimiento que se podrá obtener en la pesquería de anchoa durante el período de 1982-83.

La producción de huevos como método para estimar la biomasa de la puesta de la anchoa resulta de 376,000 Toneladas métricas. Esto se basa en una producción de 12.30×10^{12} huevos diarios y una poblacion (machos y hembras) con fecundidad de 3.253×10^7 Toneladas métricas de huevos diarios. El error normal de las estimaciones por el método de producción de huevos es de 97,200 Toneladas métricas para un coeficiente de variación de 25.7%.

En 1982 la población de anchoa en la zona central de California estaba distribuida por la franja costera del seno del sur de California, desde las islas del Canal de Santa Bárbara, hasta el norte de Baja California. Un grupo de menor importancia se observó entre las Bahías de Monterrey y San Francisco.

INTRODUCTION

The biomass of the central subpopulation of northern anchovy (*Engraulis mordax*) has been assessed periodically using three independent methods: larval census (Smith 1972; Stauffer and Parker 1980; Stauffer 1980; Stauffer and Picquelle 1981); sonar mapping (Smith 1970; Mais 1974; Hewitt et al. 1976); and egg production (Parker 1980; Stauffer and Picquelle[1]). The anchovy management plan adopted by the Pacific Fishery Management Council (PFMC 1978) specifies that harvest quotas will be established by an optimum yield formula based on annual estimates of spawning biomass. Because of technical complexities in converting acoustic returns to fish biomass, the sonar mapping method is most useful for describing the disposition of adult schools. The egg production method is an improvement over the larval census method because it does not require multiple surveys and because it measures and incorporates variability in adult reproductive output. However, the optimum yield (OY) formula was developed based on larval census biomass estimates. The alternative estimation methods mentioned above produce estimates that consistently differ in magnitude from larval census estimates. Consequently, use of one of these estimates would systematically alter the optimum yields calculated from the larval-census-based formula. In order to avoid this

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[Manuscript received February 7, 1983.]

[1] Stauffer, G. D., and S. J. Picquelle. MS. Egg production estimates of spawning biomass of the northern anchovy, *Engraulis mordax*, for 1980 and 1981. Southwest Fisheries Center, La Jolla, California.

problem, the PFMC has interpreted the OY formula to require a "larval census equivalent" spawning biomass estimate.

The Scientific and Statistical Committee of the PFMC reviewed egg production and larval census surveys conducted in 1979 and 1980, and recommended that replicate egg production surveys, concurrent with a larval census survey, be conducted in 1981. These were successfully accomplished, and the harvest quotas continued to be established using larval census estimates of biomass. In 1982 the National Marine Fisheries Service, in cooperation with the California Department of Fish and Game, conducted only an egg production survey. This report describes the survey results, the egg production estimate of biomass, and the equivalent larval census estimate of biomass.

The egg production method defines the spawning biomass as the quotient of the daily production of eggs in the sea and the daily fecundity (per ton of spawners) of the population (Parker 1980). The larval census method defines the spawning biomass as proportional to the average standing stock of larvae summed over four quarters of the year, and assumes constant reproductive output (per ton of spawners) and constant survival of the young. The proportionality constant was defined from a regression of sardine biomass on sardine larvae and assumes a relative fecundity between anchovy and sardine (Smith 1972).

No larval census was conducted in 1982; however, an equivalent larval census can be estimated by measuring larval mortality and projecting the number of larvae resulting from the measured egg production.

DESCRIPTION OF SURVEY

The 1982 egg production survey for the central subpopulation of the northern anchovy was conducted on board NOAA ship *David Starr Jordan* and F/V *Oregon Beaver* during the period January 18 through March 9, 1982. (For detailed descriptions of operations, see the respective cruise reports on file at the Southwest Fisheries Center, La Jolla, California, and California Department of Fish and Game, Long Beach, California.) A total of 992 egg samples was obtained on the *Jordan* using a small-mesh plankton net retrieved vertically from 70 m (Figure 1); adults were sampled on the *Beaver* and the *Jordan* with 187 midwater trawls (Figure 2); and the disposition of adult schools was described by sonar operated aboard the *Beaver* (Figure 3). In addition, the larvae were sampled with the 505-micrometer mesh bongo plankton net used for the larval census method. These samples are used to determine the posthatch survival of the larvae. Sea temperature, salinity, and weather observations were also recorded.

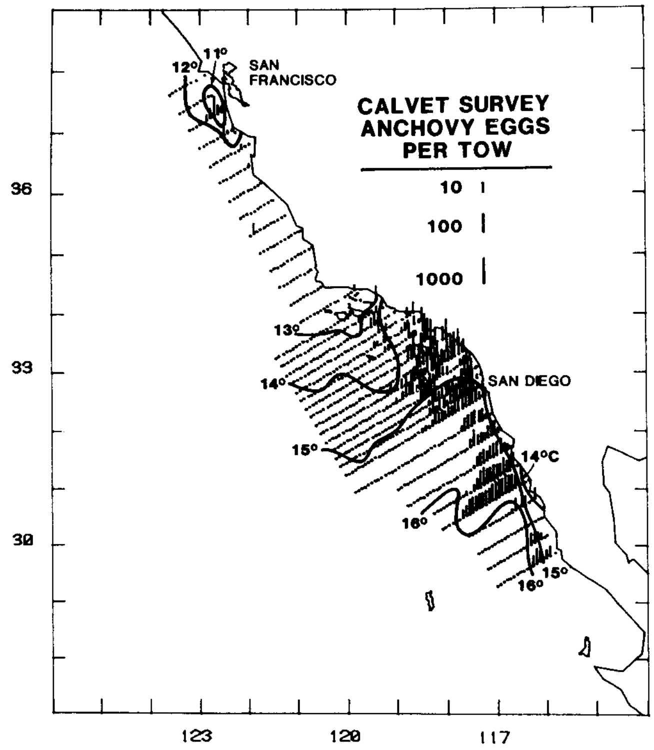

Figure 1. Geographic distribution of anchovy eggs in 1982. Spawning did not occur in cold water southeast of Point Conception or immediately adjacent to the northern Baja California coastline; some spawning was evident between Monterey and San Francisco bays.

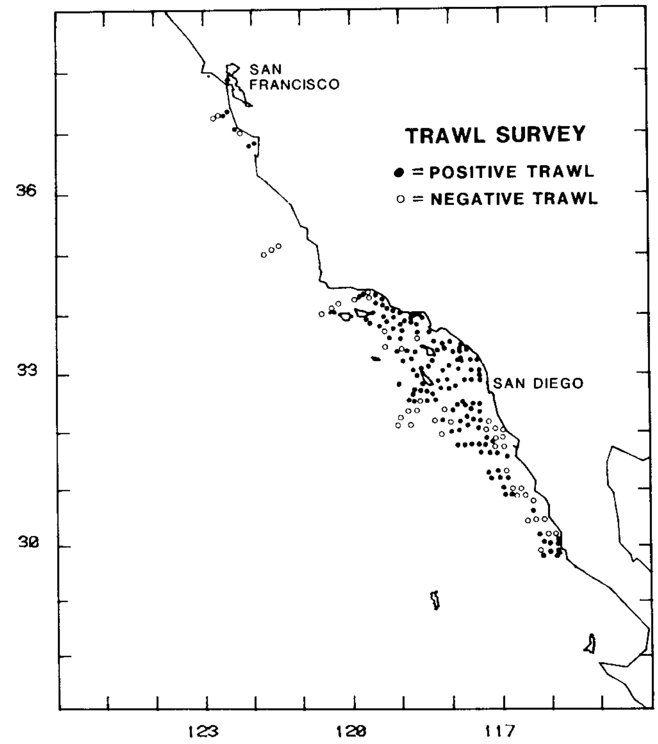

Figure 2. Geographic distribution of trawl sampling effort and trawls that caught adult anchovy (positive trawls). The distribution of adults matched the distribution of eggs (Figure 1).

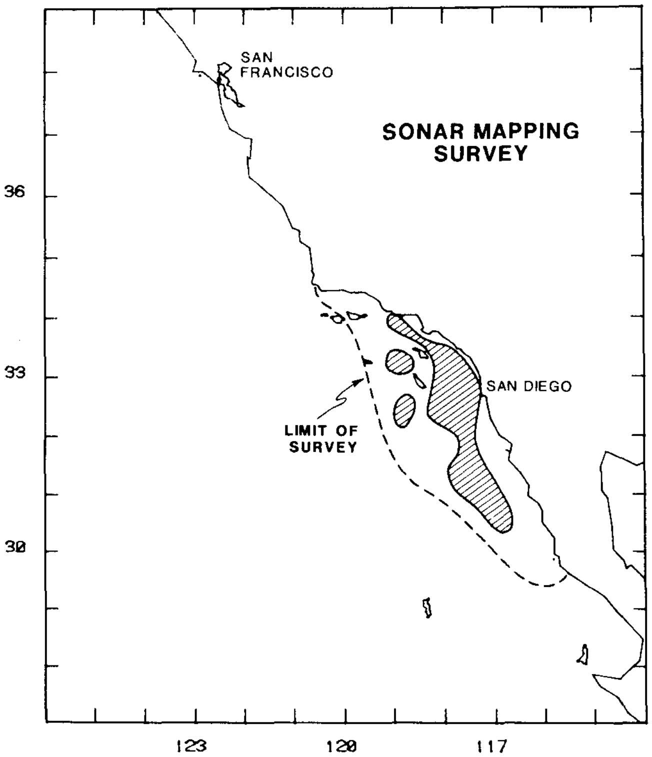

Figure 3. Geographic areas of heaviest anchovy concentration as mapped by sonar (K. Mais, CDF&G). The general distribution matches those of eggs and adults obtained by direct sampling.

Anchovy eggs were distributed along the northern Baja California coast and in the Southern California Bight as far north as the Santa Barbara Channel Islands (Figure 1). As in previous years, the geographic pattern of spawning was correlated with the pattern of surface temperature isotherms (Lasker et al. 1981). Spawning did not occur in water colder than 14°C south of Point Conception, although this is not considered a lethal temperature. Cold water was observed as a large plume extending southeastward from Point Conception into the Southern California Bight and immediately adjacent to the northern Baja California coastline (Figure 1). A much smaller area of spawning was sampled between Monterey and San Francisco Bays in 11-12°C water.

The geographic distribution of positive trawl samples agrees with the distribution of eggs (Figure 2). Adult fish were caught in the Southern California Bight, along the northern Baja California coast, and between Monterey and San Francisco. Adults were not caught in trawls taken in the Santa Barbara Channel and immediately adjacent to the northern Baja California coastline.

The geographic distribution of fish schools as detected by sonar agrees with the distribution of eggs and positive trawls (Figure 3). The area of heaviest anchovy concentration extends along the northern Baja California coastline (approximately 50 km offshore) and into the inshore portion of the Southern California Bight as far north as the Santa Barbara Channel Islands. Two smaller areas of heavy concentration were mapped in the offshore portion of the Southern California Bight.

In summary, northern anchovy, in the spring of 1982, were distributed continuously in the Southern California Bight from the Santa Barbara Channel Islands south to Cape Colnett. A second group was distributed between Monterey and San Francisco bays. In both groups fish were spawning, thus facilitating the use of reproductive surveys to estimate adult biomass.

EGG PRODUCTION ESTIMATE

Estimation Equation

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

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

where B = spawning biomass (MT),

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

W = average weight of mature females (grams),

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

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

S = fraction of mature females spawning per day,

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

k = conversion factor for grams to metric tons.

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

$$\begin{aligned} \mathrm{Var}\,(B) &\cong B^2 \times \\ &\left\{ \frac{\mathrm{Var}\,(P_o)}{P_o^{\,2}} + \frac{\mathrm{Var}\,(W)}{W^2} + \frac{\mathrm{Var}\,(R)}{R^2} + \frac{\mathrm{Var}\,(F)}{F^2} + \frac{\mathrm{Var}\,(S)}{S^2} + \right. \\ &2\left[\frac{\mathrm{Cov}\,(P_oW)}{P_oW} - \frac{\mathrm{Cov}\,(P_oR)}{P_oR} - \frac{\mathrm{Cov}\,(P_oF)}{P_oF} - \frac{\mathrm{Cov}\,(P_oS)}{P_oS} - \frac{\mathrm{Cov}\,(WR)}{WR} - \right. \\ &\left.\left. \frac{\mathrm{Cov}\,(WF)}{WF} - \frac{\mathrm{Cov}\,(WS)}{WS} + \frac{\mathrm{Cov}\,(RF)}{RF} + \frac{\mathrm{Cov}\,(RS)}{RS} + \frac{\mathrm{Cov}\,(FS)}{FS} \right] \right\}. \end{aligned} \tag{2}$$

Daily Production of Eggs in the Sea

The parameter P_o, the daily production of eggs in the sea, is the number of eggs spawned per night, per unit area, averaged over the range and duration of the survey. An ichthyoplankton survey is used to sample anchovy eggs to provide data on the density of the eggs by age. An exponential mortality model is then fit to the data, and the time-zero intercept of the fitted function is the estimate of egg production.

The sampling design of the survey is two-stage sampling with postsurvey stratification. The first stage is a systematic sample of block areas. The total area of the survey is divided into 4 × 20- (or 4 × 10-)nm blocks. The second stage is the selection of a 0.05-m^2 sampling unit in the center of the block (Stauffer and Picquelle[2]). This sampling design assumes that the distribution of eggs within one block is independent of the distribution within adjacent blocks. This assumption is based on experimental data showing that 4 miles is sufficient distance to ensure a negligible autocorrelation (P. Smith, pers. comm.). Advantages of this sampling plan are convenient and efficient use of ship time, even coverage of the total sample area, and improved precision of abundance estimates by maximizing the heterogeneity between adjacent sampling units (Jessen 1978).

Because of time and budget constraints, the sampling intensity was decreased in regions where fewer eggs were expected to be found. In the two 1981 surveys and the 1980 survey, the majority of the anchovy population was found in the Southern California Bight; a narrow band of eggs was typically found off Baja California; and very few eggs were collected off the central California coast. Therefore, the sampling fraction in the bight is increased to one sample per 4 × 10-nm block; elsewhere there is one sample per 4 × 20-nm block. To compensate for the uneven sampling intensity, each station is assigned a weight, w_{ij}, that is proportional to the relative area that the *j*th station represents in the *i*th stratum.

The total survey area is divided into two strata in order to reduce the variability about the egg abundance estimates. The geographic area of the survey is specified without knowing the actual area that the anchovy stock is currently occupying. Therefore, a portion of the surveyed area is beyond the range of the stock, contributing a large number of zero stations, which potentially inflates variance estimates. After the data are examined, a boundary for the current anchovy habitat can be drawn. The boundary is determined by following each line seaward until the last positive tow was taken. Thus all stations seaward of the boundary are zero, and all positive stations are shoreward of the boundary, along with many imbedded zero stations. The area within the boundary is allocated to stratum 1, and the area outside the boundary is put into stratum 0.

	Stratum 1	*Stratum 0*	*Total*
Area (nm^2)	24,190	35,039	59,229
Number of samples	396	596	992

Because the strata can be defined only after the data are collected, this technique is called postsurvey stratification. The area of each stratum, A_i, is not predetermined, so A_i is a random variable, and all variance estimates must be adjusted to include this source of variation (Jessen 1978).

The anchovy eggs from each sample are counted and staged according to the degree of embryonic development. The eggs are then classified into one-day age intervals based on the time of collection, surface water temperature, developmental stage, and laboratory-determined development rates. The ages are then further refined by adding the portion of a day that has elapsed between 2200 (the assumed time of spawning[3]) and the time of collection. This aging procedure is facilitated by the fact that eggs in a particular sample are either spawned on the same evening, or are separated by one-day increments, thus making it easier to separate the modes of egg abundance over stages into one-day age groups. Sea-surface temperatures for the majority of the cruise ranged between 13° and 17°C with an egg-weighted average of 14.9°C. At this temperature, eggs begin to hatch after 2.91 days. Eggs less than 2.67 days old were used in the analysis.

The daily production of eggs, P_o, and its variance are then estimated by regressing the counts of eggs on their age, using the exponential mortality model:

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

where P_{ijk} is the number of eggs in the *k*th day age category from the *j*th station in the *i*th stratum; t_{ijk} is the age in days measured as the elapsed time from the time of spawn for the *k*th day category eggs to the time of sampling of the *j*th station in the *i*th stratum; P_{oi} is the daily production of eggs per unit area (0.05 m^2) in stratum *i; Z* is the daily rate of instantaneous egg mortality; and ϵ_{ijk} is the additive error term. This model assumes that all eggs are spawned and fertilized each day at time 2200, and eggs have a constant positive rate of instantaneous mortality[4].

The mortality function (equation [3]) is fit to the data by regressing the aged egg counts $\{P_{ijk}\}$ on their age $\{t_{ijk}\}$ for stratum 1 with a weighted nonlinear

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[2] See footnote 1 on page 16.

[3] See footnote 1 on page 16.

[4] See footnote 1.

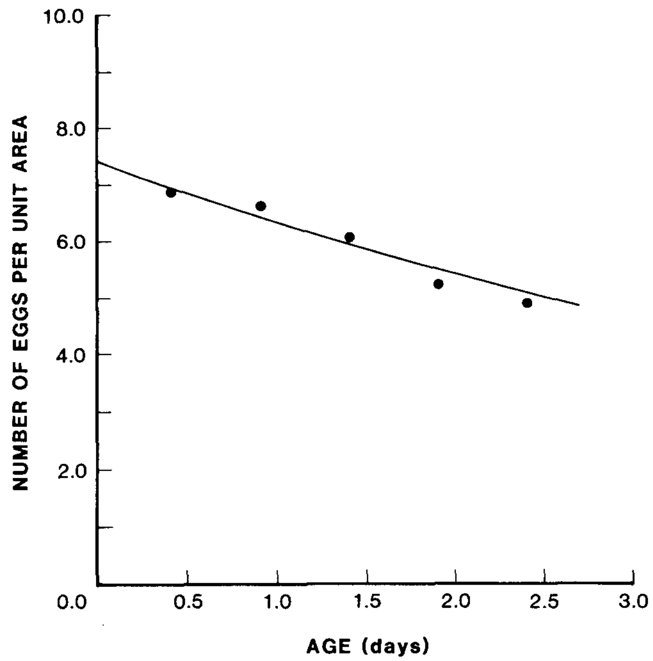

Figure 4. Mean egg production per 12-hour interval for stratum 1 is plotted against age in days. The exponential mortality model was estimated by regressing the individual egg counts on age.

least squares routine using a pseudo-Gauss-Newton algorithm (Dixon and Brown 1979). The individual weighting factors are the station area weights, $\{w_{ij}\}$. The resulting estimate of P_{oI} is 7.40 eggs per day per 0.05 m^2, and Z is 0.158 per day with variances 1.25 and 0.0110, respectively. A plot of the mean egg production per 12-hour interval and the estimated regression for stratum 1 are shown in Figure 4.

The final stratified estimate of P_o is the weighted average of the two strata where the strata weights u_i are proportional to A_i, the area of the ith stratum. P_{oi} for stratum 0 is zero by definition, thus:

$$u_i = \frac{A_i}{A_I + A_O}$$

$$P_o = u_I P_{oI} + u_O P_{oO} = u_I P_{oI}, \qquad (4)$$

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

$$\widehat{\text{Var}}(P_o) = (1 + \frac{1}{n}) \Big[\sum_{i=1}^{2} u_i (\widehat{\text{Var}}(P_{oi}) \Big] \qquad (5)$$

where n is the total number of observations = 992; $\widehat{\text{Var}}(P_{o1}) = 1.25$ is estimated from the regression (3) for stratum 1, and; $\widehat{\text{Var}}(P_{o0}) = 0$ by definition.

The stratified estimate of P_o is 3.023 eggs per day per 0.05 m^2 for the entire survey area, with an estimated variance of 0.5119 and coefficient of variation of 23.67%. This estimate of P_o applies over the 59,299-nm^2 area of the survey ($A = 4.068 \times 10^{12}$ area units of 0.05 m^2 each).

Adult Parameters **W, F, S,** *and* **R**

The parameters W, F, S, and R are estimated from samples of adult anchovies collected by the midwater trawl survey. The sampling design consists of three stages: (1) placement of trawl stations, (2) trawl catch, and (3) subsample of fish. The statistical technique of judgment sampling is used in selecting the location for the trawls in order to achieve a high proportion of positive trawls. Station locations were selected where concentrations of anchovies were detected by the occurrence of anchovy eggs or larvae in the plankton samples, and the presence of apparent schools on the sonar (Figures 1, 2, and 3). Because more stations are selected where heavy concentrations of anchovies are suspected, the sample design follows the precepts of probability sampling (Cochran 1963).

One trawl is taken at each selected location, and the trawl catch is assumed to be a random sample of fish at the station. Each station is given equal weight by subsampling an equal number of fish from each trawl, m^*. This is appropriate if the probability of choosing a station is exactly proportional to the number of anchovies at the station; however, these probabilities are impossible to enumerate, so that the actual sampling design is only an approximation of the ideal design (judgment sampling rather than probability sampling). If the trawl catch size were a good measure of the abundance of fish at the station, this information could be used to improve the approximation of the ideal sample design. However, trawl catch size and abundance of fish are unrelated for anchovies; catch size depends more on the depth of the school, the avoidance of the net by the fish, and luck. This conclusion is supported by the historical lack of agreement between trawl catch size and the factors that indicate concentrations of anchovies (sonar detection, eggs and larvae in plankton samples).

Even though equal subsample sizes are attempted, they are not always attainable: the catch may have few mature females, or the catch may be extremely small. In these cases the stations should receive less weight to compensate for the error in judgment sampling; if there are few mature females in the catch then it is assumed that there are few mature females at the station, and if the catch is very small then it is assumed that the actual number of anchovies at the station is relatively small. Thus, each station is given a weight of the relative subsample size.

The estimates and variances, ($\bar{\bar{y}}$) and var($\bar{\bar{y}}$), of the four parameters—*W, R, F,* and *S*—are the weighted sample mean and sample variance (Cochran 1963)

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

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

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

The method described by equations (6) and (7) is used in the succeeding sections to estimate parameters *W, F, S,* and *R* and their respective variances.

Average Female Weight

The average female weight, *W*, is calculated as the weighted average of W_{ij}, the weight of the *j*th mature female from trawl *i*, using equation (6). The weight of females with hydrated eggs in their ovaries is temporarily inflated because of water retention, therefore their weight is adjusted using the regression of whole-body weight on ovary-free weight estimated from females that do not have hydrated eggs,

$$\hat{W}_{ij} = -0.0701 + 1.06\, W_{ij}^{*} \qquad (8)$$

where W_{ij}^{*} is the ovary-free weight; the regression has an $r^2 = 99.6\%$. The desired subsample size is $m^* = 15$ mature females. The estimated average female weight is 18.83 g with a variance of 0.1319 (equation [7]) and coefficient of variation of 1.93%. The mode of the frequency distribution of $\bar{W}_i$, the average weight of mature female anchovies in the *i*th trawl, is at 19 g (Figure 5).

Batch Fecundity

For the estimate of batch fecundity, *F*, the individual observations, F_{ij}, are not observed directly but are estimated from a relationship between batch fecundity and ovary-free weight. This relationship is estimated from a sample of 109 hydrated females that were collected over the duration of the cruise. These hydrated females have a distribution of adjusted weights (equation [8]) similar to the weight distribution of females for the whole cruise (Figure 6). A linear regression of fecundity on weight was selected because the fitted exponent for the power function was not significantly different from one, indicating that any curvature present in the data is

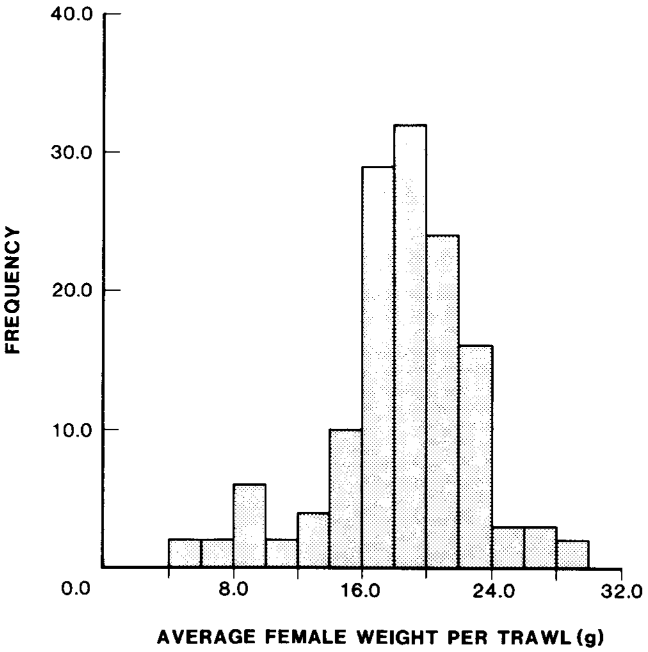

Figure 5. The frequency distribution of the average weight of mature females per trawl.

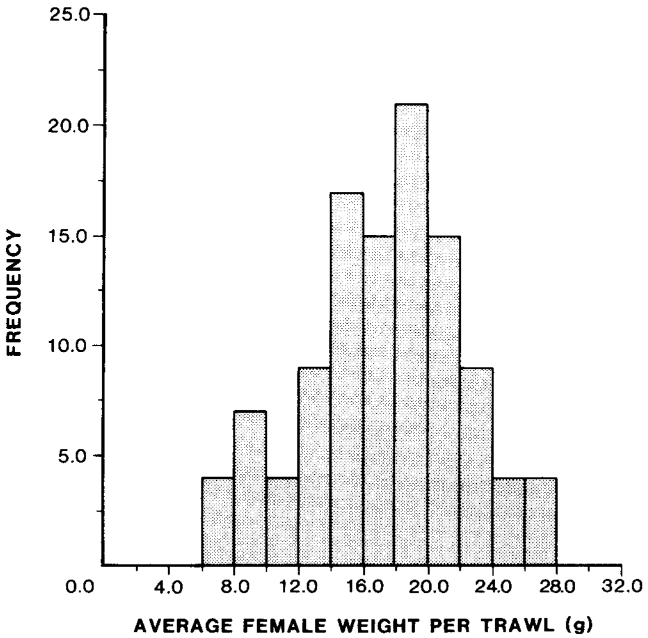

Figure 6. The frequency distribution of whole body weights for the hydrated females used in regression (9). The weights of the hydrated females were adjusted to nonhydrated weights using regression (8). The frequency distribution of adjusted weights is similar to that of the average weights of mature females (Figure 5).

very slight. The selected regression model is

$$\hat{F}_{ij} = -179.7 + 617.2\, W_{ij}^{*} \qquad (9)$$

with an $r_2 = 52.4\%$ (Figure 7).

Based on this regression, the F_{ij} are estimated for each of the $m^* = 15$ mature females from each trawl. Estimated average batch fecundity is 10845 (equation [6]), with a variance of 171730 (equation [10]) and coefficient of variation of 3.82%. Because the trawl averages ($\bar{F}_i$) are not based on actual observations, but are estimates with their own variance, the variance estimate for F includes this additional source of variation (Draper and Smith 1966):

$$\widehat{\mathrm{Var}}\,(\bar{\bar{F}}) = \sum_{i=1}^{n} \qquad (10)$$

$$\frac{\left(\frac{m_i}{\bar{\bar{m}}}\right)^2 \left[\frac{(\bar{F}_i - \bar{\bar{F}})^2}{n-1} + \frac{S_h^2}{109} + (\bar{W}_i^* - \bar{W}_h^*)^2\, \widehat{\mathrm{Var}(b)}\right]}{n}$$

where $S_h{}^2 = 6658675$ is the variance about the regression (9); $\bar{W}_i{}^*$ is the average ovary-free weight for the ith trawl; $\bar{W}_h{}^* = 16.54$ is the average ovary-free weight for the 109 hydrated females; $\hat{\mathrm{Var}}(b) = 3172$ is the variance of the slope of regression (9); and $n = 135$ positive trawls.

Specific fecundity, expressed as eggs per gram of whole-body weight, is similar to those observed in 1981.

Year	1980	1981	1981	1982
Survey	8003/4	8102	8104	8202
Mean weight (g)	17.4	13.4	16.2	18.8
Eggs/gram	444.4	623.0	546.0	575.9

Spawning Fraction

Spawning fraction, S, is estimated from $m^* = 15$ mature females, and $S_{ij}^{1} = 1$ if the ovary of the jth mature female in the ith trawl is classified as having day-1 postovulatory follicles (day-1 spawners), and $S_{ij}^{1} = 0$ otherwise (see Hunter and Macewicz 1980 for histological definition of day-1 and day-0 spawners). Thus $\bar{S}_i^1$ is the proportion of mature females in the ith trawl that are in the day-1 spawning category (S^1).

Another measure of spawning activity is the proportion of mature females that are classified as day-0 spawners, S^0. In past surveys, it has been suspected that the proportion of day-0 females is a biased estimate because of oversampling of females that spawn on the night of capture. This was indicated by a large discrepancy between S^1 and S^0, with the deviation between these two measures reaching a maximum during the peak hours of spawning. There was also a co-occurrence of high values of $\bar{S}_i^0$ and low values for sex ratios for trawls taken during these hours, which suggested that males and day-0 spawning females segregate out from other females at the peak hours of spawning at a depth where they are more vulnerable to the midwater trawl[5]. In previous surveys, m_i was adjusted by assuming that the actual number of day-0 females is the same as the observed number of day-1 females.

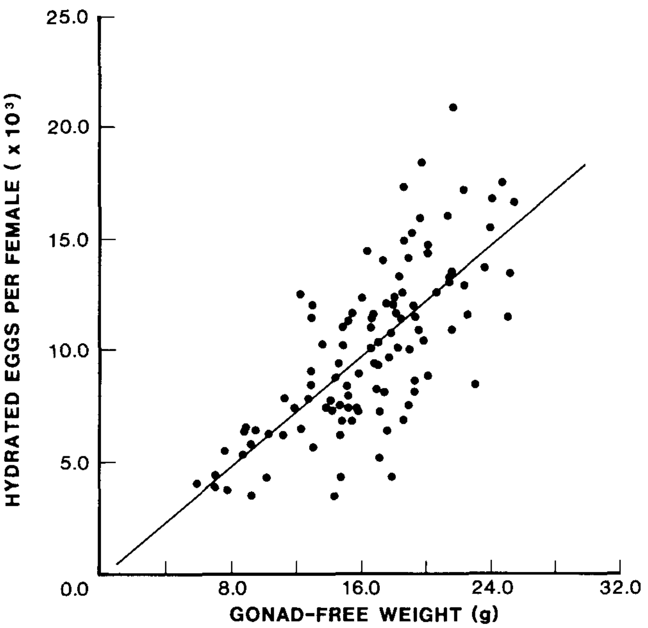

Figure 7. Batch fecundity regressed on ovary-free weight of 109 hydrated females using a linear model (equation [9]).

The apparent oversampling of day-0 females was reduced in this year's data; this may have been due to a slight change in the trawl gear. The difference between S^1 and S^0 is still greatest during the peak spawning time 2200-2259 (Figure 8), and there is still a dip in the sex ratio over the time 2000-2259 (Figure 9), but the discrepancy is very small relative to past years. In fact, the values of S^1 and S^0, 0.120 and 0.127, respectively, are not significantly different from each other. Thus, we concluded that day-0 spawning females were not oversampled this year. Hence, m_i is not adjusted and is simply the number of mature females in the ith trawl. The estimate of spawning fraction is 0.120 (equation [6]) with variance $= 9.47 \times 10^{-5}$ (equation [7]) and coefficient of variation $= 8.13\%$.

Sex Ratio

The parameter R, sex ratio, is the fraction of females in the anchovy stock based on fish weight.

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[5] See footnote 1 on page 16.

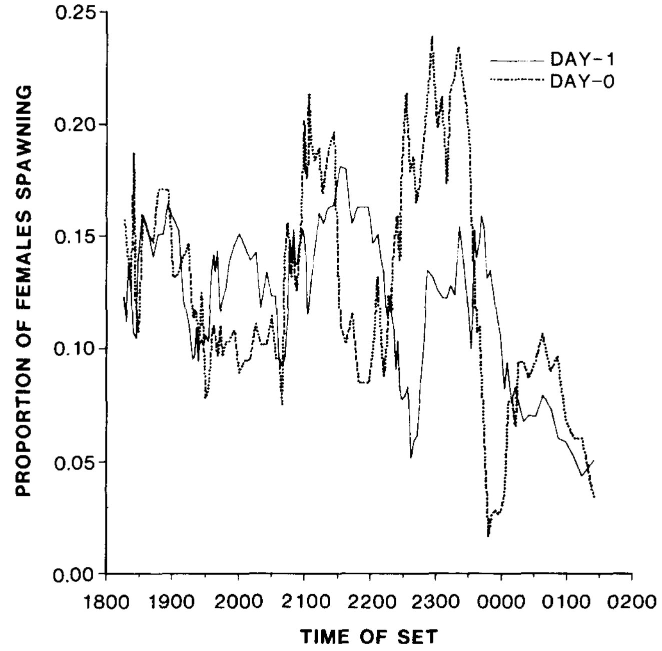

Figure 8. The running averages for S^0 (day-0 spawning fraction) and for S^1 (day-1 spawning fraction) plotted against the time of trawl. The running averages are based on 10 observations. The discrepancy between S^0 an S^1 is largest during the time interval 2200-2259, the peak time of spawning.

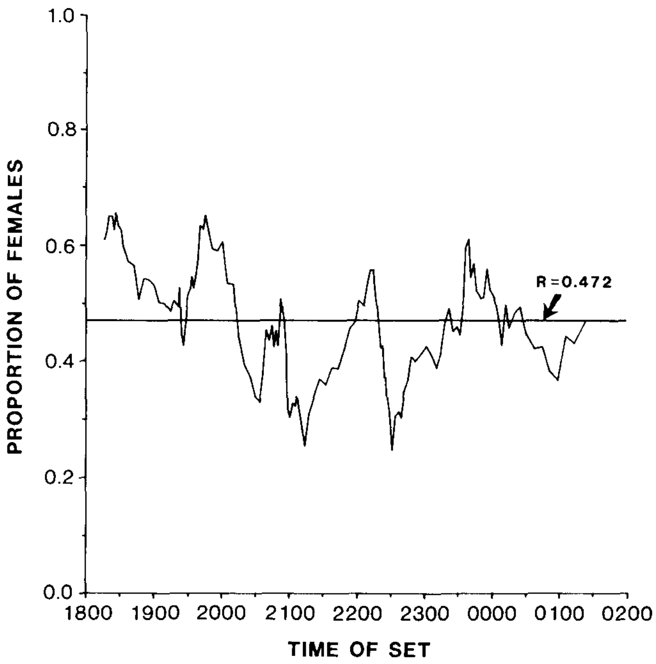

Figure 9. The changes of observed sex ratio with time. The running average for sex ratio is based on 10 observations. The horizontal line is the estimated mean sex ratio.

TABLE 1
Estimates of Egg Production Parameters and Spawning Biomass for 1982

Parameter	Symbol	Mean	Variance	Coefficient of Variation
Egg production (eggs/0.05 m^2-day)	P_o	3.023	0.5119	0.237
Area of survey (0.05 m^2 units)	A	4.068×10^{12}	—	—
Average female weight (grams)	W	18.8	0.132	0.0193
Sex ratio by weight (females/total)	R	0.472	4.90×10^{-4}	0.0469
Batch fecundity (eggs per batch per mature female)	F	10845	171730	0.0382
Fraction of mature females spawning per day	S	0.120	9.47×10^{-5}	0.0813
Spawning biomass (MT)	B_e	378,000	945×10^9	0.257

The sex ratio for each trawl is determined from the first 50 fish. Average weights by sex per trawl are estimated from the first 5 males and the first 20 females, where the weight of hydrated females is adjusted using equation (8). The trawl average, $\bar{R}_i$, is the estimated total weight of the females in the first 50 fish subsampled, divided by the estimated total weight of the first 50 fish. The m_i in equations (6) and (7) for this parameter is the estimated total weight of the first 50 fish. For both sexes, both mature and immature fish are included because of the difficulty of distinguishing between mature and immature males. The estimate for sex ratio is 0.472 (equation [6]), and its estimated variance (equation [7]) and coefficient of variation are 4.90×10^{-4} and 4.69%, respectively.

Biomass Estimate and Variance

The parameter estimates and their variances given above are summarized in Table 1. The resultant estimate of anchovy spawning biomass using equation (1) is 378,000 MT (417,000 short tons). The approximate variance is calculated according to equation (2), where covariance terms are included only for those pairs of variables with sample correlations that are significantly different from zero. The sample correlations between P_o and the adult parameters are assumed to be zero because they are derived from two different surveys (the plankton survey and the trawl survey) and thus cannot be estimated. Of the adult parameters, only cov(W,F), cov(R,W), and cov(F,R) are significant, with values of 110, 0.00271, and 1.57, respectively. The approximate variance of the biomass estimate is 9.45×10^9, and standard error is 97,200 MT, for a coefficient of variation of 25.7%. The approximate 95% confidence interval is ± 194,000 MT.

EQUIVALENT LARVAL CENSUS ESTIMATE OF BIOMASS

The anchovy management plan presently requires that the annual harvest quota for the U.S. fishery be based on an annual estimate of spawning biomass (Smith 1972; Huppert et al. 1980). The PFMC has interpreted the plan to require an equivalent larval census biomass estimate. The 1982 survey was designed to generate an estimate of the biomass based on the egg production and fecundity of the population, but was not designed to directly generate a larval census estimate of biomass.

It is possible to generate an equivalent larval census estimate of biomass by estimating the number of larvae resulting from the measured production of eggs (Stauffer 1983). To do so, the mortality rates of both eggs and larvae are required. The abundance of larvae can then be extrapolated to an annual census using historical proportions of quarterly abundances. The spawning biomass is assumed to be proportional to the annual census; the constant of proportionality was determined from a regression of adult sardine biomass on the annual census of sardine larvae, and an assumption of sardine to anchovy annual fecundity of 1:2 (Smith 1972).

During the 1982 egg production cruise, 96 plankton samples were obtained using the bongo net at standard CalCOFI stations (Figure 10). Anchovy larvae were found at 69 of the stations. In the following sections we discuss: (1) the production curve of the larvae derived from the size-specific catch curve; (2) an equivalent annual larval census derived from the population production of eggs and the subsequent mortality of both eggs and larvae; and (3) the discrepancy between the egg production estimate of biomass and the equivalent larval census estimate.

Production Curve

The larvae were grouped into 12 size categories (yolk-sac to 15 mm), and catches were adjusted for variations in the volume of water filtered per m of depth. Bias corrections were also applied for extrusion of small larvae through the meshes of the net and avoidance of the net by large larvae. The adjusted catches were divided by the duration of growth, through each size class, to estimate the age-specific production of larvae (P_t). The adjustments were accomplished by fitting a weighted negative binomial model to the sample frequency distributions of each size class. Each observation is weighted by a factor that is the product of the various adjustments, and the means of the final distributions are unbiased estimates of production (P_t). The procedure was developed in a series of papers: Bissel 1972; Zweifel and Smith 1981; Hewitt 1981, 1982; Hewitt and Methot 1982; Hewitt and Brewer 1983. The calculations are summarized in Table 2, and the results are described in Figure 11.

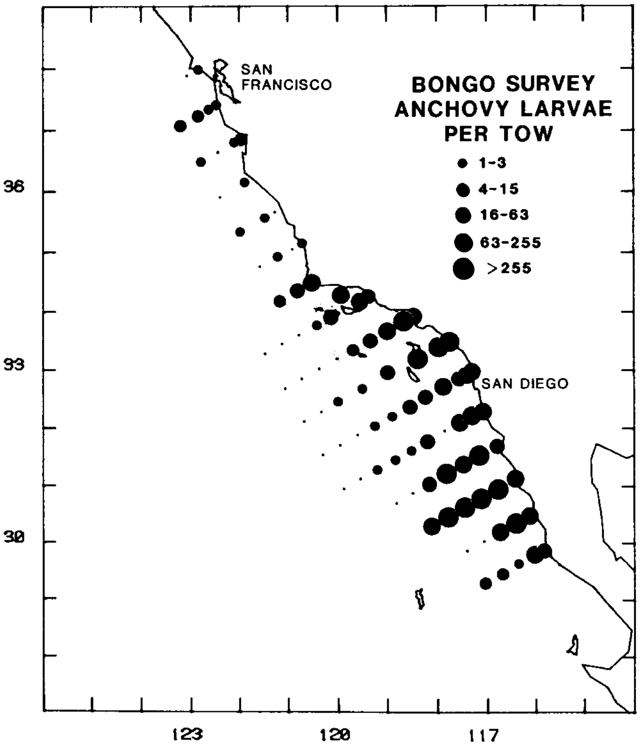

Figure 10. Geographic distribution of anchovy larvae as determined from standard CalCOFI ichthyoplankton bongo tows taken at 96 stations during the 1982 egg production survey.

It is clear, from a log-transform plot, that a constant mortality model, $dp/dt = -cP$ will not adequately describe the data. A variable mortality model may be devised by defining c as a function of age.[6] Several forms would adequately describe the data, but for reasons of mathematical tractability we may use:

$$\frac{dP}{dt} = -\frac{\beta}{t}P . \qquad (11)$$

As t increases, the instantaneous rate of change of production decreases (improving survival with age). The above expression may be rearranged, integrated, and the integration constant determined at the age of hatching (t_h):

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

---

[6] Variable mortality rate may be defined as a function of age, size, or population abundance. The important point is that the number of deaths is modeled as a portion of those living. N. Lo, SWFC, suggested the form used here.

TABLE 2
Size-Specific Catches of Anchovy Larvae and Age-Specific Estimates of Daily Production

Preserved size (mm)	Fraction retained by net[1]	Average adjustment for sampling and sorting variability[2]	Average duration of growth[3] (days)	Average catch $\left(\frac{\text{larvae}}{\text{tow}}\right)$	P_t[4] $\left(\frac{\text{larvae}}{\text{m}^2\text{-day}}\right)$	Age[3] since fertilization (days)
2.50	0.21	1.91	3.59	29.99	20.82	4.42
3.75	0.51	1.99	3.51	26.91	7.56	8.00
4.75	0.69	1.98	2.58	16.91	4.80	11.07
5.75	0.73	2.18	2.38	12.12	3.20	13.62
6.75	0.73	2.18	2.24	8.93	2.51	15.74
7.75	0.68	2.20	2.16	6.75	2.09	18.13
8.75	0.61	2.22	2.12	5.10	1.78	20.24
9.75	0.60	2.09	2.11	3.38	1.28	22.67
10.75	0.54	2.86	2.12	1.70	0.52	24.92
11.75	0.56	2.27	2.14	1.06	0.39	27.01
12.75	0.46	1.75	2.19	0.51	0.29	28.88
13.75	0.57	2.11	2.29	0.33	0.12	31.93

[1] Extrusion corrections are based on relative retention rates between 75-micrometer and 505-micrometer mesh nets (Lo, SWFC pers. comm.) Avoidance corrections are based on night and day catch comparisons using bongo data from 1978 and 1979 (Hewitt and Methot 1982). Fraction of larvae retained in the net is estimated as Σ col. 5/Σ (col. 5/col. 2); $r = 0.4$.

[2] Accounts for partial sorting of samples and standardizes sampling volume to 1 m^2 per m of depth.

[3] Temperature-dependent embryonic growth is determined from laboratory experiment (Lo, SWFC pes. comm.), and post-yolk-sac growth follows Methot's (1981) description.

[4] Production rates (P_t) may be estimated by dividing the average catch by the product of columns 2, 3, and 4. In practice, however, P_t is the mean of a weighted negative binomial model fit to the distribution of individual observations (ie., plankton tows).

This expression defines the larval production curve. The average standing stock of larvae is the area under the curve, and it may be determined by integrating the above expression between t_h and 30 days (the maximum age effectively caught with a standard plankton tow). Thus:

$$N = A \int_{th}^{30} Ph \left(\frac{t}{th}\right)^{-\beta} dt$$

$$= A \frac{Phth}{\beta-1}\left(1 - \left(\frac{th}{30}\right)^{\beta-1}\right) \qquad (13)$$

where N is the average standing stock of larvae and A is the area of the survey.

Equivalent Annual Larval Census

An equivalent larval census estimate of biomass may be derived by reducing the production of eggs to the production of hatching larvae via egg mortality and then integrating the larval production curve over age to estimate average standing stock of larvae. The average standing stock is converted to the annual larval census by a factor[7] of 2.12. The standard sampler would retain a fraction (r) of these larvae; the remainder are extruded through the meshes, and a small portion avoid capture. Finally, the annual larval census is converted to spawning biomass using the historical conversion factor of 8.9 × 10^{-8} MT/larva. Thus:

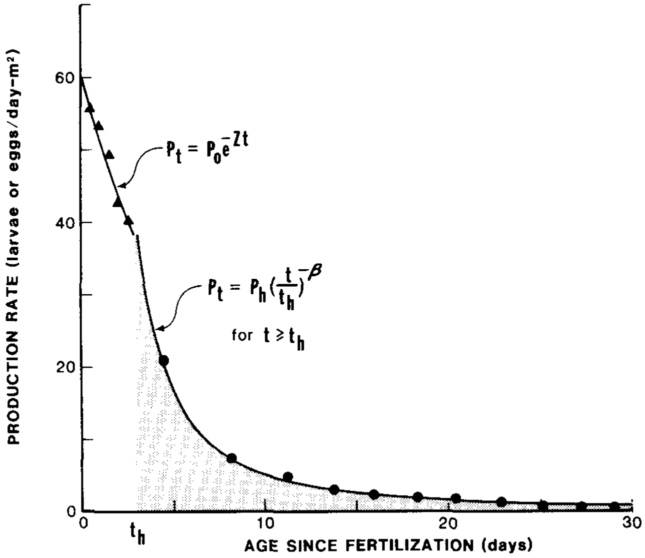

Figure 11. Changes in the production rate of eggs and larvae with time since fertilization. Production of eggs (triangles) was estimated from the CalVET sample, and the production of larvae (dots) was estimated from the CalCOFI bongo sample. The shaded area under the larval production curve is the average standing stock of larvae (*N*).

$$\hat{B}_l = N(2.12)\, r(8.9 \times 10^{-8}) \qquad (14)$$

where: r = fraction of larvae retained in standard sampler,

$P_hA = P_0As$

$$N = P_0As\left(\frac{th}{\beta-1}\right)\left(1 - \left(\frac{th}{30}\right)^{\beta-1}\right)$$

---

[7] The annual larval census is the sum of the average standing stock in each quarter. Stauffer and Picquelle (1980) describe the historical proportions of the quarterly values as 1/1/.06/.06, so that the annual larval census is equal to 2.12 times the average standing stock over the first 2 quarters.

TABLE 3
Projected and Observed Larval Census Estimates of Spawning Biomass and Related Parameters

	1980	1981		1982
		Feb.	Apr.	
Population production P_oA of eggs (eggs/day)	23.97×10^{12}	19.07×10^{12}	11.46×10^{12}	12.30×10^{12}
Egg mortality rate z	0.453	0.138	0	0.158
Time to hatch (days) t_h	2.71	2.75	2.75	2.91
Survival to hatch $s = e^{-zt_h}$	0.293	0.684	1.000	0.631
Coefficient in larval mortality β model	1.7999	1.7058	1.7058	1.7085
Retention r	0.4	0.4	0.4	0.4
Projected larval census B_l estimate of spawning biomass (MT)	1.533×10^6	3.126×10^6	2.746×10^6	1.866×10^6
Larval census estimate of B_l spawning biomass (MT)	1.611×10^6	2.544×10^6	2.544×10^6	—
Daily fecundity $\left(\frac{\text{eggs/day}}{\text{ton}}\right)$ q	30.28×10^6	33.03×10^6	33.84×10^6	32.53×10^6

and P_hA is the population production of hatching larvae, P_OA is the population production of eggs, s is the fraction of egg production surviving to hatch, and $\hat{B}_l$ is the equivalent larval census estimate of spawning biomass (MT).

When equation (14) was applied to 1980 and 1981 surveys, which generated both egg production and larval census estimates, the larval census was similar to that estimated from the production of eggs (average ratio = 1.09; range 0.95 to 1.23; Table 3). By rewriting equation (1) as:

$$B_e = \frac{P_OA}{q}$$

where B_e is the egg production estimate of spawning biomass, P_OA is the daily population production of eggs, and q is the daily fecundity on a weight basis $= RFS/kW$, we may relate the equivalent larval census estimate of biomass ($\hat{B}_l$) to the egg production estimate of biomass (B_e) using equation (14):

$$\hat{B}_l = B_e\, qs \left(\frac{t_h}{\beta-1}\right)\left(1-\left(\frac{t_h}{30}\right)^{\beta-1}\right) r\,(18.9 \times 10^{-8}). \quad (15)$$

Thus the equivalent larval census estimate of spawning biomass may be calculated from the egg production estimate of biomass by adjusting the latter for fecundity, egg survival, larval survival, and larval retention in the standard ichthyoplankton sampler historically used for larval census estimates. Because the larval census estimate of biomass assumes a fixed fecundity, $\hat{B}_l$ may be calculated from the population production of eggs, without consideration of the adult reproductive parameters, using equation (14).

Equation (14) was applied to the data presented in this report; the parameter values are listed in Table 3. The 1982 equivalent larval census estimate of spawning biomass is 1.866×10^6 MT (2.060×10^6 short tons); the equivalent annual larval census is $20{,}966 \times 10^9$ larvae.

Discrepancy between the Biomass Estimates

The equivalent larval census estimate of spawning biomass (1.866×10^6) is nearly five times the egg production estimate of spawning biomass (0.378×10^6 MT). One or more of three factors may be the cause of this discrepancy: (1) sampling errors between the ichthyoplankton gears; (2) variability in the conversion factor relating the larval census to the spawning biomass (resulting from variability in the population fecundity and survival of young, which are assumed to be constant in the larval census method); and (3) systematic inaccuracy in the conversion factor relating anchovy larvae to anchovy spawners.

The projected abundance of larvae and the measured abundance of larvae agree reasonably well for three surveys (Table 3). This indicates that the two sampling gears (CalVET net, used to sample eggs, and the CalCOFI bongo net, used to sample larvae) yield consistent and compatible estimates of ichthyoplankton production. It is possible to predict the catch of one gear from the catch of the other. The discrepancy between the biomass estimates is thus not due to inaccuracy or imprecision in the ichthyoplankton sampling.

The population fecundity and survival of larvae did not vary considerably among the three surveys (Table 3). Egg survival, however, did vary, ranging from an estimated 29% survival in 1980 to 100%

TABLE 4

Adjustment of Larval Census Estimates of Spawning Biomass for Variability in Egg Survival

Year	1980	1981		1982
		Feb.	Apr.	
S	0.293	0.684	1.000	0.631
B_e	792×10^3	577×10^3	339×10^3	378×10^3
B_l	1611×10^3	2544×10^3	2544×10^3	1866×10^3
$\frac{0.650}{S}$	2.218	0.950	0.650	1.030
Adj. B_l	3573×10^3	2417×10^3	1654×10^3	1922×10^3
$\frac{\text{Adj. } B_l}{B_e}$	4.5	4.2	4.9	5.1
$\frac{0.300}{S}$	0.977	0.439	0.300	0.475
Adj. B_l	1574×10^3	1117×10^3	763×10^3	886×10^3
$\frac{\text{Adj. } B_l}{B_e}$	2.0	1.9	2.3	2.3
$\frac{1.000}{S}$	3.412	1.462	1.000	1.585
Adj. B_l	5498×10^3	3719×10^3	2544×10^3	2957×10^3
$\frac{\text{Adj. } B_l}{B_e}$	6.9	6.4	7.5	7.8

survival in April 1981. Low egg survival implies that a low larva-to-spawner ratio actually existed and that spawner biomass was underestimated relative to surveys where egg survival was high. To investigate this effect, we assumed that an egg survival rate of 65% prevailed during all the surveys, and we proportionally adjusted the larval census estimates of spawning biomass (Table 4). The adjusted larval census estimates of spawning biomass are consistently 4 to 5 times greater than the egg production estimates of spawning biomass, indicating a systematic bias. If we assume an egg survival of 30%, the ratio decreases to 2; whereas an egg survival of 100% implies that the larval census overestimates spawning biomass by a factor of 7 (Table 4). Thus by considering variability in egg survival we have shown that the discrepancy between the two biomass estimates can be reconciled by a single factor for all the surveys.

Finally, we consider the conversion factor relating the annual census of anchovy larvae to anchovy spawners. This factor was determined for the sardine by regressing virtual population estimates of the adult stock on the annual sum of quarterly larval census estimates (Smith 1972). The proportionality was extended to the anchovy by estimating the relative annual fecundity (anchovy: sardine) to be 2 (Smith 1972); i.e., each anchovy larva represented only half the weight of adult fish that a sardine larva did. We demonstrated above that the larval census estimate of biomass (when adjusted for variations in egg survival) exceeds the egg production estimate of biomass by a fixed factor. We suggest that this bias results from inaccuracy in the anchovy/sardine relative annual fecundity (on a weight basis). The average of the four observations of egg survival is our best estimate of the long-term average egg survival (65%); use of this value implies that the relative fecundity is approximately 4.5 times the previously accepted value. We suggest that the anchovy spawns approximately 9 times as many eggs per gram throughout the year as does the sardine. This may be explained by increasing the batch fecundity per gram and shortening the interval between spawnings (these relationships between the reproductive parameters of anchovies and sardines have been observed in Peru by P. Smith [pers. comm.]).

Thus the discrepancy between the larval census estimates and the egg production estimates of spawning biomass can be explained by variation in egg survival and inaccuracy in estimating the average proportionality between the larval census and the spawning biomass. We further consider the egg production method to be more precise (because it considers the rate at which eggs die) and more accurate (because of the underestimate of anchovy fecundity) than the larval census method.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

IDYLLWILD, CALIFORNIA

OCTOBER 26, 1982

THE LARGER PELAGIC FISHES OF THE CALIFORNIA CURRENT

Since 1978 CalCOFI has been expanding its scope to include a wider range of biological and oceanographic investigations. Before 1978, CalCOFI was constrained by its charter to examine causes of variability in the "wetfish" (anchovy, sardine, etc.) fisheries. It is only slight exaggeration to say that all previously necessary knowledge of higher predators could be summarized in a single anchovy statistic: natural mortality rate.

In 1978, the CalCOFI Symposium examined "The Nonconsumable Living Resources of the California Current." That symposium gave particular emphasis to seabirds and marine mammals as apex predators. The present symposium complements the earlier one, and examines the larger fishes, which also are apex predators. These two symposia will help form the basis for an emerging perspective of the California Current as an ecosystem. It is only with such a broad perspective that CalCOFI will be able to fulfill its goal of understanding the nature and variability of the California Current.

Alec D. MacCall, Convenor

PACIFIC MACKEREL: A RESURGENT RESOURCE AND FISHERY OF THE CALIFORNIA CURRENT

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ABSTRACT

The Pacific mackerel, *Scomber japonicus*, supported one of California's major fisheries during the 1930s and 1940s but by the mid-1960s was a depleted stock. After a decade of virtual economic extinction, a series of successful spawns in the mid-1970s restored the fishery to levels of the early 1940s.

Subsequent to the collapse, regulation efforts culminated in the first Pacific mackerel management measure—a commercial fishing moratorium. Fishery and management developments during the years of resurgence were complicated by the incidental catch of Pacific mackerel in the jack mackerel fishery and by the difficulty of accurately assessing the biomass of Pacific mackerel. The rationale behind measures adopted for managing a recovered rather than a recovering resource is discussed.

RESUMEN

La caballa, *Scomber japonicus*, ha mantenido desde 1930 una de las pesquerías más importantes de California durante dos décadas; pero a mediados de la década de 1960-1970, sus poblaciones disminuyeron notablemente, y después de diez años de extinción virtual, sobrevinieron épocas de buena reproducción con supervivencia larval elevada, dando por resultado que, a mediados de la década entre 1970 y 1980 las poblaciones de caballa llegaron a alcanzar los niveles de principios de la década de 1940-1950.

Al decaer la pesquería, los esfuerzos regulatorios culminaron con la primera reglamentación prohibiendo la pesca comercial de esta especie. La reglamentación y pesca durante el período de resurgencia resultaba complicada, debido a que la caballa se capturaba también durante la pesca del jurel (*Trachurus symmetricus*), lo cual dificultaba la estimación exacta de las poblaciones de *Scomber japonicus*. Se discuten las bases para establecer las regulaciones de la pesquería, adoptadas para una reserva que se ha recobrado, y no para poblaciones en período de recuperación.

INTRODUCTION

For a period of almost four decades beginning in the mid-1920s, Pacific mackerel (*Scomber japonicus*) supported one of California's most important commercial fisheries. As canneries developed better processing capabilities and more marketable packs, the small but important fishery of the late 1920s quickly became second only to the Pacific sardine (*Sardinops sagax caeruleus*) fishery in annual landings. Mackerel landings increased to a peak of 73,000 short tons in 1935. Then came a long fluctuating decline to a catch of less than 4,000 tons in 1953. The fishery rebounded in 1954, but landings remained below expectation, averaging less than 17,000 tons per year for the next decade. After 1963 the fishery experienced a quick and dramatic decline; by 1966, for all practical purposes, it ceased to exist (Figure 1). More detailed descriptions of the fishery prior to the 1960s collapse include Fry (1931), Croker (1933, 1938), Roedel (1952), Fitch (1952), Roedel and Joseph (1954), Blunt and Parrish (1969), and Parrish and MacCall (1978).

The precollapse history is devoid of regulations to control the fishery, but not necessarily because of a lack of warnings or management recommendations. The earliest warnings were sounded just subsequent to the peak landing year (Fry 1937; Croker 1938). Later Fitch (1951) concluded that the fishery was not good; closed seasons, overall yearly bag limits, and minimum size restrictions would no doubt help relieve the situation. In 1951 the California Fish and Game Commission (FGC) recommended legislation to empower it to set seasonal limits on both Pacific mackerel and sardines. Similar warnings and management attempts are less apparent during the next decade, but just prior to the eventual collapse, the California Department of Fish and Game (DFG) concluded that the outlook was not bright and the population was at a low level (Anonymous 1961).

After the collapse, management efforts eventually resumed. The first regulations were established in 1970, and the resource and fishery began their respective and rapid recoveries during the late 1970s. By 1979 the total biomass was estimated (Klingbeil 1982) as approximately equivalent to the average biomass, 143,000 tons, for the years 1937-43 (Parrish and MacCall 1978).

The purpose of this paper is twofold: (1) to describe management efforts during the years of depletion, and (2) to document fishery and management developments during the years of resurgence.

[Manuscript received March 17, 1983.]

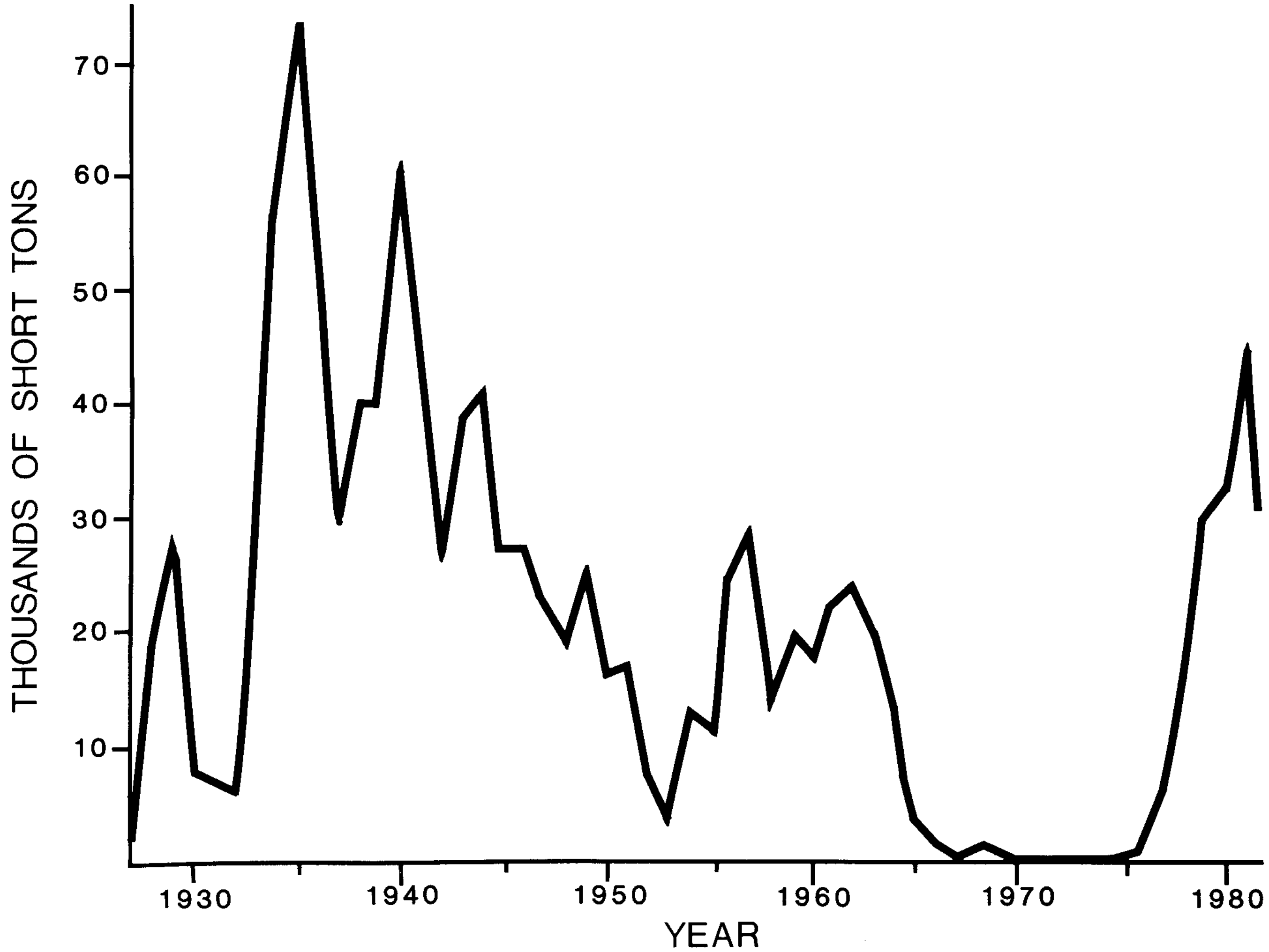

Figure 1. Pacific mackerel landings in California, 1928-82.

MANAGEMENT EFFORTS DURING THE YEARS OF DEPLETION, 1965-75

Although the fishery collapsed in 1965, it was not until 1969 that management legislation was introduced. The exact reasons for this lag are not well documented. Parrish and MacCall (1978) point out that the scientific community was in a politically awkward position at the time, and there is little doubt that a variety of social, economic, and political forces interacted to delay meaningful management.

With the depletion of both Pacific mackerel and Pacific sardines off California completed by the mid-1960s, the fishing industry dependent on these resources became extremely depressed. Government, including both state and federal agencies, and the fishing industry seemed to concentrate their efforts during this period toward developing "replacement" fisheries. The northern anchovy, *Engraulis mordax*, was the major species of interest, and the FGC authorized an anchovy reduction fishery in late 1965. Controversies continued, and administrators, scientists, and commissioners continued to interact frequently, usually amid considerable controversy, as the anchovy fishery and its management slowly evolved. Talbot (1973) and Messersmith (1969) discuss in detail the controversies and problems of managing California's pelagic fisheries during this period.

Meanwhile, warnings of the critical condition of the Pacific mackerel fishery continued (Parrish 1968; Blunt and Parrish 1969). In March 1968 DFG scientists formally presented the problem to fishing industry representatives and raised the question of placing a moratorium on Pacific mackerel. Industry reaction was generally skeptical that overfishing was the cause of the decline or that a moratorium was necessary (Anonymous 1968). At the same meeting the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Steering Committee, consisting of scientists from the DFG, the United States Bureau of Commercial Fisheries (now known as National Marine Fisheries Service), and Scripps Institution of Oceanography offered the following opinion: "The stakes in scientific management are greater than the potential yield of the Pacific mackerel fishery . . . despite scientific evidence attesting to its decline, presented over many years, no action has been taken which might rehabilitate this resource. . . . This prima facie evidence substantiates allegations that the State cannot manage its resources on a scientific basis" (Baxter et al. 1968).

On May 2, 1968, Assembly Joint Resolution No. 26 was passed. It requested the DFG, in conjunction with the Bureau of Commercial Fisheries, to arrange meetings with Mexican scientists to ascertain the exact status of the Pacific mackerel resource. In retrospect, this action seems to have been little more than legislative foot dragging. State and federal scientists had been conducting research cruises off Baja California for many years; they were aware of decreased landings in Mexico, and probably expected to gain little additional insight into the exact status of the population. A three-page report to the assembly in January 1969 supports these conclusions (Anonymous 1969).

In February 1969 the DFG tried again. Assembly Bill (AB) No. 570 was introduced to prohibit the commercial take of Pacific mackerel, except for a 15% by weight incidental catch tolerance in a load of other fish. The tolerance provision was needed to allow for a "reasonable" incidental catch of Pacific mackerel for fishermen targeting on other species, primarily jack mackerel (*Trachurus symmetricus*). Since the two species often school together, the intent of the proposed regulations was to limit both the exploitation of Pacific mackerel and to minimize any negative impacts this action might have on the jack mackerel fishery. This legislation was not enacted during 1969. Industry opposition caused management to postpone the bill. Meanwhile, commercial interests agreed to support legislation to increase fish landing taxes and license fees, and to work with the DFG for a moratorium during the 1970 legislative session.

It was not until August 1970 that a Pacific mackerel management measure became law. AB 1732 provided that Pacific mackerel could not be taken commercially for two years except for an 18% by weight tolerance for incidental catches. In 1972 lawmakers extended the moratorium indefinitely and provided for a quota fishery should the stock recover. The moratorium would remain in effect until the spawning biomass exceeded 10,000 tons. If recovery occurred, an annual harvest of 20% of the spawning biomass in excess of 10,000 tons plus 30% of the spawning biomass in excess of 20,000 tons would be allowed.

Assessing the effect of the delayed implementation of a moratorium, after the fishery had already collapsed, is difficult. Recruitment was virtually nonexistent after 1962, and by the fall of 1968 six poor year classes in a row had been documented (Blunt and Parrish 1969). Landings remained low, with the annual catch averaging less than 2,000 tons from 1965 to 1969. A majority of this harvest was caught incidentally with jack mackerel, and a substantial amount of these catches were small, immature fish-of-the-year (Parrish and MacCall 1978).

During the early years of the moratorium, 1970 to 1975, Pacific mackerel were rarely taken incidentally with jack mackerel; recruitment remained poor, and annual landings seldom exceeded 100 tons. Assessments of stock size remained well below the level needed to initiate a fishery (Frey and Knaggs 1973; Knaggs 1974; Knaggs and Sunada 1975).

FISHERY AND MANAGEMENT DEVELOPMENTS DURING THE YEARS OF RESURGENCE, 1975-80

During 1975, Pacific mackerel party boat (commercial passenger-carrying fishing vessel) catch increased, as did the occurrence of Pacific mackerel in jack mackerel landings. Although both these increases were relatively weak, the 1974 year class, which produced these catches, was judged a success relative to what had been observed during the previous decade (Klingbeil 1976).

The occurrence of incidental catches rose dramatically in 1976. Age composition data indicated that the increased catches were primarily the result of the 1974 year class and in spite of a 1975 spawning season that appeared to be yet another failure (Klingbeil 1979). However, reason for optimism developed with early signs of a successful 1976 spawning season.

During the summer of 1976 live-bait fishermen who were operating daily in nearshore waters throughout southern California reported frequent catches of young-of-the-year Pacific mackerel while targeting on anchovies. This had been a rare event during the previous 15 years. During the subsequent fall these yearling fish were being caught incidentally by purse seiners engaged in the offshore anchovy reduction fishery. In addition, the DFG young-fish survey in the autumn of 1976 detected these fish in 37% of midwater trawls, the highest trawl success ratio for Pacific mackerel since the inception of midwater trawl surveys in 1966 (Mais 1974).

These young fish, averaging approximately 200 mm FL (8 inches) began occurring in jack mackerel landings during the following winter under the incidental catch tolerance provision. However, by early spring 1977, unlike the 1974 year class, the 1976 year class was available and vulnerable to the extent that fishermen maintained the fish were interfering with fishing for jack mackerel.

The complaints of fishermen centered around their ability to identify and set on schools of "mackerel" that contained 18% or less Pacific mackerel. Most fishermen asserted that this was often an impossible situation and that the composition of a school could only be estimated after the net had been pursed, and brailing had begun. A few fishermen felt that this was mainly a problem when setting on "sonar" or "fathometer" schools, rather than on surface schools. Whatever the scope of the problem, boat operators had two choices once they had determined that a catch exceeded the allowable tolerance: (1) roll the catch, with considerable but unknown mortality to both Pacific and jack mackerel, or (2) continue to brail and run the risk of having the load seized by law enforcement officers at off-loading facilities. By mid-spring 1977, after several citations and a decline in jack mackerel landings, this problem became acute enough for fishermen to seek remedial legislative action.

During May, AB 1783 was introduced as urgency legislation for the purpose of relaxing the incidental catch provision of a moratorium law. In its final form, the new law increased the allowable incidental tolerance to 40% by weight and allowed for landings of "pure" loads of Pacific mackerel if they did not exceed three tons. The law also stipulated that only the pure loads and the tonnage exceeding 18% in mixed loads could be counted against any quota established for the 1977-78 season. Because of the urgent nature of this legislation, a time-lock provision was included so that the new provisions would only remain in effect until January 1, 1978.

The intent of these actions seems to have been to ease the negative impacts on the "unregulated" jack mackerel fishery of a resurgent biomass of Pacific mackerel. The problem for management was to insure the recovery of a depleted stock, while minimizing the regulatory interference on the harvest of what most scientists felt was an underutilized resource (MacCall et al. 1980). The DFG feared that any law that encouraged targeting on Pacific mackerel might lead toward increased catches that would preempt recovery, and that too liberal a tolerance provision would result in fishermen topping-off catches of jack mackerel primarily with still immature 1976-year-class Pacific mackerel.

In retrospect, the urgency legislation, which took effect in June 1977, had the desired effect. Although several small lampara net vessels often took advantage of the pure load provision to target on Pacific mackerel, and larger purse seiners periodically topped-off, landings of Pacific mackerel remained relatively low. Since the beginning of 1977, Pacific mackerel had averaged less than 7% of total mackerel landings; this increased to only 13% of total landings from June through December 1977. Meanwhile, jack mackerel landings soared to a 25-year high of 50,000 tons.

Aside from apparently accomplishing the desired effect, AB 1783 was a unique piece of fisheries management legislation. It allowed (1) a quota to be fished before it was established, and (2) for only a portion of the catch to be counted against the quota.

While hindsight easily allows me now to label Pacific mackerel landings during the latter half of 1977 as "relatively low," that was not the case at the time. During the spring of 1977 the spawning biomass was tentatively assessed as exceeding 14,200 tons, and a quota of 1,500 tons was recommended for the season scheduled to open October 1, 1977 (Klingbeil 1977). However, the catch of Pacific mackerel during the summer and fall had already exceeded 3,000 tons by mid-November under the urgency provisions. A reassessment of the spawning biomass became imperative, especially in view of the fact that management would revert to the moratorium law on January 1, 1978.

The reassessment took into account comparisons of current and historical data including age composition, young-fish surveys, CPUE, spawner-recruit relations, and airborne monitoring abundance indices. These comparisons resulted in a reassessment of the 1977 spawning biomass to approximately 30,000 tons. The quota for the 1977-78 season was set at 5,000 tons, of which approximately 4,000 tons could be taken in an open *permit* fishery after January 1, 1978 (Klingbeil 1978, addendum 1).

The permit fishery allowed the DFG to prescribe conditions for the taking of Pacific mackerel as long as the fishery was operating on a quota. Once a quota was filled, regulations would revert to those dictated by the current law (18% incidental tolerance, and no pure loads until the following season). Because of the small 1977-78 season quota, and in order to postpone reverting to the 18% tolerance, permit restrictions were used to stretch out landings over as long a period as possible. The initial permit restrictions called for 15-ton daily boat limits when Pacific mackerel accounted for 60% or more of a catch. However, at the insistence of boat owners, permits also allowed for "paper transfers"—a concept that let boats land more than 15 tons and transfer the excess, in 15-ton increments, to boats that did not have fish for the day. None of this was necessary, of course, if a landing contained more than 40% jack mackerel. There seemed to be good reasons for fishermen to target on jack mackerel.

Although few, if any, landings were seized for violation of these restrictions, this was more a result of their unenforceability than because fishermen abided by them. With Pacific mackerel readily available, landings against the quota increased dramatically during January and February 1978. In late February, permit restrictions were tightened in order to reduce catch rates. Pacific mackerel could only be landed in loads containing 40% or less by weight. The daily limit and paper transfer provisions were deleted. However, on March 10, 1978, the 1977-78 season was closed when the 5,000-ton quota was filled.

After the closure, fishermen were as unable to live with the 18% tolerance provisions as they had been the previous spring. Urgency legislation (AB 3704) was again introduced. The intent was to allow for an increase in the 1977-78 season quota and to give the DFG more flexibility in adjusting permit restrictions and quotas. During most of the spring, while the new law was being formulated, fishermen's unions at San Pedro went on strike. The issues were the mackerel price, shares for aerial fish spotters, and payment of crewmen's social security taxes by boat owners. The strike continued until early July 1978, when AB 3704 was signed into law.

This management measure established a different quota formula, which called for a seasonal (October 1-September 30) harvest equal to 20% of the *total biomass* in excess of 20,000 tons. It also provided that the DFG could (1) adjust the season's allowable catch quota, if an earlier determined biomass estimate is revised, (2) set incidental catch tolerances during a season between 18% and 50% by number of fish, and (3) set daily limits for pure loads of Pacific mackerel. These provisions were supposed to remain in effect until January 1, 1981.

Because the law took effect immediately, the 1977-78 season quota was increased from 5,000 tons to 9,300 tons, based on a total biomass assessment of 66,500 tons for the summer of 1977. The season was reopened on July 10, 1978, to allow the additional 4,300 tons to be caught. Permit restrictions limited pure loads to 3 tons and allowed a 50% tolerance for larger catches to prevent the additional tonnage from being caught too quickly. Fishing was considered excellent for larger vessels during the next two months, for the 50% tolerance was seldom exceeded. Mixed schools, with jack mackerel predominating, seemed to be the rule in the areas where these boats fished. However, larger vessels were able to fish on pure schools of Pacific mackerel because they frequently topped off catches of jack mackerel with Pacific mackerel, and vice versa. The smaller seiners and lampara vessels generally could not find good concentrations of jack mackerel or mixed schools within their range, and during most of this period were limited to landing 3-ton pure loads of Pacific mackerel. By mid-September the quota addition had been caught. The season was again closed, and for approximately 2 weeks interseason restrictions reverted to 18% tolerance with no pure loads.

The first full season of regulating the take of a resurgent stock of Pacific mackerel was finally over. The season had progressed through two urgency statutes, numerous revisions of permit restrictions, two reassessments of biomass, a fishermen's strike, and considerable interaction between fishermen and DFG's law-enforcement officers. In the end approximately 12,000 tons were harvested during the 12-month accounting season (October through September). It was not known, at the time, whether this amount was excessive in terms of damaging the changes for full recovery. However, there was little doubt that the exploitation rate would have been much higher without any regulatory mechanisms. Meanwhile, the biomass had been bolstered somewhat by the recruitment of the 1977 year class, and a quota of 14,000 tons was set for the 1978-79 season, based upon a total biomass assessment of approximately 90,000 tons (Klingbeil 1978).

The DFG and fishermen were skeptical that 14,000 tons was enough to last through 12 months, without necessitating reversion to the 18% tolerance provision. Continuing permit restrictions were designed to retard catch rates and extend the season. At the outset pure loads were restricted to no more than 3 tons. This was raised to 8 tons within a few weeks to appease small-boat fishermen. The tolerance for larger catches was set at the maximum 50% by number.

The season progressed with little controversy through the fall, with moderate landings of primarily 1976 and 1977 year-class Pacific mackerel. However, when the 1978 year class began its recruitment, considerable enforcement problems resulted. These fish became readily available on local fishing grounds late in the year, and the schools exhibited very little mixing with jack mackerel. During one week in late December at least eight seiners landed Pacific mackerel in violation of permit restrictions. This trend continued into the new year, and on January 22, 1979, new permits were issued increasing pure load limits to 25 tons. Landings, of course, increased, but catch rates were held down considerably by marketing considerations. The large majority of mackerel catches in southern California are canned for human consumption, and canneries prefer a certain size-range of fish for maximum efficiency on automated fish cutters and cleaners. The 1978 year class had not yet grown to the minimum acceptable size (10-11 inches FL) by the spring of 1978, and canneries cut back orders when they realized that these fish were dominating the catch. However, a considerable number of these small fish were delivered for pet food production and fresh fish consumption.

Although mackerel landings continued, a large part of the effort of the southern California wetfish fleet during the spring was diverted to fishing anchovies for reduction. But when the anchovy reduction season was closed in early June, fishermen again turned their attentions to mackerel, and the industry requested a reassessment of the biomass and an increase in the quota.

Justification for an increase in the 1978-79 season quota became a problem. On the biological side of the equation it was felt that an increase could not be justified. The law required that a season's catch be based on the total biomass just prior to the season opening. Thus, the biomass assessment for the 1978-79 season could not technically take into account the 1978 year class, and biologists could not see any reason to increase previous assessments of the 1977 and older year classes. On the social and economic side of the equation (1) the anchovy season was closed until September 15; (2) market squid (*Loligo opalescens*), Pacific bonito (*Sarda chiliensis*), and bluefin tuna (*Thunnus thynnus*) were largely unavailable; (3) jack mackerel were becoming less available; (4) a closed season for Pacific mackerel by July meant 3 months of fishing under the 18% tolerance with no pure loads; and (5) no increase in the quota probably would have resulted in the introduction of industry-sponsored urgency legislation. Under these circumstances the 1978-79 season quota was increased from 14,000 to 18,000 tons. In later years it became apparent that this increase was far from excessive.

With the attention of managers and fishermen focused on an open fishery, concern about filling the quota too quickly surfaced again. Pacific mackerel permits were modified in late June to reduce the pure-load limit from 25 to 8 tons. Permits were modified again in early July to allow 40-ton pure-load weekly limits or 8 tons per day. Any load having more than 50% Pacific mackerel was supposed to be counted against the pure-load limits. These provisions proved logistically impossible to enforce. The catch of Pacific mackerel increased dramatically in July, and before the end of the month the 1978-79 season was closed. The interseason restriction of 18% incidental tolerance took effect immediately. Landings of jack mackerel continued at a brisk rate for a couple of weeks, and then the fishery virtually shut down until the new season began on October 1, 1979.

The second "season" of managing a recovering Pacific mackerel resource as a part of a dual-species mackerel fishery had been only slightly less hectic than the first. The 12-month landings of Pacific mackerel from October 1978 through September 1979 (21,000 tons) represented a 16-year high in seasonal landings. One-third of this tonnage was contributed by the apparently very successful 1978 year class.

The 1979-80 season opened on October 1, 1979, with a quota of 25,000 tons. This was based on a total biomass assessment of approximately 145,000 tons for the summer of 1979 (Klingbeil 1979). The biomass of the 1978 year class was estimated at approximately 70,000 tons. At this level, the 1978 year class represented the largest year class in 37 years, when compared with historical biomass estimates produced by cohort analysis (Parrish and MacCall 1978). Also, it meant that the 1978 spawning season was one of the most successful on record (Figure 2), assuming that the assessment of spawning biomass for the summer of 1978 was also reasonable (Klingbeil 1978). At the time, there was some concern that the assessment was too liberal. Two years later it became apparent that the 1978 year class was larger than any since the early 1930s and possibly the largest on record.

Because of the size of the 1979-80 season quota, and the ability to adjust it on fairly short notice, management resisted suggestions for permit restrictions, in particular a special allocation for owners of small boats. The season began without regulatory interfer-

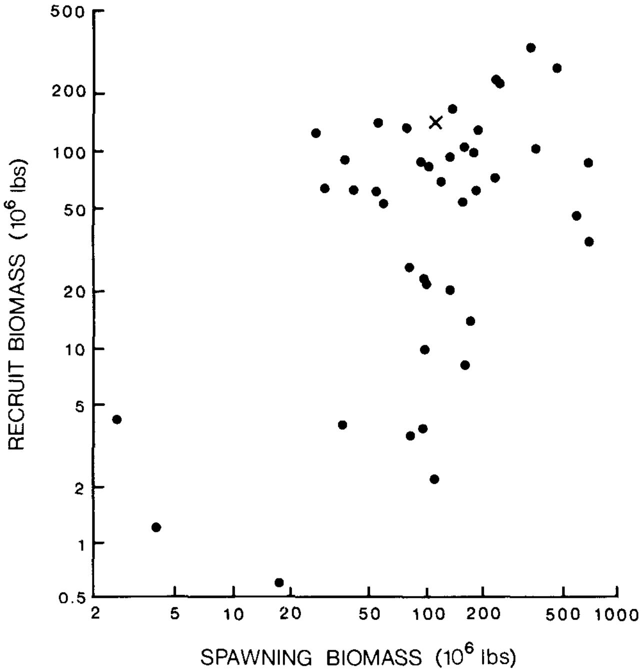

Figure 2. Spawner-recruit relationship (dots reproduced from Parrish and MacCall 1978; "x" represents estimated relationship between 1978 year class at one year of age and 1978 spawning biomass).

ence, other than the quota itself, for the first time since the resurgence commenced. But not even a 25,000-ton quota was enough to quell fishermen's anxieties about returning to an 18% interseason tolerance. Not even the hope of an early 1980-81 season opening (July 1 rather than October 1) because of new management proposals was enough to dissuade management from regulating lower catch rates. In early February 1980, with approximately 9,000 tons left on the quota, permits were amended to slow the catch rate. This time, the permits limited daily landings that contained more than 18% Pacific mackerel to 25 tons, and prohibited the possession of such loads on Friday, Saturday, and Sunday of each week.

In the fall of 1979, the DFG had begun planning new management legislation. The intent was to produce guidelines for managing a recovered rather than a depleted or recovering Pacific mackerel resource—one which could not be managed without considering the harvest of the underexploited jack mackerel.

The planning phase of the new management proposals had several objectives:

1. to maintain quota management of Pacific mackerel
2. to retain the ability to establish a moratorium if the resource again declined
3. to minimize impacts on the harvest of jack mackerel
4. to provide the flexibility needed to set and adjust "more reasonable" incidental catch provisions during the interseason
5. to allow for seasonal quotas, but limit the time in which the DFG could adjust them
6. to protect against growth overfishing, particularly at low biomass levels
7. to align the fishery, as much as possible, with the unregulated seasonal and size considerations of the 1930s
8. to establish the season opening in a way that took into account the regulated season closures of the anchovy reduction fishery.

The mechanisms for obtaining these objectives were formulated and presented to industry representatives late in 1979. The proposals were introduced as urgency legislation in early 1980, and, with one minor change, they were enacted into law in early May 1980.

The first two objectives were met by retaining the provision for a seasonal allowable catch quota of 20% of the total biomass over 20,000 tons. A moratorium with an 18% incidental catch tolerance would ensue should the biomass decrease below 20,000 tons. The third and fourth objectives were fulfilled by giving the DFG authority to assess the need for, to establish, and to adjust interseason incidental catch provisions. After a seasonal quota was reached, the DFG could set tolerance levels between 18% and 50% by number. The possibility that interseason catches could be substantial, if tolerances were established at 50%, was partially offset by retaining a fairly conservative harvest formula.

The fifth objective recognized the need to adjust quota levels during a season. This flexibility was formalized in the new law. Specifically, managers recognized that biomass assessments made in the spring of each year were always tentative and often intuitive, that little might be known about the most recently recruited year class, and that the performance of the fishery during the subsequent first part of a season could be invaluable in reassessing previous estimates. The political nature of a decision to raise or lower a quota was recognized by stipulating that quota adjustments had to be made prior to February 1 of each season. This provision forced one decision rather than allowing for a series of incremental adjustments as a season wound down.

Protection against growth overfishing restricts fishing on a year class until the gain in weight of individuals is overcome by the loss in numbers (Cushing 1977). A size limit, often thought of as protection against the harvest of too many immature fish, can also protect against growth overfishing by delaying recruitment until a year class experiences its maximum biomass. Because of a lack of detailed data on juvenile mortality, it is more feasible to design the size limit around the season of most rapid growth in body weight. For Pacific mackerel this growth occurs during its first 16 months of life and is generally complete after its first 6 months in the fishery (Figure 3). The new management proposals included a size-limit provision to discourage targeting on an emergent year class until this growth spurt was near complete.

Original proposals called for an 11-inch FL size limit from October to July of each year, with a 50% tolerance for undersized fish. The adopted provision set the size limit at 10 inches FL from January to July with a 50% tolerance for sublegals. It included a caveat that the size limit could be lowered to 9 inches if a year class had not grown above 10 inches by the second January of its life. The provision was designed to work in the following way: establish the size limit during the winter of each year when 0-age-group fish are becoming more vulnerable to nets; lift the size limit in the summer after the period of rapid growth; allow these fish to grow through the size limit during the subsequent summer and fall; reestablish the size limit the following winter to protect the next incoming group of small fish (Figure 4). The 50% tolerance

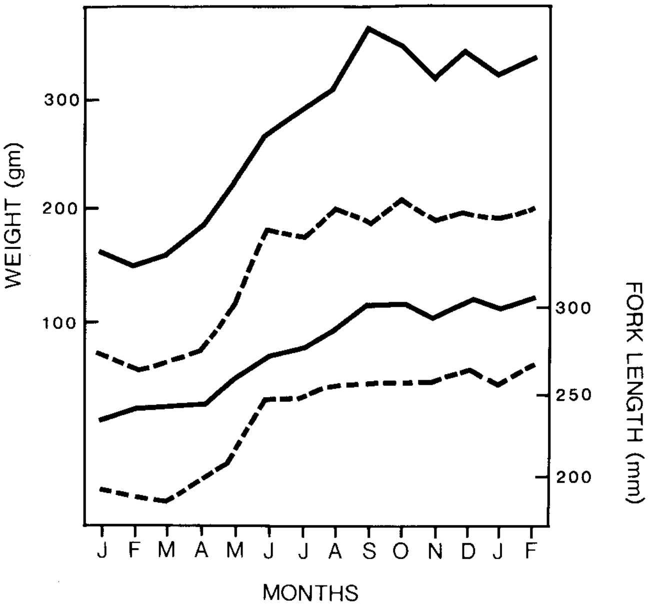

Figure 3. Monthly mean lengths and weights of 1976 (solid lines) and 1978 (dashed lines) year classes during approximately first 12 months in fishery.

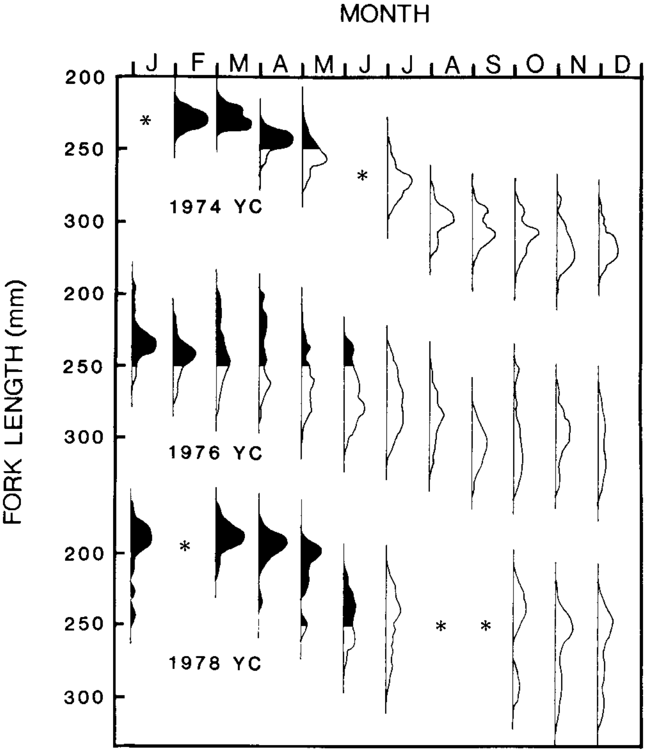

Figure 4. Monthly length frequency diagrams of 1974, 1976, and 1978 year classes during approximately first 12 months in fishery. Darkened areas show fish protected by seasonal (January to July) 10-inch FL size limit (* no sampling data).

provision was not considered too liberal, because 7-9-inch FL Pacific mackerel seldom can be found schooling with a larger size class of fish. The seasonality of the size limit also recognized the practical difficulties fishermen might have if a year class was readily available during the time that it was growing through the size limit.

The size limit was also a way of more closely aligning the fishery with industry-enforced considerations of the 1930s. Fry (1936) noted in a graph (Figure 5) that canneries often enforced a 13-inch TL (approximately 12 inches FL) size limit by refusing deliveries of smaller fish. This probably helped production in the early years of the fishery. Croker (1933) noted that canneries preferred to take fish from midsummer to midwinter. Pacific mackerel were considered firmer and of higher quality during this time. In fact, during the 1930s slightly more than 80% of annual catches were taken from July through December. The moving of the season opening from October to July was in recognition of this fact; however, it was also an attempt to coordinate the seasons for anchovy reduction and Pacific mackerel.

The anchovy and mackerel fisheries have been the mainstays of the southern California wetfish fleet for many years. Management of the anchovy reduction fishery had included season closures since its inception in 1965. During the late 1970s Pacific Fisheries Management Council's guidelines provided for an anchovy reduction season off southern California from September 15 to June 30 with a midseason closure during February and March. By retaining the October opening for Pacific mackerel the DFG would have enhanced the probability that fishermen might often be faced with two closed fisheries during the summer. Opening the Pacific mackerel season in July allows fishermen to begin fishing a new quota for mackerel immediately upon the closure of the anchovy reduction fishery. The months that were most likely to be closed for Pacific mackerel after a quota was filled (April, May, June) remained open for the anchovy reduction fishery.

These regulations took effect during the late spring of 1980 and resulted in only a 9-month accounting season for 1979-80. Actually, the season was closed on May 15, 1980, when the 25,000-ton quota was harvested. For the next month and a half fishermen operated under the 18% incidental catch provision for the last time to the date of this publication. Fishing effort was minimal until the new season opened July 1, 1980.

THE EPILOGUE TO RESURGENCE, 1980-83

During the subsequent three seasons, the Pacific mackerel fishery was managed without urgency legislation and without any modification of permit restrictions during the open or closed portions of the 12-month accounting season. Quotas for the 1980-81 and

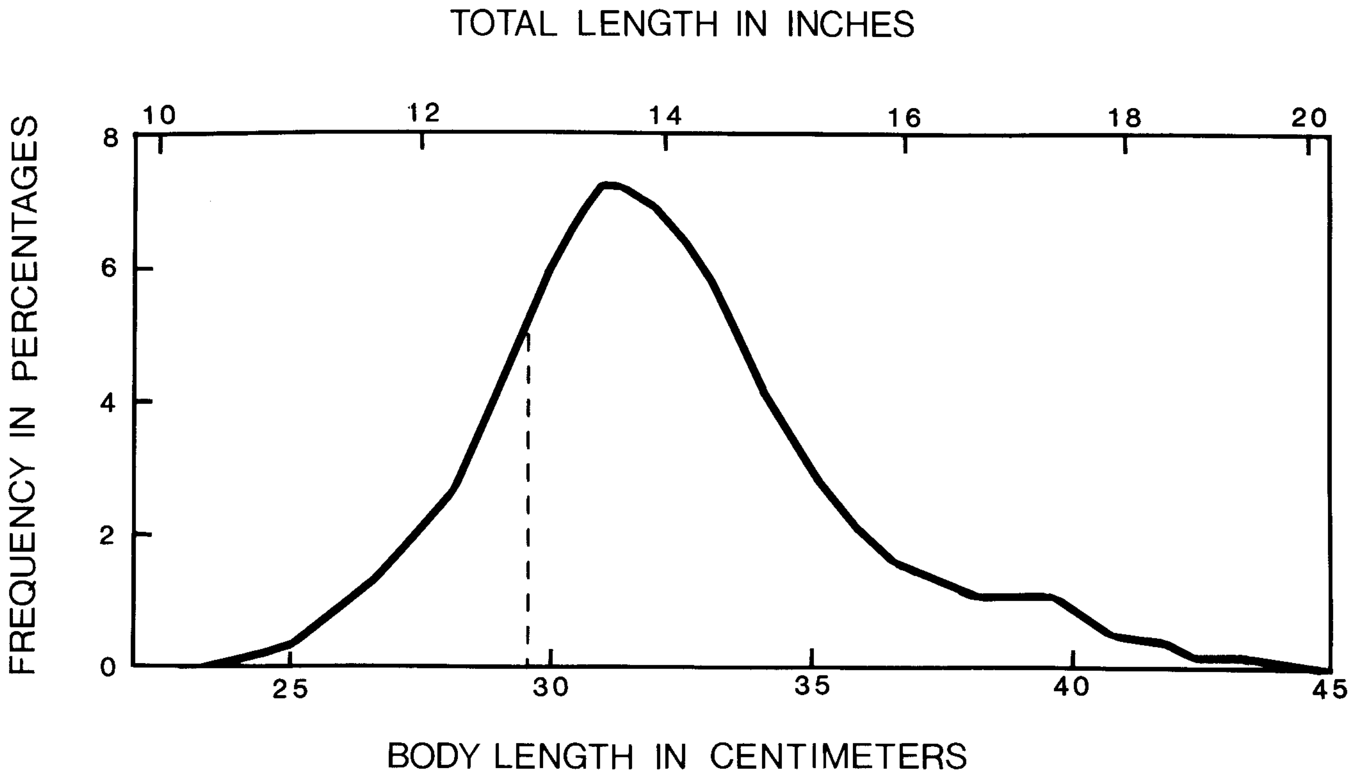

Figure 5. Size of San Pedro cannery mackerel: July, 1929-June, 1931. Vertical line at 13 inches total length, the minimum size limit sometimes set by canneries (reproduced from Fry 1936).

1981-82 seasons were initially set at 15,000 and 33,000 tons, and eventually raised to 20,000 and 38,000 tons, respectively (Table 1). Both quotas were filled during the 12-month accounting season, and interseason tolerances were set at the maximum 50% by number. The 1982-83 season quota was set at 29,000 tons, and by April 1983 approximately 8,000 tons remained to be caught.

During these three seasons the 1978 year class dominated the landings. The 1979, 1980, and 1981 year classes have been assessed as poor, weak, and moderate, respectively. Even though recruitment from the 1979 and 1980 year classes was weak, annual landings increased from 29,000 tons in 1979 to 32,000 tons in 1980 to 42,000 tons in 1981—the highest annual catch since 1940. In 1982 the catch fell, for the first time since the recovery, to 31,000 tons, but Pacific mackerel remained the dominant of the two species in "mackerel" landings for the fourth straight year (Table 2). During the first six months (July-December) of the 1982-83 season, 4-year-olds (1978 year class) and older fish accounted for 70% of the tonnage landed.

A noteworthy development during these last three seasons was the northward extension of the Pacific

TABLE 1
Seasonal Quotas, Adjustments, and Total Landings of Pacific Mackerel in California, 1977-78 to 1982-83

Season	Quota Initial	Quota Adjusted	Total[1] catch
1977-78	5,000	9,300	11,600
1978-79	14,000	18,000	20,900
1979-80[2]	25,000	—	25,410
1980-81	15,000	20,000	30,760
1981-82	33,000	38,000	42,090
1982-83	29,000	—	<30,000[3]

[1] All landings of Pacific mackerel during 12 months following season opening, i.e., quota landings plus interseason incidental catches.
[2] Nine-month accounting season.
[3] Projected catch.

TABLE 2
Species Composition of California "Mackerel" Landings, 1974-1982, Short Tons

Year	Jack mackerel	Pacific mackerel	Pacific sardine	Total landings
1974	12,729	67	7	12,803
1975	18,390	144	3	18,537
1976	22,278	328	27	22,633
1977	50,163	5,975	6	56,144
1978	34,456	12,540	5	47,001
1979	17,652	29,392	17	47,061
1980	22,225	32,349	38	54,612
1981	15,513	42,477	31	58,021
1982	28,908	31,057	144	60,109

mackerel's range. During the summer of 1981, a small commercial fishery developed in Monterey Bay for the first time since before the depletion years. Annual landings for the next two years of 1,000-2,000 tons at Monterey were held down considerably by processing capabilities and market demand. By the summer of 1982, Pacific mackerel were contributing substantially to the bag limits of sport fishermen off Fort Bragg, and were being caught by salmon trollers and commercial trawlers off Oregon for a brief period of time. Interestingly, this expansion in range seems to have occurred in response to increased age of the population as well as increased biomass, but may also be closely tied to a warming trend, which appears to have begun during 1982 in the northeast Pacific.

SUMMARY AND CONCLUSIONS

Following development of a large fishery in the 1930s the declining Pacific mackerel resource endured for a little more than 3 decades before the collapse of the 1960s. Management, despite warnings and suggestions for regulatory proposals, was nonexistent during these years, except for a brief period during the 1930s when the canning industry set its own size limit. The lack of legislative action resulted in a prolonged period of virtual economic extinction of the commercial fishery.

The initial few years of depletion, marked by concerns to develop other fisheries, can be characterized as a period of continued management inaction. This was followed by a couple of years of legislative foot dragging and management-industry trade-offs, which culminated in 1970 with the first Pacific mackerel management legislation—a moratorium. It's questionable, however, if quicker action, once the fishery had collapsed in 1965, would have shortened the depletion years. In any case the Pacific mackerel spawning biomass had been fished to a very low level and remained extremely low during the 1960s and early 1970s.

The first few years of management were mostly uneventful. The DFG refined its "moratorium law," providing for quota management in the event of resurgence, and closely monitored jack mackerel landings for signs of increased incidental catches. The recovery began in 1975 with the emergence of the 1974 year class, and continued with successful spawns in 1976, 1977, and 1978. The very large 1978 year class insured recovery to biomass levels of pre-World War II years. It is doubtful that the 1978 year class would have been as large had a moratorium not been in place.

The years of resurgence were hectic, and provided DFG with the challenge of managing a recovering resource as part of a dual-species mackerel fishery. The period was characterized by urgency legislation, frequent alteration of permit restrictions, considerable interaction between fishermen and law enforcement officers, and challenges to the validity of biomass estimates.

When legislation in 1972 first provided for future quota management based upon the annual size of the biomass, little thought had been given to how to estimate the current size of a population of pelagic fish, particularly during a moratorium. As long as the biomass obviously remained very low, the feasibility of producing valid annual estimates was seldom a matter of great concern. However, as the resurgence began and continued, much of the controversy between management and industry centered around the "accuracy" of these estimates, and still does today!

Wherever possible, I have chosen to use "biomass assessments" rather than "biomass estimates." The distinction that I have drawn is that confidence limits on an assessment cannot be quantified in any statistically valid way. This has been true for all biomass estimates of Pacific mackerel made for the purpose of establishing seasonal quotas. These assessments have relied on (1) the comparison of recent trends of the fishery with 40 years of historical landing data, (2) the age composition of these landings, and (3) the subsequent cohort analysis of this time series. The assessments of current biomasses remain "soft" (i.e., to a large degree intuitive) and in need of continual reevaluation. They have, more often than not, resulted in quotas unacceptable to fishermen. Usually these quotas have been adjusted upward during the course of a season, and other, socio-economic, considerations usually have played a large role in these decisions.

In retrospect, the system appears to have worked relatively well. Quota adjustments have not been excessive, and the costs of producing assessments have remained minimal. It seems unlikely that quotas have been too low, adversely affecting the fishery's potential, in view of recent catch levels and historical trends. The probability that catches have been too high is partially lessened by the fact that quotas have been met, seasons have been closed, and annual harvests have been less than one could have expected otherwise.

However, at the time of this writing it is becoming apparent that the Pacific mackerel fishery is in need of another large year class. It is still too early to make judgments concerning the strength of the 1982 year class. If it is weak, and mortality continues to exceed recruitment, then recovery may be short-lived. The fishery could be managed through a series of years of declining quotas, longer interseasons, and stricter incidental catch provisions. As yet, it is unclear how appropriately the present management framework will work under the circumstances created by a declining biomass.

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BIOLOGY AND FISHERY POTENTIAL OF JACK MACKEREL *(TRACHURUS SYMMETRICUS)*

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ABSTRACT

Young jack mackerel (age 0 to about 5 years) are most abundant in the Southern California Bight, where they school in open waters and near offshore banks. They progressively emigrate from these grounds, but the whereabouts of 6- to 15-year-old fish is not well known. The large fish, 15 to 30+ years old, school offshore in open ocean waters from Baja California to the Aleutian Islands. Ages 1 and older are capable of spawning, an exceptionally early age of maturity for a long-lived species. Spawning extends from central Baja California to British Columbia, with a tendency for larval abundance to progress northward from late winter to late summer. The Southern California Bight contains few jack mackerel larvae until late in the spawning season.

Year-class strengths are highly variable, with strong year classes typically separated by several relatively weak ones. On the basis of larvae collected on CalCOFI surveys, spawner abundance has been fairly constant since 1950. Spawning biomass is estimated to be 0.64 to 1.3 million metric tons (MT) in the CalCOFI region, with perhaps an equal biomass outside that region.

The estimated spawning biomass was allocated among age categories according to assumed mortality rate schedules. Because of age-specific mortality rates, potential yield was estimated by applying the Gulland approximation to each age category separately and summing the results. Overall potential yield estimates range from 130 to 260 thousand MT. The young inshore fish have a potential yield of 100 to 200 thousand MT, whereas the old offshore fish have a potential yield of 10 to 25 thousand MT. If a significant fishery were to develop on either segment, the other segment would probably be impacted indirectly.

RESUMEN

Jureles (*Trachurus symmetricus*) jóvenes, de hasta 5 años de edad son abundantes en el seno del sur de California, y sus cardúmenes se presentan en mar abierto y en las proximidades de los bancos costeros. Los jureles emigran progresivamente desde estas zonas, pero no se conoce con la debida precisión el paradero de las poblaciones con edades entre 6 y 15 años. Jureles grandes, de más de 30 años de edad integran los cardúmenes de mar abierto, desde Baja California hasta las Islas Aleutianas. Los jureles inician la reproducción al año de edad, madurez precoz y excepcional en peces que llegan a alcanzar una larga vida. La puesta se extiende desde Baja California hasta la Columbia Britanica, con una tendencia a que la abundancia de larvas progrese hacia el norte, desde finales del invierno hasta finales del verano. La zona del seno del sur de California contiene pocas larvas de jurel hasta el final de la época de puesta.

La dominancia de las generaciones es muy variable, observándose generaciones abundantes alternando con otras de escasez numérica. La abundancia de reproductores, tomando como base las larvas recolectadas durante las exploraciones del programa CalCOFI, resulta bastante constante desde 1950. La biomasa de reproductores en la región explorada por el programa CalCOFI se ha estimado entre 0.64 a 1.3 millones de Tm., y se considera que la cantidad será aproximadamente similar para las zonas adyacentes a esa región.

La biomasa estimada se distribuye entre categorías de edades de acuerdo con el valor asumido establecido para la mortalidad. Considerando los valores de mortalidad para las diversas edades se estimó el rendimiento potencial, aplicando la aproximación de Gulland separadamente para cada categoría de edad y sumando luego los resultados. Se estima que el total de rendimiento potencial oscila de 130 a 260 mil Toneladas. Los peces jóvenes costeros presentan un potencial de producción de 100 a 200 mil Toneladas, mientras que los oceánicos tendrían un potencial de rendimiento de 10 a 25 mil Toneladas. Si se desarrollase una pesquería importante en cualquiera de estos sectores, el otro sería afectado indirectamente por dicha pesca.

FISHERIES AND DISTRIBUTION

The jack mackerel, *Trachurus symmetricus*, was reported in the commercial landings of fish in California as early as 1888, but was of minor commercial importance before 1947. Of much greater commercial importance were the more profitable Pacific sardine,

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Sardinops sagax caerulea, and the more desirable Pacific mackerel, *Scomber japonicus.* Much of the jack mackerel catch between 1926 and 1946 was absorbed by fresh fish markets and consisted primarily of fish taken from mixed Pacific sardine and Pacific mackerel schools. Landings were low, varying between 180 and 14,000 MT. During these years, the fish were referred to as horse mackerel and had relatively little market appeal. In 1947 the fishing industry, after being hit hard by poor sardine landings, turned to jack mackerel and landed 58,535 MT. The following year, the U.S. Food and Drug Administration authorized the common name jack mackerel for use on labeling. This was expected to have greater consumer appeal than the original name horse mackerel. Jack mackerel have been a major contributor to California's commercial landings ever since (Figure 1).

There is presently only one fishery targeting on jack mackerel. This fishery uses purse seine gear, and operates out of southern California ports, harvesting small fish from local waters. Fisheries farther to the north take jack mackerel incidentally. The salmon troll fisheries operate in nearshore waters north of Point Conception, and take an unknown but probably large number of jack mackerel, which are discarded at sea. The foreign trawl fleets, which operate offshore north of Point Arena, take jack mackerel incidentally to fishing for Pacific whiting (*Merluccius productus*), but have actually avoided taking jack mackerel in recent years. If an expanded domestic offshore trawl fishery develops out of northern California and Oregon ports, large jack mackerel may become a target species, and will almost certainly be an incidental species of significant magnitude. Recreational fisheries all along the Pacific coast occasionally take jack mackerel but do not consistently target on the species. The various jack mackerel fisheries are described in detail by MacCall et al. (1980).

In the Vancouver Island area of Canada, large jack mackerel have been caught at the surface by purse seiners and are taken incidentally in the bottom trawl fisheries (Hart 1973). Although jack mackerel are quite abundant at times, there is no directed fishery for the species. Incidental catches are insignificant and are not included in catch records (S.J. Westrheim, Pacific Biological Station, Nanaimo, B.C., pers. comm.).

The distribution of jack mackerel extends northward into the Gulf of Alaska east of 160° W. A high-seas experimental salmon gill net survey found jack mackerel to be relatively abundant (Larkins 1964). Incidental catches along the coast of southeast Alaska occur infrequently and are not documented (D. Cantillon, Alaska Department of Fish and Game, Juneau, Alaska, pers. comm.). Jack mackerel have been found as far south as Cape San Lucas, Baja California. The offshore limit of the population is poorly defined, but various sources have been compiled by Blunt (1969) to produce a distributional map (Figure 2). The offshore limit is approximated by a line running from Cape San Lucas, Baja California, to the eastern Aleutian Islands, Alaska. A large portion of the range lies outside the 200-mile fishery jurisdiction zones of the U.S. and Mexico.

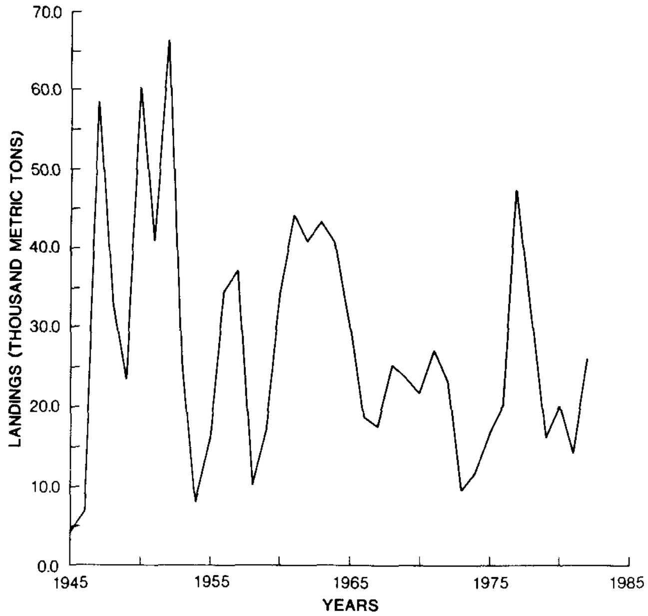

Figure 1. California jack mackerel landings (source: California Department of Fish and Game).

REPRODUCTION AND STOCK STRUCTURE

In their study of maturation of jack mackerel from the southern California fishery, Wine and Knaggs (1975) determined that most females become sexually mature at about their first birthday. Although immature fish were found at all times of the year, 50% or more of all females appear to be close to or in spawning condition from March through September. Very young spawners appear to reach a reproductive condition later in the season than do older spawners. Nothing is known of the maturity cycle of the large offshore fish.

MacGregor (1976) calculated the fecundity, in advanced eggs per gram of fish, of thirty jack mackerel. These fish could be divided conveniently into two distinct groups, representing small and large fish. The small fish ($n = 15, \bar{l} = 235$ mm) had a mean fecundity of 68.5 advanced eggs per gram of fish. The large fish ($n = 15, \bar{l} = 519$ mm) had a mean fecundity of

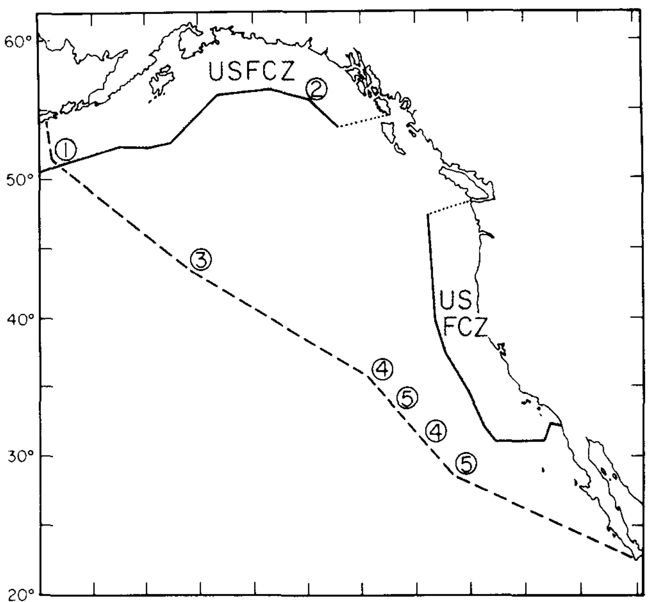

Figure 2. Distribution of the jack mackerel resource (modified from Blunt 1969). Circled numbers indicate the periphery as determined by various sampling methods: (1) gillnet catches, INPFC, 1963; (2) gillnet catches, INPFC, 1955; (3) eggs and larvae, NORPAC, 1955; (4) night-light stations, CDF&G, 1957-68; (5) eggs and larvae, CalCOFI, 1950-78.

152.3 advanced eggs per gram of fish. The small fish, which would correspond to age 2 years, had a fecundity of 65.8/152.3 = 0.43 relative to the large fish on a per unit body weight basis.

Jack mackerel eggs and larvae first become abundant in the waters far offshore of northern Baja California and southern California in March through June (Kramer and Smith 1970; Ahlstrom 1969). There is very little production of eggs and larvae in the Southern California Bight until July and August, presumably when the younger fish begin to spawn (see above). Also, the center of offshore spawning loosely moves north as the summer progresses. The northern and offshore areas of spawning have received very little sampling effort, so the seasonality and geographic limits to spawning by the offshore population are poorly known. A survey of the northeastern Pacific in August 1955 took jack mackerel eggs and larvae off Oregon and Washington from 100 to 1000 miles offshore (Ahlstrom 1956). CalCOFI cruise 7210 (October 1972) similarly found a large isolated area of spawning jack mackerel extending from 200 to 600 miles off the coast of Washington, verifying the existence of late northern offshore spawning. The northern limit of jack mackerel spawning was not determined.

There are two distinct and non-overlapping segments shown by available length frequencies (Figure 3). The southern California purse seine fishery presently catches fish ranging from 10 cm to 30 cm FL, whereas offshore and northern coastal captures tend to range from 50 cm to 60 cm FL. The intermediate lengths are distinctly lacking in either data set. The southern California fleet captured moderate quantities of fish ranging from 30 cm to 40 cm FL during the early years of the fishery (Figure 3), but whether this reflected biological availability, fishermen's tactics, or fishing pressure is not known. Length frequencies of jack mackerel taken off Monterey from 1958 to 1967 (not shown) resemble those of the early southern California fishery. The Monterey fish were slightly larger, with one-half of the catch ranging from 30 cm to 40 cm FL, but with few fish larger than 40 cm FL. Length frequency of jack mackerel captured by the California Department of Fish and Game's preseason offshore albacore cruises shows a few fish ranging from 40 cm to 50 cm FL, but no data show the 30-cm-to-50-cm fish in the abundance they must presumably have, assuming that the small fish eventually grow and join the large fish segment. Soviet research trawls taken from 1966 to 1977[1] show a clear geographic pattern of jack mackerel mean lengths, with small fish (20-30 cm FL) to the south and inshore, and large fish (ca. 53 cm FL) to the north and offshore.

As shown above, jack mackerel eggs and larvae are distributed widely in the northeastern Pacific. The quantity of spawning products released in the Southern California Bight is a small portion of the total. Nonetheless, the largest known concentrations of young-of-the-year jack mackerel are found in the Southern California Bight. Many of the southern California fish are undoubtedly spawned locally. However, it is likely that the extensive offshore spawning by large fish produces significant numbers of offspring and, judging from the scarcity of juvenile jack mackerel elsewhere, we believe these fish find their way to the Southern California Bight. Anecdotal evidence of this movement has been provided by the discovery of many young-of-the-year jack mackerel in albacore (*Thunnus alalunga*) stomachs taken off the coast of California in the summer of 1982 (M. Laurs, Southwest Fisheries Center, La Jolla, California, pers. comm.). Thus it is reasonable to assume that the southern California segment of the jack mackerel population is not self-sustaining, but depends to an unknown extent on spawning by the offshore large fish segment.

RECRUITMENT

Absolute magnitude of recruitment cannot presently be determined. However, examining the contributions

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[1] Stepanenko, M.A. Some traits of biology and reproduction rate and conditions of California jack mackerel. Presented to the 1979 U.S.-U.S.S.R. Bilateral Meeting on Fisheries Assessment in the North Pacific, Seattle, June 5-8, 1979.

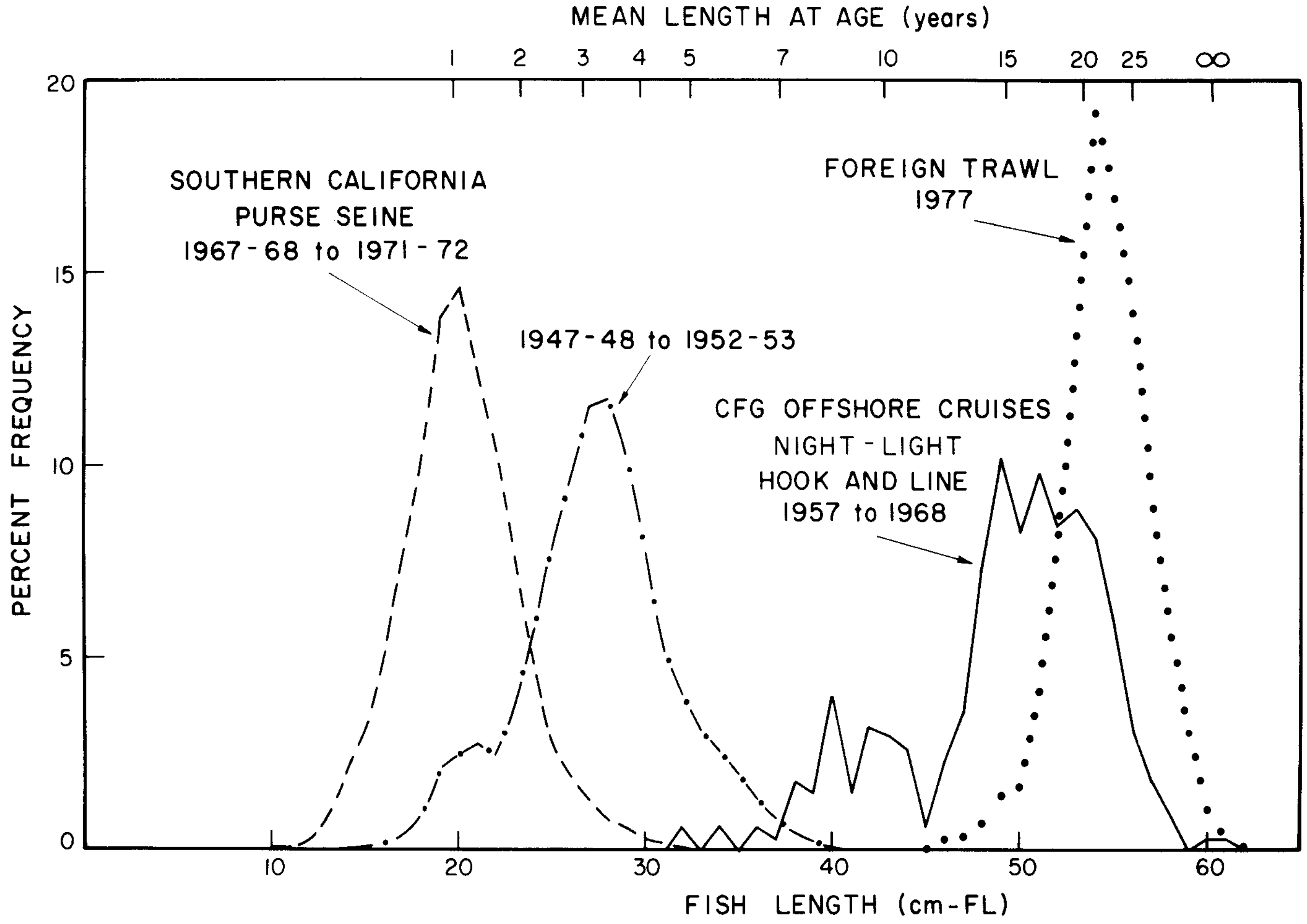

Figure 3. Length frequency of jack mackerel taken by various fishery segments and surveys. Age scale is not an accurate measure of age at length, and is provided only for comparison.

of various year classes to the southern California fishery provides a rough picture of recruitment variability. The fishery landings have been determined by processor orders rather than by availability, so actual volume of catch is not necessarily a good indicator of relative abundance. Virtual year-class strength, obtained by summing the percentage contributions of a year class to the various seasons in which it was fished, provides a rough indication of year-class variability. Age composition data were taken from Knaggs (1974a, b), Knaggs and Barnett (1975), Fleming and Knaggs (1977), and Fleming (California Dept. of Fish and Game, Sacramento, Calif., pers. comm.). Because we have used percentage contribution, an average year class will have a virtual strength of 100%. Long-term trends cannot be detected by this treatment, since year classes are effectively compared only with their near neighbors.

The resulting series of virtual year-class strengths (Figure 4) shows a pattern of runs of weak year classes interrupted by occasional strong year classes. Until the 1966 year class, recruitment seems to have been either very good or very poor, with average recruitment a rarity. In more recent years, since 1966, year classes seem to have fluctuated less severely; however, the recent fishery, from which data are not yet fully available, suggests that the 1976 year class was very strong. The 1982 year class also appears to be extraordinarily abundant, based on high catch rates by a midwater trawl survey for young fish in the Southern California Bight (Mais 1982) and on the occurrence of young fish in albacore stomachs cited above.

ABUNDANCE

CalCOFI ichthyoplankton surveys are the principal source of information on jack mackerel spawner abundance. Because the CalCOFI region does not encompass the full range of the fish (see Figure 2), some assumptions are necessary. Principally, we assume that the density of fish in the CalCOFI region bears a reasonably constant relationship to the size of the total spawning population. CalCOFI surveys have shown

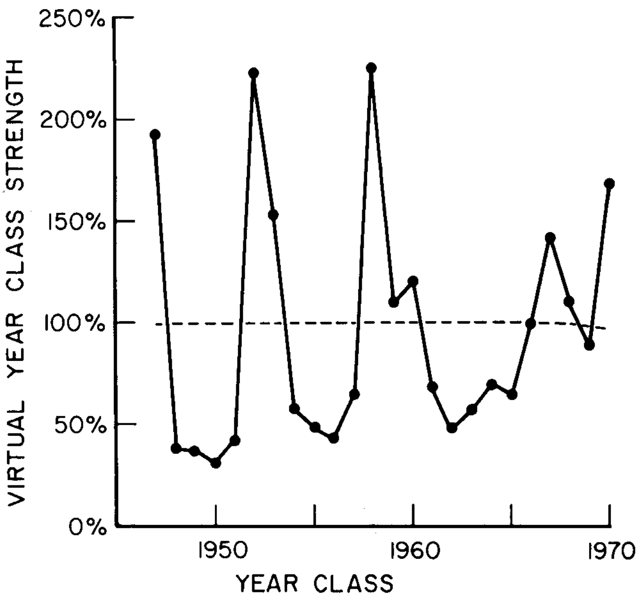

Figure 4. Relative recruitment strengths of jack mackerel year classes in southern California. Virtual year-class strength is measured by the sum of percentage contributions to seasonal landings over the lifetime of the year class. The dashed line indicates average strength.

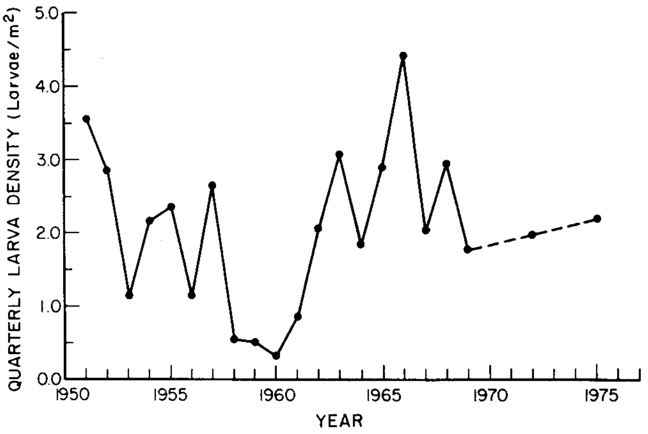

Figure 5. Density of jack mackerel larvae in selected areas of CalCOFI surveys.

that the center of spawning moves northward as the season progresses, from northern Baja California waters in March and April to as far north as Oregon in the fall (Ahlstrom 1956, 1969; Kramer and Smith 1970). Whether this shift is due to actual migration of spawners or to progressively later maturation of more northerly fish is not known.

Mean apparent density of jack mackerel larvae was calculated from CalCOFI samples in regions most consistently occupied by eggs and larvae. This density is the average quarterly density off northern Baja California in the first and second quarters of the year, and off southern California in the second and third quarters. The near inshore regions of Baja California and southern California were excluded. The densities are plotted in Figure 5. The unusually low densities from 1958 to 1961 may be due to the influence of abnormally warm oceanic temperatures from 1957 to 1960: the population may have shifted northward; gonadal maturation may have been affected; and abnormally rapid growth of larvae would decrease apparent abundance. Also, it is highly unlikely that abundance changes of the magnitude suggested by the larval density can actually occur, given the low rate of mortality exhibited by offshore jack mackerel. Data for 1958-61 will not be considered as representative of jack mackerel abundance during that period.

Larval densities show considerable year-to-year fluctuation (Figure 5), but there is no trend showing a long-term change. It would be difficult to show small changes in future jack mackerel abundance using the CalCOFI larval density because of natural variability and anomalies like those of 1958-61. Thus a minimum management response time to a decrease in abundance is probably greater than 6 years, given the present triennial schedule of CalCOFI surveys.

Ahlstrom (1968) estimated the jack mackerel resource to be 1.9 to 4.4 million MT of spawning biomass. Ahlstrom based his estimate on CalCOFI survey estimates of jack mackerel egg production (Farris 1961). He used two assumptions of fecundity: the low fecundity estimate was two spawning batches per year, based on the two modes of egg diameters observed in ovaries by MacGregor (1966); the high fecundity estimate was 3⅓ batches per year, based on a peak egg abundance (when all fish are assumed to spawn) to average egg abundance, and assuming that it takes at least 30 days to mature a batch of eggs. Ahlstrom also assumed that the total stock was 1½ to 2 times that measured in the CalCOFI area.

Knaggs (1973) used tag returns to estimate the total population available to the wetfish fleet off southern California. This estimate was 0.6 to 1.4 million MT, but must be considered tentative because sample size was very small, and many assumptions underlying tagging estimates could not be met.

Pashchenko[2] used an acoustic-trawl survey to estimate the jack mackerel biomass *outside* the CalCOFI area in the spring of 1978. Using the assumption that all fish in the path of the net were caught, he obtained a biomass of 308,000 ± 91,000 MT. If a portion of the fish in the trawl path were escaping capture, his estimate should be increased accordingly.

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[2] Pashchenko, V.M. Distribution, biology and biomass assessment of the jack mackerel. *Trachurus symmetricus* (Ayres). Presented to the 1979 U.S.-U.S.S.R. Bilateral Meeting on Fisheries Assessment in the North Pacific. Seattle, June 5-8, 1979.

We propose a new estimate of jack mackerel abundance. The approach is similar to Ahlstrom's, but assumptions regarding fecundity can be improved in light of recent work on other species (see below). Also, the methodology is changed slightly, and additional factors are considered in estimating egg production rates.

Egg production can be expressed by the following equation (Parker 1980):

$$E = Brfp \qquad (1)$$

where E is daily egg production, B is spawning biomass, r is fraction of the spawning population that is female, f is fecundity in eggs per body weight per spawning, and p is fraction of females spawning per day.

The equation can be rearranged to

$$B = E/rfp \qquad (2)$$

in order to estimate spawning biomass.

Egg production in the CalCOFI region for the years 1951-54 was estimated by Farris (1961). As was shown above, there is no visible trend in jack mackerel abundance since that time, so Farris' data are appropriate for estimating present biomass. Farris corrected his egg production estimates for a 3-day duration to hatching; however, he ignored the effects of natural mortality. Because of losses of eggs before hatching, the duration of an average egg would be somewhat less than 3 days. Paul Smith (Southwest Fisheries Center, La Jolla, Calif., unpublished data) has calculated approximate numbers of jack mackerel eggs surviving to each stage of development at 15°C. Time to hatching at 15°C is 86.4 hours, whereas mean duration of eggs is 53.2 hours, eggs being terminated either by mortality or by hatching. Thus the mean duration is 0.62 of the time to hatching. Farris' eggs were in an environment averaging 15.5°C, which is reasonably close to the above temperature. This change in assumed residence time requires that Farris's egg production estimate be multiplied by 1/0.62, or 1.62.

Peak egg production extends from March to June in the CalCOFI area, during which period 82.6% of the total year's eggs are released. Average egg production for March through June is 5.5×10^{14} eggs or 4.5×10^{12} eggs/day (Farris 1961). With the above mortality correction, the latter value is increased to 7.3×10^{12} eggs/day.

Ahlstom (1968) used a fecundity estimate of 306 eggs/gram/spawning, based on a single fish examined by MacGregor (1966). MacGregor (1976) gives fecundities of 30 fish, including 15 fish longer than 40 cm. The mean fecundity of these large fish was 153.2 advanced eggs/gram body weight, or about one-half the earlier estimate. Our biomass estimate will use MacGregor's fecundity estimates. However, it is likely that they are low. Pashchenko[3] examined 18 large female jack mackerel taken 390 miles west of San Diego in the spring of 1978. These fish were larger (mean 54.0 cm FL) than MacGregor's fish, and had a mean fecundity (362.6 eggs/gram) over twice that obtained by MacGregor. If Pashchenko's data are used, or are averaged with MacGregor's observations, resulting biomass estimates would be considerably lower.

Little is known of spawning rates of pelagic fish, and nothing is known for jack mackerel. Ahlstrom (1968) used a minimum estimate of two spawnings per year, because there were two modes of egg diameters in the single fish examined; and he used 3.3 spawnings per year as a high estimate, assuming 30 days is necessary to mature each batch of eggs. In comparison, similar spawning rates were suspected for the northern anchovy (*Engraulis mordax*), for essentially the same reason. However, recent work on anchovy gonad histology (Hunter and Goldberg 1980) has strongly indicated that about 15% of the mature female anchovy population is spawning each day during the peak spawning months. This spawning rate translates as approximately one spawning per week, and indicates that a batch of eggs may require fewer than 7 days to be produced. Because jack mackerel gonad morphology and the protracted spawning season are similar to those for anchovy, we assume that spawning rates are similar to those for anchovy. In our estimate of jack mackerel abundance we will use 15% spawning per day as an arbitrary upper limit, and 7.5% spawning per day as a lower limit. Lower percentages could be considered; the biomass estimate changes inversely with this percentage, which is a major source of imprecision. It is assumed that males exist in equal weight to females, so the proportion of females is 0.5.

Using the values in equation (2), $E = 7.3 \times 10^{12}$ eggs/day, $r = 0.5$, $f = 152.3$ eggs/gram of large female fish, $p1 = 15\%$ female fish spawning/day, $p2 = 7.5\%$ female fish spawning/day, we obtain spawning biomass estimates of 0.64 and 1.3 million MT in the CalCOFI region. If the fish migrate extensively, with virtually all fish spawning in the CalCOFI region and then dispersing, these may be direct abundance estimates. If the fish are less migratory, and only a fraction of the population spawns in the CalCOFI region, total abundance will be greater. Ahlstrom (1968) assumed that one-half of the total jack mackerel

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[3] See footnote 2.

spawning biomass resides outside the CalCOFI area. Pashchenko[4] also feels that one-half of the resource may be spawning outside the CalCOFI area. Although the exact fraction of the resource outside the CalCOFI area cannot be quantified, we will assume the total spawning biomass to be 1.36 million MT (1.5 million short tons) as the working estimate.

This working estimate of 1.36 million MT of spawning biomass is considerably lower than Ahlstrom's (1968) range of 1.9 to 4.4 million MT. However, it is more consistent with current knowledge of the likely spawning frequency of pelagic fishes. This working estimate would suggest that available southern California biomasses are smaller than estimated by Knaggs (1973). However, Knaggs's estimate may be high because of emigration, and our estimate gives total biomasses approaching Knaggs's lower range of 0.6 million MT.

MORTALITY RATE

The natural mortality rate of jack mackerel has not been estimated previously. The necessary data for a direct estimate are very difficult to obtain, given the stock structure and poorly known migratory habits of the fish. Because of the size selectivity and geographic character of existing fisheries, age-frequency analysis is not feasible because mortality rates are confounded with rates of emigration. However, other information correlating with mortality rates is available, allowing reasonable values to be hypothesized. Pauly (1980) examined a large number of fish stocks, from which he derived an empirical natural mortality rate approximation based on von Bertalanffy growth parameters and water temperature. Wine and Knaggs (1975) obtained von Bertalanffy parameter estimates of the asymptotic length ($L_\infty = 60.3$ cm) and the growth rate coefficient ($K = 0.0935$/year). Using the 10-m annual mean water temperature off central California of about 14°C (Lynn 1967), Pauly's method gives a tentative natural mortality rate of $M = 0.23$. Fitch (1956) reports that some large jack mackerel are over 30 years of age, according to growth rings on their otoliths. The average mortality rate would have to be quite low to allow a significant number of fish to reach such an age, confirming the magnitude of the Pauly approximation.

It is highly unlikely that jack mackerel exhibit a constant natural mortality rate throughout their life. Small young fish living in the predator-rich nearshore area are likely to have much higher mortality rates than the large offshore fish. Based on this speculation, the following age-specific natural mortality rate schedule is postulated for jack mackerel: $M_0 = 0.5$, $M_1 = 0.5$, $M_2 = 0.45$, $M_3 = 0.4$, $M_4 = 0.35$, $M_5 = 0.3$, $M_6 = 0.25$, $M_{7+} = 0.2$. Other tentative mortality rate schedules could be proposed (see MacCall et al. 1980).

FISHERY ANALYSIS AND POTENTIAL YIELD

A simple "piece-wise" dynamic pool model can be used to represent the long-term average or steady-state population structure. Natural and fishing mortality rates and weights at age are used to estimate relative biomass at age from the working estimate of 1.36×10^6 MT (1.5×10^6 short tons) spawning biomass. The total spawning biomass is allocated among the ages according to these relative contributions. The biomass of young of the year (age 0.5) was calculated by the ratio of cohort weights at age 0.5 and age 1.

As discussed previously, it is likely that young jack mackerel have a lower batch fecundity and may spawn fewer times than do older mature fish. Spawning biomass, being based on egg censuses, is expressed in terms of body weight equivalents of fully mature spawning females. Total fishable biomass is therefore likely to be greater than spawning biomass. Two alternative fecundity models are used here. The first model simply assumes that all fish are equally fecund on a unit body weight basis (Table 1). The second model assigns partial fecundities to young fish. If mature fecundity is given a relative value of 1.0, ages 1 through 4 are assigned relative fecundities of 0.2, 0.4, 0.6, and 0.8, respectively (Table 2).

The above method of allocating biomass among age categories is subject to considerable imprecision. Both assumed rates of natural mortality and relative fecundity of young fish have strong influences on the age structure and total biomass of the model population. Since the spawning biomass is fixed, different mortality rate schedules will result in inverse changes in allocation of biomass to small fish (ages 0-8) and large fish (ages 15-30). As can be seen in Table 2, assumption of reduced fecundity of young fish results in an increase in estimated total biomass.

The dynamic pool model was used to estimate fishing mortality rates by an iterative process. Fishing mortality rates at age (F_j) are given by

$$F_j = C_j / \bar{B}_j \qquad (3)$$

where C_j is catch of age j fish, and B_j is mean biomass. Mean biomass was approximated by

$$\bar{B}_j = (B_j + B_j + 1) / 2 \qquad (4)$$

The iterative process is as follows: initially, fishing mortality rates of 0 are input to the dynamic pool model, and biomasses are estimated (allocated). Esti-

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[4] See footnote 2.

TABLE 1
Dynamic Pool Model of Jack Mackerel Population and Estimates of Potential Yield, Using Assumed Schedule of Natural Mortality Rates

Age	Assumed natural mortality rate	Fishing mortality rate	Relative number	Length (mm-FL)	Mean weight[1] (g)	Initial biomass (10^3 MT)	Mean catch[2] (10^3 MT)	Potential yield (10^3 MT) Low $X=0.3$	Potential yield (10^3 MT) High $X=0.5$
0	(0.5)	—	1,000	—	—	—	—	—	—
0.5[3]	(0.5)	0.018	779	—	60	(123.3)	2.360	9.3[4]	15.4[4]
1	0.5	0.043	602	198	85	135.0	5.728	20.2	33.7
2	0.45	0.046	350	234	140	129.3	5.664	17.4	29.1
3	0.4	0.058	213	267	207	116.5	6.340	14.0	23.3
4	0.35	0.032	135	297	285	101.2	3.024	10.6	17.7
5	0.3	0.012	92	324	370	89.7	1.048	8.1	13.4
6	0.25	0.004	67	349	461	81.8	0.337	6.2	10.3
7	0.2	0.002	52	372	556	76.6	0.124	4.6	7.6
8	0.2	0.001	43	392	653	73.5	0.025	4.4	7.3
0-8	—	—	—	—	—	926.8	24.649	94.8	157.9
9-15	0.2	—	145	411-493	959	367.0	—	22.0	36.7
16-30	0.2	—	45	503-576	1598	190.3	—	11.4	19.1
0-30						1360.8 (spawning) 1484.1 (total)		128.3	213.7

[1] Weight is based on length-weight relationship with correction for σ_L = 21.5 mm (Pienaar and Ricker 1968)
[2] Catch includes only San Pedro landings.
[3] Age O fish are assumed to be unavailable for the first half year; mean weight is approximate; and biomass does not spawn.
[4] Potential yield reduced by ½ because fish are only available for ½ year.

mates of F_j are then made by equations (3) and (4), given the mean catch of fish at age for the 1952-53 through 1971-72 fishing seasons (Fleming and Knaggs 1977). These fishing mortality rates are then used in the dynamic pool model to produce new biomass estimates for the second iteration. The estimates of F converge to two significant digits with three iterations.

Estimates of F are given in Tables 1 and 2 and reflect a southern California fishery of approximately 24,649 MT per year, which is the average San Pedro catch for the 1952-71 period. Fishing mortality on older fish caused by incidental catches and the foreign trawl fishery has been ignored, because of lack of information on magnitude and age composition. Recent foreign trawl catches are up to 2,000 tons per year, but the 1952-71 average is much smaller—not large enough to significantly affect the model.

The potential yield estimator of Gulland (1970) is intended to provide a reasonable limit to exploratory expansion of a fishery. It is not meant to be an esti-

TABLE 2
Dynamic Pool Model of Jack Mackerel Population and Estimates of Potential Yield, Using Assumed Natural Mortality Rates and Partial Fecundity of Young Fish

Age	Assumed fecundity	Assumed natural mortality rate	Fishing mortality rate	Initial biomass (10^3 MT)	Potential yield (10^3 MT) $X=0.3$	Potential yield (10^3 MT) $X=0.5$
0.5[1]	0	(0.5)	0.032	(148.2)	11.2[2]	18.5[2]
1	0.2	0.5	0.036	161.0	24.1	40.3
2	0.4	0.45	0.038	155.1	21.0	34.9
3	0.6	0.4	0.048	140.9	16.9	28.2
4	0.8	0.35	0.026	123.6	13.0	21.6
5	1.0	0.3	0.010	110.3	9.9	16.5
6	1.0	0.25	0.003	100.8	7.5	12.6
7	1.0	0.2	0.001	94.3	5.6	9.4
8	1.0	0.2	0.001	90.6	5.4	9.1
0-8	—	—	—	1124.9	114.6	191.1
9-15	1.0	0.2	—	452.5	27.1	45.3
16-30	1.0	0.2	—	234.6	14.1	23.5
0-30				1360.8 (spawning) 1812.0 (total)	155.8	259.9

[1] Age 0 fish are assumed to be unavailable for the first half year; mean weight is approximate; and biomass does not spawn.
[2] Potential yield reduced by ½ because fish are only available for ½ year.

mate of maximum sustainable yield (MSY), but is an interim limit to catches while data sufficient to estimate MSY are being accumulated. Thus Gulland's estimator should not be treated as a goal for fishery development. In some cases it may be considerably in excess of true MSY, but we cannot know for the case of the jack mackerel fishery until more information is gained.

The potential yield estimator is given by

$$Y_{\text{pot}} = X\, M\, \bar{B}_0 \qquad (5)$$

where Y_{pot} is potential yield; M is natural mortality rate; $\bar{B}_0$ is mean virgin biomass; and X is a coefficient based on M, on Von Bertalanffy growth parameter K, and on c, the ratio of length at first capture to asymptotic length. The present biomass is only very lightly fished, and can be used for $\bar{B}_0$. A value of $X = 0.5$ is commonly used and will be used here for a "high" estimate. The value obtained from Gulland (1970) for $M/K = 2.5$ to 5.0, and relative length at first capture $c = 0.3$, is $X = 0.3$, providing a "low" estimate of potential yield. Gulland's estimator assumes a constant mortality rate, but M varies with age in the dynamic pool model. Therefore, the Gulland estimator is applied to each age separately, and potential yields are summed afterward (Tables 1 and 2).

The sensitivity of potential yield estimates to different assumed rates of natural mortality is somewhat different than sensitivity of biomass estimates. For the large-fish segment, decreases in natural mortality rate (M) result in offsetting increases in estimated biomass ($\bar{B}_0$), making potential yield estimates relatively constant (cf. equation 5). However, the sensitivity is compounded for the small-fish segment, where decreased overall rates of mortality result in a decreased portion of the total biomass being allocated to the small-fish segment, and potential yield drops considerably. Without good estimates of biomass and mortality rates, these estimates of potential yield must remain only tentative. Other estimates of potential yield, based on alternative mortality rate schedules and other assumptions, are given by MacCall et al. (1980).

Potential yield is estimated for three segments of the resource. Ages 0.5 through 8 represent the inshore small-fish fishery, and have a potential yield of about 100 to 200 thousand MT. The historical fishery has exploited fish aged 1 through 4 years more heavily than the other ages in the small-fish fishery. Based on yield-per-recruit considerations, there would be no detriment in obtaining an equivalent total yield from younger fish (e.g., ages 1-4) rather than in proportion to their biomasses over the entire range of ages. This argument does not extend to the large-fish segment, which is harvested independently. Potential yield of large fish ranges from 10 to 25 thousand MT. The intermediate group of ages 9 to 15 years has a potential yield of 20 to 50 thousand MT. The total stock has a potential yield of 130 to 260 thousand MT.

COMPARISON WITH OTHER *TRACHURUS* FISHERIES

The world catch of *Trachurus* is composed of about 13 species from the Atlantic, Pacific, and Indian oceans, and Mediterranean Sea (Berry and Cohen 1972). Two or more species often co-occur in the same region (e.g., Stephenson and Robertson 1977). In these cases one species typically attains a maximum size of 60-70 cm, and the other reaches a size of 40-45 cm. The smaller species is usually a coastal pelagic schooling fish vulnerable to purse seine fisheries. The larger species tends to be distributed widely offshore, forming semidemersal or pelagic schools, which are caught by bottom or midwater trawls. *Trachurus symmetricus* is the sole inhabitor of the northeast Pacific, and appears to fill both of these ecological niches.

Except for growth, population parameters are poorly known for most stocks of *Trachurus*. Rates of growth are relatively slow. Age at first maturity ranges from 1 to 4 years. Longevity varies from 6 years for *T. japonicus* to 35 years for *T. trachurus* (Macer 1977), the latter value being similar to that for *T. symmetricus*. Differences in longevity can be attributed to differences in age determination techniques and exploitation rates as well as inherent differences among species. Stock abundance, recruitment, and mortality rates have not been estimated for any of the *Trachurus* stocks, making *T. symmetricus* among the best-known cases. Fisheries on these stocks have developed with very little management information on their status or potential yield.

The total world landings of *Trachurus* have increased in the last 20 years from about 0.9 to 2.7 million MT in 1980 (Table 3). The major fisheries occur along the eastern Atlantic from the English Channel to South Africa; the total annual Atlantic harvest has exceeded 1 million MT since 1971, although some fisheries such as *T. trachurus capensis* off South Africa have declined severely. The large fishery off Japan has declined steadily from 0.6 million MT in 1965 to 0.06 million MT in 1980. This decline suggests that the stock was overfished, but has not collapsed catastrophically. The South American fishery off the coasts of Peru and Chile has increased rapidly since the collapse of the Peruvian anchoveta fishery in 1972, although the extent to which stock abundance or productivity has increased is unknown. The South American catch has exceeded 1 million MT since 1978, and accounts for all of the recent increase in

TABLE 3

World Catch of *Trachurus* spp by Oceanic Regions for 1965 to 1980 in 1,000 MT[1]

	Atlantic Ocean				Pacific Ocean					
	North eastern	Central eastern	South eastern[2]	Medit. Sea	North western	South western	North eastern	South eastern	Indian Ocean	Total
1965	124	52	311	42	553	—	30	15	—	1,127
1966	109	37	300	41	487	<1	19	22	—	1,015
1967	119	102	245	62	334	<1	17	30	—	909
1968	143	166	206	43	315	<1	25	27	—	925
1969	152	258	148	42	286	<1	24	23	—	969
1970	249	297	232	37	222	<1	22	117	—	1,176
1971	241	480	384	42	283	14	27	168	<1	1,639
1972	260	456	363	56	156	19	24	180	<1	1,514
1973	356	486	482	65	131	16	9	164	3	1,712
1974	285	501	346	43	169	19	10	324	4	1,700
1975	277	444	444	45	193	14	17	299	5	1,738
1976	354	433	679	64	138	16	18	377	5	2,084
1977	224	492	753	64	95	18	50	848	35	2,579
1978	146	330	968	76	64	11	32	1,025	10	2,662
1979	143	250	768	118	93	8	17	1,287	8	2,692
1980	137	490	695	94	57	7	22	1,195	35	2,732

[1] Source is FAO catch statistics.

[2] Includes a few tons from southwestern Atlantic off South America.

world catch of *Trachurus*. *Trachurus symmetricus* off California, and the New Zealand and Indian Ocean species appear to be the only remaining lightly exploited *Trachurus* stocks.

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THE BIOLOGY OF THREE PELAGIC SHARKS FROM CALIFORNIA WATERS, AND THEIR EMERGING FISHERIES: A REVIEW

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ABSTRACT

The rapid growth of a drift gill net fishery for pelagic sharks off southern California has caused concern among fishery biologists because elasmobranchs tend to have slow growth and low reproductive rates. The primary targets of this developing fishery are the common thresher shark, *Alopias vulpinus,* and the bonito shark, *Isurus oxyrinchus.* Not marketed, but also taken in large numbers, is the blue shark, *Prionace glauca.* From 1976 through 1981, annual shark landings increased from 360 to over 1575 metric tons (MT). During the same period, the drift gill net fleet grew from 15 to 200 vessels. During 1982, thresher shark landings alone exceeded 1059 MT. Bonito shark landings reached nearly 231 MT. We report our results to date on the age, growth, and reproduction of these three pelagic species.

Ages between 0 and 15 years were estimated for 167 thresher sharks ranging from 360 to 5733 mm total length (TL). Male thresher sharks mature at 3330 mm TL, and females at 2600 to 3150 mm TL. Age at maturity ranges from 3 to 7 years. Females give birth to 4 pups annually. Little is known about stock distribution or abundance.

Ages between 0 and 17 years were estimated for 44 bonito sharks ranging from 900 to 3210 mm TL. Bonito sharks mature at 1800 mm TL. The number of offspring reportedly varies between 2 and 16. Ages between 0 and 9 years were estimated for 130 blue sharks ranging from 280 to 2521 mm TL. Blue sharks reach maturity at 2200 mm TL. The number of offspring may be as high as 82. Because of the limited area over which the current southern California fleet operates, and the lack of information concerning the distribution and stock structure of these three pelagic species, the future of the southern California gill net fishery cannot be predicted.

RESUMEN

El rápido incremento de la pesca de tiburones pelágicos en el sur de California, usando trasmallos, ha causado preocupación a los biólogos pesqueros, ya que estos Elasmobranquios presentan un crecimiento lento y un índice de reproducción bajo. Esta pesquería se enfoca principalmente al *Alopias vulpinus* (pez zorro), *Isurus oxyrinchus* (marrajo), capturándose también un número elevado de *Prionace glauca* (tintorera), aunque estos últimos no se cotizan todavía en el mercado. Desde 1976 hasta 1981, los desembarcos de tiburones aumentaron de 360 hasta más de 1575 toneladas métricas. Durante este período, la flota que utiliza trasmallos aumentó de 15 a 200 embarcaciones. Los desembarcos de *Alopias vulpinus* sobrepasaron las 1059 Tm. en 1982, mientras que *Isurus oxyrinchus* llegaba a las 231 Tm.

Se incluyen los resultados obtenidos sobre la edad, crecimiento y reproducción de estas especies de tiburones. 167 ejemplares de *Alopias vulpinus* incluían peces de menos de un año y de hasta 15 años de edad, con tallas de 360 hasta 5733 mm de longitud total (LT). Los machos de *Alopias vulpinus* maduran a los 3330 mm de longitud, y las hembras entre los 2600 mm y 3150 mm de longitud total. La edad que tienen al alcanzar la madurez sexual oscila entre 3 y 7 años. Las hembras producen 4 crias cada año. Se conoce poco sobre la distribución y abundancia de las poblaciones de esta especie.

44 *Isurus oxyrinchus* oscilaban entre edades de menos de un año y 17 años, con tallas de 900 mm hasta 3210 mm de longitud total. *Isurus oxyrinchus* madura cuando alcanza 1800 mm de longitud total. El número de crias que producen al año varía entre 2 a 16.

Se obtuvieron 130 *Prionace glauca* con tallas de 280 a 2521 mm de longitud total, y edades entre menos de un año y 9 años. Las tintoreras alcanzan su madurez sexual a los 2200 mm de longitud total. El número de crias puede ascender a 82 por año.

Debido a que la zona cubierta por la flota que actualmente opera en aguas del sur de California es muy limitada, y la carencia de información sobre la distribución y estructura de las poblaciones de estas tres especies pelágicas, no se puede predecir el futuro de la pesquería con trasmallos que está operando en el sur de California.

[Manuscript received March 14, 1983.]

INTRODUCTION

During the last few years, commercial fishing for pelagic sharks has increased rapidly in California's coastal waters. Historically, sharks were used primarily for their oils and for reduction (Byers 1940) and for the vitamins in their livers (Frey 1971). Today, however, their principal use is for human food. In 1977 a new fishery began to develop off the coast of southern California. Long gill nets, drifted near the surface in deep offshore waters, were used successfully to land pelagic sharks. Recent increases in the retail demand for fish had led wholesale buyers to look for new sources, and shark meat looked promising to many. Wholesalers began to pay a good price for sharks, creating a new and attractive market for commercial fishermen. The new shark fishery grew rapidly.

Fishery biologists began to express some concern over the rapid expansion of the commercial shark fleet. Historically, shark fisheries have tended to decline soon after their initial success, principally because of the relatively slow growth and reproductive rates that seem to characterize elasmobranchs as a group (Holden 1973, 1974, 1977). Perhaps the new pelagic shark fisheries might also be subject to a similar decline. Unfortunately, there was little life-history information (generally considered an effective prerequisite for management) available on any of the main pelagic shark species. Aging techniques had not been evaluated for any of the three pelagic sharks being fished in California, and very little was known of their reproductive biology. This kind of information could prove critical in the development of management measures. We have been working for several years toward a better understanding of the biology of these species, particularly in regard to age, growth, and reproduction.

We here describe the California pelagic shark fishery, both in terms of fishing methodology and historical development. We then review what is currently known about the biology of these most important species.

DESCRIPTION OF THE FISHERIES

The southern California drift gill net fleet targets on pelagic sharks (the common thresher, *Alopias vulpinus*; the bonito or short-fin mako, *Isurus oxyrinchus*; and the blue shark, *Prionace glauca*) and swordfish (*Xiphius gladius*) in the deeper waters surrounding the Channel Islands chain.

The basic gear includes a hydraulically driven spool or drum on which the net may be rolled. The spool is most often located on the stern of the vessel. The net is constructed of nylon twine, and the mesh sizes of nets used in this fishery may range from 8 inches (20.3 cm) to 20 inches (50.8 cm) stretched. Mesh sizes of 14 inches (35.6 cm) and 16 inches (40.6 cm) seem to be favored. Most nets range from 10-20 fathoms (18.3-36.6 m) in depth, and may be as long as 1000 fathoms (1828.8 m).

When fished, the drift gill net hangs vertically in the water column, stretched between a buoyant corkline on one side, and a lead line on the other (Figure 1). The entire net is suspended by a series of floats attached at intervals of about 10 fathoms (18.3 m). The floats are attached to the corkline via extension lines, usually ranging from 1-3 fathoms (1.8-5.5 m) in length. As a result, the net is suspended beneath the surface commensurate with the length of these extensions. While fishing is underway, the boat remains attached to the net at one end. Attached to the opposite end of the net is a buoy on which a strobe light and radar reflector are mounted.

Drift net fishing operations are conducted during nighttime hours. Until 1982, drift net fleet activities extended from south of Point Conception to the Mexican border. In the summer of 1982, drift gill net operations began to expand northward to Morro Bay. Currently, a few vessels are fishing on an exploratory basis as far north as Monterey Bay. Drift gill net op-

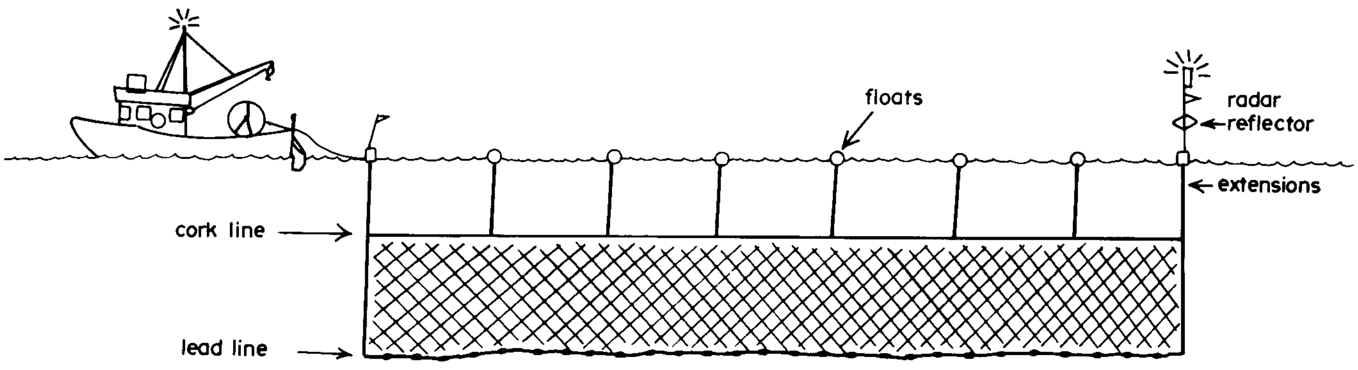

Figure 1. Drift gill net in operation.

erations north of Point Conception are severely limited by sea conditions.

The drift gill net fleet has undergone rapid expansion from 15 participating vessels in 1977 to the current level of about 200. Aside from the dramatic increases in the ex-vessel price of common thresher and bonito sharks, the discovery that large-mesh drift gill nets provided an efficient method of taking swordfish served to fuel that expansion.

Landings of various shark species in California have historically been little more than incidental byproducts of other fisheries. Until recently, the only exception was the soupfin shark fishery, which began in 1937 (Byers 1940) and continued for a period of approximately ten years (Figure 2). Even so, it was not the shark's flesh which prompted this fishery. It was the high concentration of vitamin A in the soupfin's enormous liver that led to the demand for this species. When vitamin A was synthesized in a laboratory following the end of World War II, the soupfin fishery collapsed just as suddenly as it had begun (Ripley 1946).

During the 1970s, the rising cost of red meat and growing public awareness of health benefits from decreasing one's animal fat consumption probably contributed to the increase in consumer demand for fresh fish. As this demand grew, wholesale fish dealers began to look for new sources of fish protein. An interest in sharks was renewed, this time for their food value. Over the period from 1976 to 1981, shark landings increased from 391 MT (800,000 lbs) to nearly 1600 MT (3,500,000 lbs) annually (Table 1).

In addition to drift gill nets, at least one vessel out of San Pedro has targeted on the blue shark using longline with 2-m stainless steel leaders baited with anchovy or squid. This process allows these sharks to be cleaned immediately after live capture, and prevents the flesh from becoming unpalatable as the fish's high urea content rapidly decomposes in the dead blue sharks.

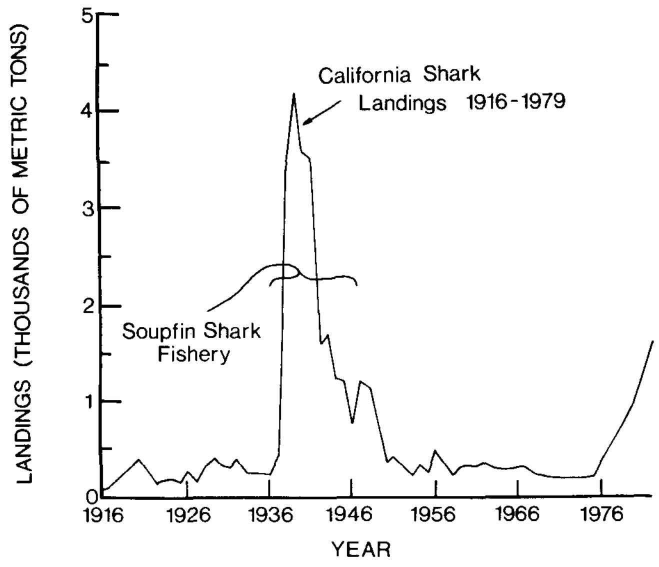

Figure 2. Annual landings of sharks (all species) in California.

DRIFT GILL NET FLEET MONITORING

In September 1980, a program was established for direct observation of on-board activities and catch of the drift gill net fleet. California Department of Fish and Game personnel boarded certain fishing vessels before they left port, and remained on those vessels during entire fishing trips. While aboard, the observers kept a complete record of activities pertaining to all interactions between crew members and marine life. Additionally, the observers gathered biological information on the size, age, sex, and reproduction of the target species.

Between October 1980 and November 1982, 17 different drift gill net vessels were observed during 53 separate fishing trips, for a total of 270 nights of fishing. These observations represent approximately 3% of the fleet's fishing activity. The limited and nonrandom number of observable vessels and observations restricts statistical inferences that might be made about the fleet as a whole. However, we are confident that our observations of the drift gill net fleet are representative. To support this assertion, we make the following points:

1. This fishery targets on pelagic species that are not uniformly distributed around the entire fishing ground. When a group of fish is located in an area, the fleet, generally moving as a unit, converges on that specific area.
2. The major components of the fishing gear and the methodology behind its use are well standardized throughout the fleet.
3. The catch of marketable species from observed vessels closely parallels the reported catch from unobserved vessels. This has been verified by comparison of wholesale market receipts.

TABLE 1
Shark Landings in All of California from 1976 to 1981

Year	Landings (metric tons)
1976	391
1977	580
1978	748
1979	1,006
1980*	1,488
1981	1,599

*Preliminary information.

AGE, GROWTH, AND REPRODUCTION STUDIES

For this portion of the study, most blue shark specimens were collected between September 1974 and October 1977 in Monterey Bay, California, by longline and hook and line. Most collections of common thresher and bonito sharks, and several specimens of blue shark were obtained from commercial fisheries in southern California, and from the California Department of Fish and Game's pelagic gill net observer program. Additional preserved specimens of all three species were obtained from several California museums.

All sharks were measured (mm), weighed (kg), and their sex and reproductive status was noted, if possible. The main measurements used were total length (TL), fork length (FL), and alternate length (AL, the distance between the origin of both dorsal fins). All length measurements were converted to total length for uniformity using conversion factors based upon measurements from our own specimens and from the literature (Bigelow and Schroeder 1948; Applegate 1967). To estimate total length from alternate length and fork length (all in mm), we used $TL = (5.73 \times AL) - 54.29$, and $TL = 1.85 \times FL$, respectively.

For age determination, a section of the vertebral column was removed, usually just anterior to the first dorsal fin, because this appears to be the area where vertebrae are largest and most calcified (Ridewood 1921). However, in some cases such as common threshers collected from fish markets, we could only obtain caudal vertebrae from carcasses. For details on processing and cleaning the vertebrae, see Cailliet et al. (in press, a). The aging technique used for blue sharks was modified from a procedure attributed to Von Kossa, in Stevens (1975). This basically involved replacing the calcium salts in the centrum with silver, providing distinct silver-impregnated bands, which become quite dark after illumination under ultraviolet light. A dissecting microscope with illumination focused laterally on the centrum was used to count bands. The cleaned centra from the common thresher and bonito sharks were X-rayed with a Hewlett-Packard Faxitron Series X-ray system (Model No. 43805N) and Kodak Industrex M film (Readypack M-2). These X-radiographs were viewed through a dissecting microscope using transmitted light from below. For both of these techniques, procedures for counting the concentric lines were standardized.

For simplicity and the widest applicability of this preliminary age information, we fit our data on age and length for all three species to the von Bertalanffy (1938) growth equation using methods for calculating the parameters L_∞, K and t_0 from Allen (1966), Gulland (1969), and Everhart et al. (1975). The parameter estimates producing the best fit (least mean square error) from one of these methods were then selected to plot the growth curve for each species. These parameters were calculated for all individuals of each species combined, and separately for male and female blue and common thresher sharks. Sexes were not separated for bonito sharks, because the data set consisted of only 44 fish. For the bonito shark, we also used the logistic growth equation (Ricker 1979).

As an initial evaluation of the temporal periodicity of band formation, we plotted size-frequency histograms of all specimens of each species collected during the entire study period, and superimposed over these the means and standard deviations of the sizes categorized into each age division by band counts. Visually, we then compared these mean sizes with modes in the size-frequency distribution.

For the blue shark, we compared our growth curve with information presented for North Sea blue sharks by Stevens (1975, 1976), and we sent two of our centra to him for independent band counts. Our bonito shark growth data were compared with those presented by Pratt and Casey (in press) for the same species in the Atlantic Ocean. For all three species, we also compared the size and age at birth, at first maturity, and the maximum size reported in the literature with the values estimated from our growth curves to gain insight into the accuracy of our counting methods.

The reproductive biology of the common thresher sharks from waters off California was examined during at-sea observations of the pelagic shark fleet. Estimates of size at maturity for males and females, length of the gestation period, and litter size were made[1].

Common Thresher Shark (**Alopias vulpinus**)

Fisheries statistics. Prior to the use of open-water drift gill nets, landings of thresher shark were incidental in hook and line, purse seine, and nearshore gill net fisheries. When the first experiments with offshore drift nets were started in 1977, approximately 15 part-time gill netters landed 59 MT (129,000 lbs) of thresher shark. The years following have seen a dramatic increase in the landings of this pelagic species (Table 2). Thresher sharks are caught off southern California from spring to fall (Figure 3).

We have attempted to characterize fishing pressure on the thresher shark stock through two indirect means: analysis of length-frequency data, and examination of the trends of catch per unit of effort (CPUE). Length-frequency data illustrate the size

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[1] Bedford, D. B. Sexual maturity and fecundity in the common thresher shark (*Alopias vulpinus*) off southern California. Manuscript, 10 pages.

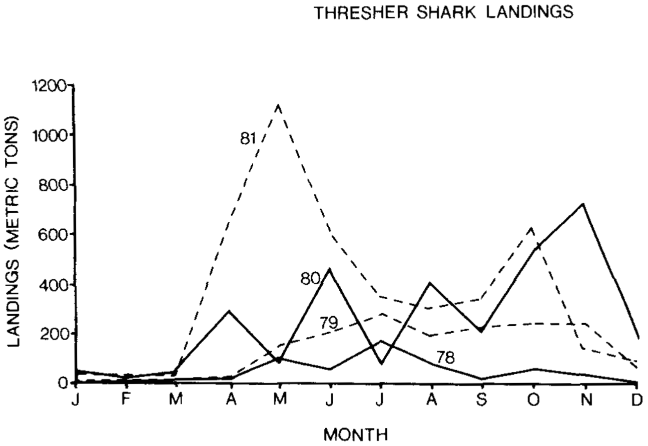


Figure 3. Monthly landings of thresher shark by drift gill net.

structure of the segment of the population that is vulnerable to capture. Length-frequency curves prepared for the 1981 and 1982 seasons based on market sampling in San Diego, San Pedro, Santa Barbara, and Morro Bay (Figure 4) indicate no obvious size-structure shifts, but the two-year time series is too short to allow resolution of trends.

CPUE data provide a measure of the relative density of the available population. We assume that the density of fish on the fishing grounds is an index of the magnitude of the total population. An index of CPUE has been prepared for the seasons 1977-82 using the number of landing receipts listing any thresher shark as an indicator of a completed trip (Figure 5). One trip is considered one unit of effort.

This index, based on landing receipts, is very crude. However, if the population was in immediate danger of depletion, even a tenuous index such as this one might illustrate that danger through a rapid decrease in both total catch and CPUE. On the other hand, the early years of a fishery are a period of learning and gear improvement, and this may obscure actual trends in abundance. Neither length-frequency data nor trends in CPUE yet show apparent impacts of the fishery on this migratory shark species.

TABLE 2
Thresher Shark Landings by the Drift Gill Net Fleet and the CPUE Indices

Year	Thresher (metric tons)	Number receipts	CPUE (MT/trip)
1977	59	349	0.17
1978	137	433	0.32
1979	334	745	0.45
1980	638	880	0.73
1981	895	1632	0.55
1982*	994[1] (1059)[2]	1851[1]	0.54

*Preliminary
[1]through September
[2]through December

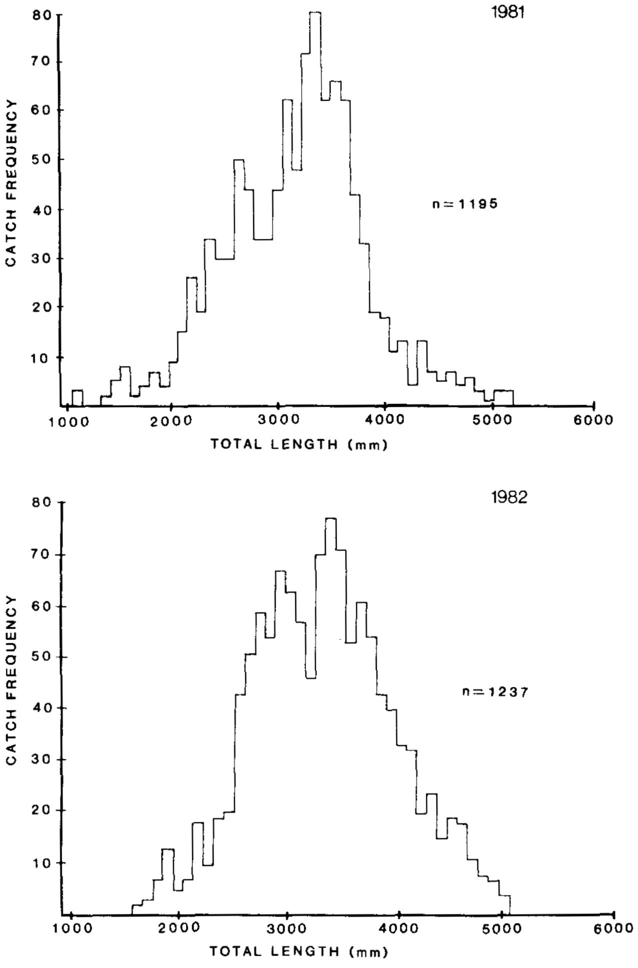


Figure 4. Length-frequency histogram of thresher shark landings.

Distribution. The common thresher shark is an inhabitant of most temperate and subtropical waters, including the Pacific, Atlantic, and Indian oceans, and the Mediterranean and Red seas (Bigelow and Schroeder 1948; Roedel and Ripley 1950; Miller and Lea 1972; Gubanov 1978). In the eastern Pacific, the thresher shark has been reported from Vancouver Island to Chile, although it seems likely that the stocks are discontinuous across the equatorial regions. One survey of Pacific oceanic sharks indicated that the thresher is abundant in nearshore waters only, but may make long-range movements (Strasburg 1958).

Age and growth. For age determination, 167 common thresher sharks were collected from the southern California gill net fishery and museum collections. The specimens ranged in size from embryos of 360 mm TL and free-living juveniles of about 1450 mm

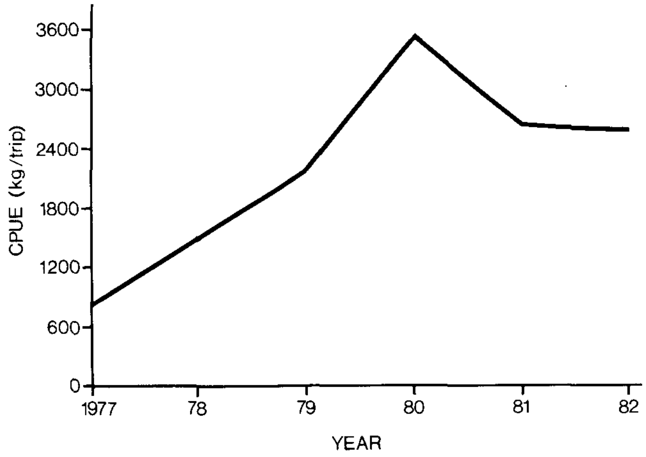
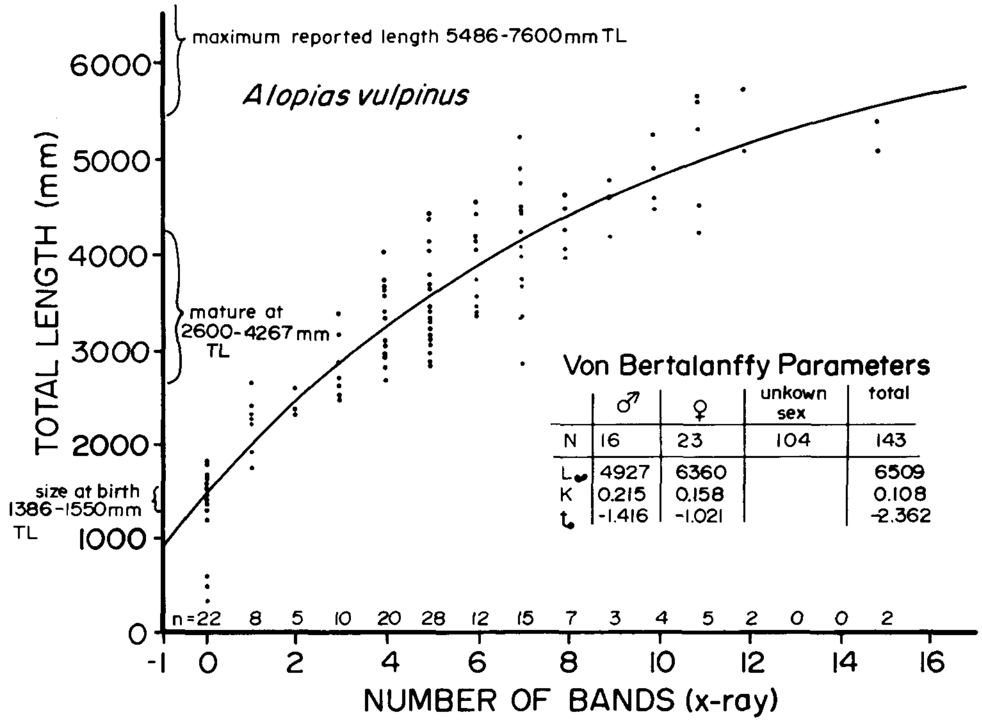


Figure 5. Catch per unit of effort for thresher shark.

TL to adults up to 5733 mm TL. Because common threshers are reported to reach maximum lengths of 6096 mm TL (Bigelow and Schroeder 1948) to 7600 mm TL (Hart 1973), our sample does not contain sufficient representatives of the larger size classes. However, Hart (1973) reports that 13- to 16-foot (3800-4900 mm TL) specimens are "common" in the northeastern Pacific, and therefore our sample includes representatives of the locally occurring larger size classes of this species.

The X-radiography technique was used to age common thresher sharks because it enhanced bands well, and many vertebrae could be processed easily in a short time. The von Bertalanffy growth curve for the 143 aged common thresher sharks ranging between 360 and 5733 mm TL rose gradually and began to level toward the estimated asymptotic length (L_∞) of 6509 mm TL for both sexes combined (Figure 6), which is only 14% smaller than the maximum reported length (6500 mm TL), and within the size range of the commonly occurring largest specimens collected in the Pacific (Strasburg 1958; Hart 1973). Females were estimated to reach a longer length (6360 mm TL) than males (4927 mm TL). The two oldest fish aged had 15 bands and measured 5102 and 5389 mm TL, and the youngest were eight embryos ranging between 360 and 1605 mm TL, having no bands. Unfortunately, sexes were unknown for most of the fish examined, because they were taken cleaned from fish markets.

Our estimate of size at birth, derived from the von Bertalanffy growth model (1580 mm TL), was slightly higher than reported smaller sizes of free-living young, which can be as small as 1168 mm TL (Bigelow and Schroeder 1948) and range up to around 1500 mm TL (Hixon 1979). One explanation for this difference is that our aging technique is not precise enough to distinguish time intervals smaller than one year. Another might be that different stocks living in differing oceanic conditions might exhibit different reproductive characteristics. In fact, this appears to be true when comparing size at birth and number of offspring reported by Gubanov (1978) for Indian Ocean speci-



	♂	♀	unkown sex	total
N	16	23	104	143
L_∞	4927	6360		6509
K	0.215	0.158		0.108
t_0	-1.416	-1.021		-2.362

Figure 6. Von Bertalanffy growth curve for 143 common thresher sharks collected in California waters and aged using X-radiography. Dots represent individuals of both sexes. Von Bertalanffy parameters for males, females, and the total sample are given in the insert. References used for size at birth, size at maturity, and maximum reported size include Bigelow and Schroeder (1948), Roedel and Ripley (1950), Hixon (1970), Miller and Lea (1972), Hart (1973), and Gubanov (1978).

TABLE 3
Estimates of Age (Number of Bands), Length, and Weight for Thresher Sharks from the Eastern Pacific Ocean

Age estimate (yrs)	Total length (mm)	Dressed weight (kg)
1	1981	15.9
2	2446	28.7
3	2954	48.9
4	3234	63.1
5	3569	83.1
6	3870	104.2
7	4140	126.1
8	4383	148.0
9	4601	169.4
10	4797	190.5

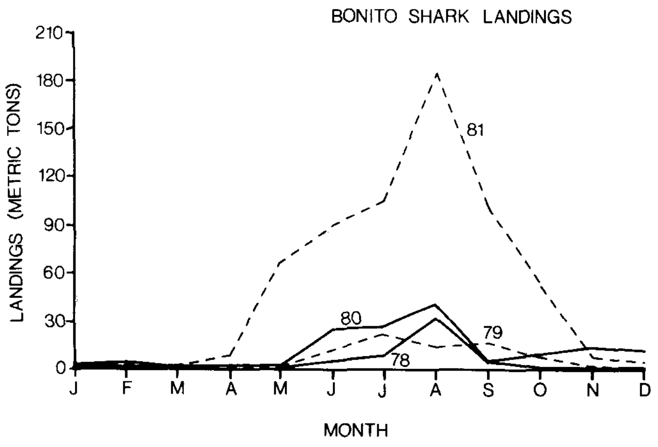


Figure 7. Monthly landings of bonito shark by drift gill net.

mens and those examined by Bedford (see Reproduction, below).

Because most length data in the literature were reported as total lengths, yet most field work could only measure fork length or alternate length, we converted all measurements to total lengths. The average dressed weight (kg) from sample data from southern California, when combined with estimates of total length at age (Figure 6), yields Table 3.

Mortality. At present, there are no estimates of natural or fishing mortality rates for the thresher shark in the Pacific Ocean. Natural mortality is assumed to be quite low, because thresher sharks are born alive, and are already about 1500 mm TL at birth. As a result, predation upon juvenile threshers is likely to be minimal. Even food does not seem to be an immediate problem for newborn threshers. At birth, their stomachs are often distended by a mass of yolk material consumed while still in the uterus (Bedford[2]).

Reproduction. Common thresher shark females range in length at reproductive maturity from 2600 mm TL in the Indian Ocean (Gubanov 1978) to 3150 mm TL in the Pacific Ocean (Strasburg 1958) and 4267 mm TL in the Atlantic Ocean (Bigelow and Schroeder 1948). Using the length of the inner margin of the claspers versus total length, we estimated that males off southern California reach maturity at about 3330 mm TL. These three lengths at maturity represent sharks ranging between 3 and 7 years old (Figure 6). Using our asymptotic length of 6509 mm TL, we found that common threshers apparently mature at a size between 39% and 66% of this length, overlapping somewhat with Holden's (1977) generalization of 60% to 90%. However, if we use the maximum reported size of 7600 mm TL, these sharks mature at between 34% and 55% of their maximum length.

From observations aboard drift gill net vessels, we found that thresher sharks in the northeastern Pacific appear to pup annually from March through June. Because gestation appears to last about nine months, mating most likely takes place around July and August. A pregnant female will typically carry four young (Bedford[3]). In our observations off southern California, we found that all mature females examined during the early spring were pregnant. The numbers of males and females in the population off southern California appear to be equal.

Migration. Adults are pelagic and considered to be highly migratory. Large numbers of threshers taken off the coast of California carry Japanese longline hooks, indicating an origin outside the U.S. Fishery Conservation Zone. Both adult and subadult threshers seasonally congregate in inshore waters of southern California; the greatest concentrations occur during spring and summer.

Stock structure and status. Differences in size at maturity, and in the number of offspring for Indian Ocean threshers reported by Gubanov (1978), for a thresher from the tropical central Pacific as reported by Strasburg (1958), and for those occurring off southern California suggest that separate stocks exist. Alternatively, these differences may simply reflect different physical conditions and forage levels.

Bonito Shark (Isurus oxyrinchus)

Fishery statistics. The bonito shark is considered one of the more palatable sharks, resulting in a relatively high ex-vessel price of \$.23-\$.45/kg (\$.50-\$1.00/lb). By comparison to the other targeted species of the drift gill net fishery, the average bonito shark is quite small, weighing in at only 9-14 kg (20 to 30 lbs). Thus the bonito shark is considered a "welcome incidental," rather than a true target.

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[2] See footnote 1 on page 60.

[3] See footnote 1 on page 60.

TABLE 4
Annual Landings of Bonito Shark (1978-82)

Year	Metric tons landed
1978	12.4
1979	16.0
1980	27.6
1981	125.7
1982*	187.8

*Through September.

Bonito shark landings have increased over the last five years in a manner similar to thresher landings (Table 4). But in the last two years landings of bonito shark have increased even beyond that which could be attributed to effort increases for the thresher shark, suggesting either fluctuations in availability or increased targeting.

At least two recent changes in the drift gill net fishery may have contributed to this sudden increase in bonito shark landings. First, there has been the anomalously warm water off southern California during the 1981 and 1982 seasons. Bonito sharks are known to have a distribution within the warmer ocean waters of the Pacific. Second, the legalization of drift gill net use in the swordfish fishery (Bedford and Hagerman 1983) may have played a role. Catch records for bonito shark (Figure 7) indicate peak seasonal availability between thresher shark (Figure 3) and swordfish.

Distribution. The bonito shark is an inhabitant of the warm and temperate oceans of the world (Bigelow and Schroeder 1948). In the eastern Pacific, it has been reported from Chile to the Columbia River, including the Gulf of California (Miller and Lea 1972). The bonito shark is pelagic, and may be found from nearshore to open-ocean waters.

Age and growth. Few specimens (50) of the bonito shark were available from the 1978-82 commercial catches and museum collections. The smallest specimen was a free-living 900-mm TL male, and the largest a 3210-mm TL female. Although this size range does not approach the largest individuals reported worldwide (3962 mm TL; Bigelow and Schroeder 1948; Roedel and Ripley 1950), nor the largest individual found off California (3507 mm TL; Applegate 1977), it is representative of the normal size range off California (2134-2438 mm TL; Roedel and Ripley 1950).

Both age determination techniques enhanced bands, but the X-radiography technique was used to age bonito sharks in this study because it was faster. The von Bertalanffy growth curve for the 44 bonito sharks we aged demonstrates a relatively slow growth rate that levels off at an asymptotic length of only 3210 mm TL (Figure 8). The oldest fish was estimated to have 17 bands, and was our largest individual (3210 mm TL), with exactly the same length as our estimated asymptotic length. In addition, the estimated asymptotic length is only 9% less than the maximum California reported length of 3507 mm TL (Applegate 1977), but is 16% less than the largest Indian Ocean specimen (3800 mm TL; Gubanov 1974), and 19% less than the maximum world size of 3962 mm TL (Bigelow and Schroeder 1948; Roedel and Ripley 1950; Miller and Lea 1972). Using the logistic growth equation on the same data produces a different curve, and a more reasonable estimate of asymptotic length of 4081 mm TL (Figure 8), which is only 3% higher than the reported maximum sizes worldwide. The differences between the curves produced by these two methods may be due to their differential sensitivity to the ages assigned to the smallest and largest individuals; hence, increased samples of these size classes should improve the curves.

Our estimates of size at birth, derived from either the von Bertalanffy or the logistic growth curves, agree with the scanty information available about the smallest, free-living bonito sharks (Figure 8). Garrick (1967) examined two embryos 605 mm TL, and one free-living male measuring 705 mm TL, whereas the smallest free-living shark examined by Gubanov (1978) was 900 mm TL, and by Strasburg (1958), 1251 mm TL. The mean size for one-year-old bonito sharks corresponds to the first size mode in sharks collected.

Reproduction. Bonito sharks reportedly do not mature until they reach lengths of 1800 mm TL (Gubanov 1978), 1828 mm TL (Bigelow and Schroeder 1948), or up to 2800 mm TL (Stevens 1983), which corresponds to a minimum age of about 7-8 years (Figure 8). Thus they reach maturity at a size that is only 56% to 87%, or 44% to 69% of the asymptotic lengths estimated by the von Bertalanffy and logistic growth models, respectively. They reach maturity at a size which is only 51% of the maximum length reported off California, and 45% of the maximum world size, both below Holden's (1977) generalization of 60% to 90%. The number of pups born to a bonito shark appears to range from 2 to 16 per birth (Bigelow and Schroeder 1948; Gubanov 1978; Stevens 1983). The length of gestation and the seasonality of pupping are unknown.

Blue Shark (Prionace glauca)

Fishery statistics. During our 270 night observations of the drift gill net fleet, equal numbers of blue sharks and thresher sharks were caught. Catch rates as

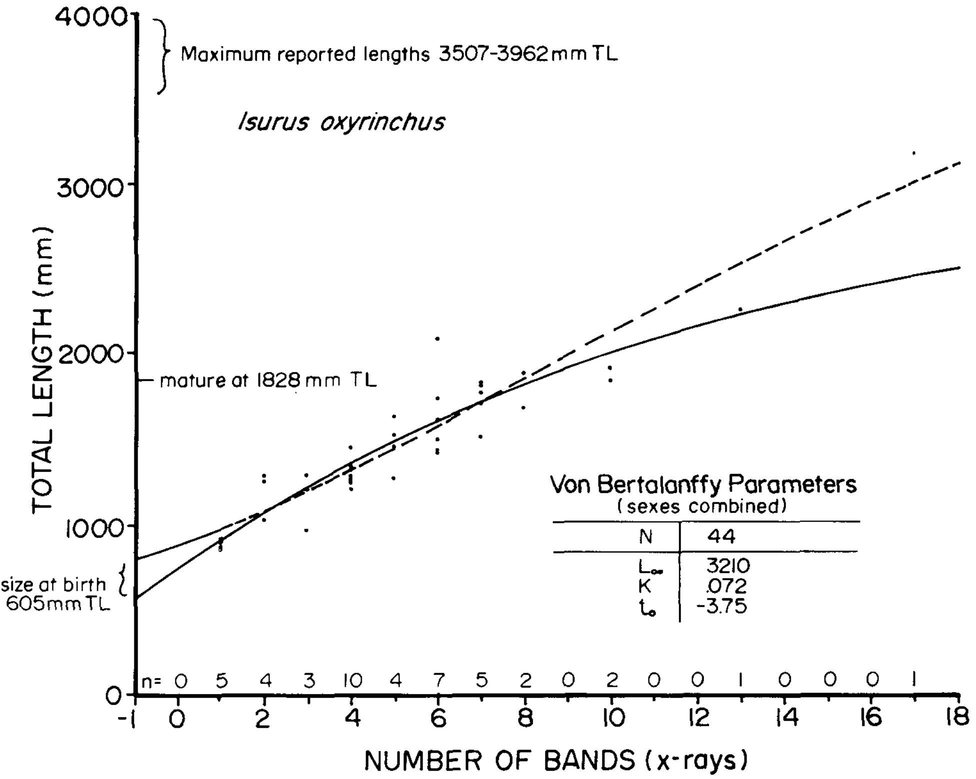

Figure 8. Von Bertalanffy (solid line) and logistic (dashed line) growth curves for 44 bonito sharks collected in California waters and aged using X-radiography. Sexes were combined because of small sample size, and von Bertalanffy parameters are for all 44 specimens. Reported size at birth, size at first maturity, and maximum size are from Bigelow and Schroeder (1948), Roedel and Ripley (1950), Garrick (1967), Applegate (1977), and Gubanov (1978).

high as 15,000 fish could contribute substantially to the income of commercial fishermen, except that unresolved spoilage problems render this fish unmarketable. Once wrapped in a gill net, these fish suffocate. Blue sharks must be bled, dressed, and cooled down while still freshly caught; otherwise the urea within the tissue begins to change to foul-smelling ammonia. Because the nets are left in the water overnight, by the time some blue sharks are retrieved they may have been dead long enough for this type of spoilage to have ruined the flesh for food purposes.

As with other shark species, there is a growing market demand for blue sharks, but not those caught by drift gill nets. An experimental longline fishery off southern California has proven successful in both capturing and processing blue sharks so that a high-quality marketable product results.

At this time, no one can predict with any certainty whether the high catch rates by the drift gill net fleet could result in a serious depletion of blue sharks. It seems advisable that the wastage be minimized, if that is possible. The most promising solution—larger mesh sizes—has been recognized by some commercial fishermen since this fishery first developed, but a trade-off situation exists because larger mesh sizes are also less efficient in capturing the targeted species. A second important potential solution involves the hanging distance of individual meshes along the corkline of the net; i.e., whether the net hangs fully stretched or loosely, creating a bagging effect. A fully stretched net captures fewer blue sharks, but the same trade-off exists as with mesh size. The escapement characteristics of both mesh size and hanging distance require further exploration.

Distribution. The blue shark inhabits all the temperate and subtropical seas of the world. It is abundant in both nearshore and open-ocean waters, and may be the most common of all the pelagic sharks (Strasburg 1958; Beckett 1970; Stevens 1976).

Age and growth. We caught a total of 120 blue sharks by longline in Monterey Bay between 1974 and 1977, and obtained an additional 42 specimens from museum collections and the commercial catch in southern California over a wider range of years. The Monterey Bay collections produced specimens ranging from 958 to 2045 mm TL, and fish smaller and larger than these sizes were added from the additional sources. The resulting size range was between 300 and 2705 mm TL. Because blue sharks are born at approximately 400 mm TL, and reach a reported maximum size of about 3962 mm TL (Bigelow and Schroeder 1948; Tucker and Newnham 1957; Strasburg 1958; Miller and Lea 1972; Hart 1973; Pratt 1979), our sample sizes are low for the smallest and largest size classes. Although the blue shark is known to make extensive, sexually segregated migrations (Strasburg 1958;

Beckett 1970; Stevens 1976), our samples suggest that the larger individuals are uncommon off central California or are not as vulnerable to commercial gear. Even with extensive collecting efforts, blue sharks over 2600 mm TL are quite rare in eastern North Pacific waters (Strasburg 1958).

Both silver nitrate and X-radiography produced clear bands, but the silver nitrate technique was chosen to age blue sharks because it was the first technique available; it worked consistently well; and it was also used by Stevens (1975) on this species. Because we counted bands in centra and not the finer rings, all counts taken before fixing in sodium thiosulfate were identical to those taken immediately after.

The von Bertalanffy growth curve for the 130 aged blue sharks ranging between 280 and 2521 mm TL rose steeply, and leveled at an estimated TL of 2655 mm for both sexes combined (Figure 9). Males were estimated to reach a larger asymptotic size (2953 mm TL) than females (2419 mm TL), but as in Stevens' (1975) study, there were insufficient samples to recognize significant differences in male and female growth rates. The oldest fish in our sample was a 2450-mm TL male that had nine bands; the youngest were two near-term embryos between 350 and 400 mm TL, having no bands.

The male asymptotic length was close to that of the largest common specimens collected in the Pacific (around 3100 mm TL; Strasburg 1958), but was considerably smaller than the largest reported blue shark (3962 mm TL; Bigelow and Schroeder 1948). With additional larger specimens, our estimate of asymptotic length might increase. This would agree more with the maximum reported size, unless Pacific blue sharks do not grow comparably to those in the Atlantic.

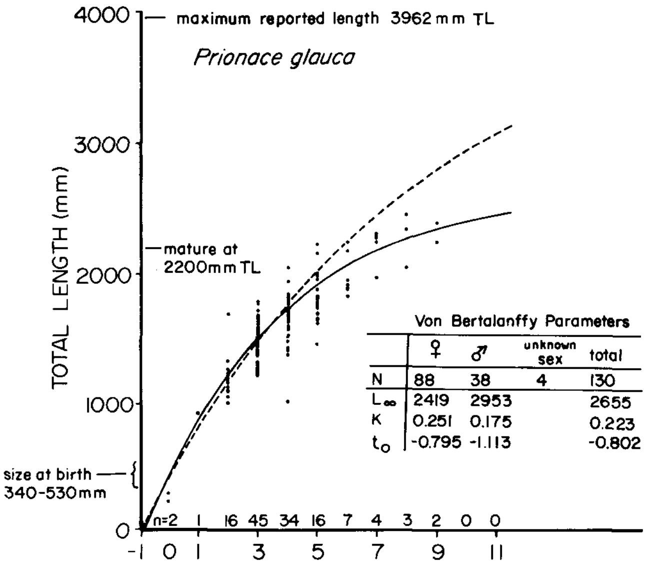

Figure 9. Von Bertalanffy growth curve for 130 blue sharks collected in California waters. Age was estimated using silver nitrate. Dots represent individuals of both sexes. Von Bertalanffy parameters for males, females, and the total sample are given in the insert. Dashed growth curve is based on Stevens (1975), and references used for size at birth, size at maturity, and maximum size were Bigelow and Schroeder (1948), Strasburg (1958), Hart (1973), Gubanov (1978), and Pratt (1979).

Our estimate of size at birth (435 mm TL), derived from the von Bertalanffy growth curve, was between the reported sizes of free-living young (340 and 530 mm TL) (Bigelow and Schroeder 1948; Tucker and Newnham 1957; Strasburg 1958; Hart 1973; Pratt 1979). Also, the mean sizes of the younger age classes corresponded to the size modes of blue sharks collected. With larger and older fish, the correspondence weakened, probably because of (1) small sample size, (2) mixing of several age classes into a larger size class because of different individual growth rates, or (3) slower growth rates in general.

Stevens (1975), using size frequencies and the silver nitrate technique on centra of 81 blue sharks of both sexes off England, produced a von Bertalanffy growth curve that corresponds to ours for the first three or four age classes, but his estimates of mean length of sharks between five and six years of age were higher. Stevens (1976), from tag-recapture size information, estimated growth at approximately 320 mm per year for sharks between 800 and 2040 mm TL, which is higher than our average estimate of about 210 mm per year taken from the growth curve for similarly sized blue sharks. Also, our measurements of radii in centra were somewhat smaller at higher band counts than those of Stevens (1975), providing further evidence that the growth rates in California blue sharks may be a bit less than in those found off England. Stevens (1975) used both his centrum band counts and Aasen's (1966) size-frequency data to generate growth curves and to estimate asymptotic lengths, for both sexes combined, of 3950 and 4230 mm TL, respectively. Both are considerably higher than the asymptotic length we derived from observed sizes and ages (2655 mm TL for both sexes combined; Figure 9). Because Stevens's counts of bands on two centra from our study were identical, his estimate of yearly growth rates from recaptured blue sharks (Stevens 1976) corresponds with our growth curve up to about 2000 mm TL. Stevens's (1975) size and age data fit within the range of observations we have found for similar age classes, the only differences between these two studies occurring in the small sample of larger fish. Blue sharks living under different oceanic conditions could exhibit different growth characteristics.

Total length (mm) and weight data from the central

TABLE 5
Estimate of Age (Number of Bands), Length, and Weight for Blue Sharks from the Pacific Ocean

Age estimate (yrs)	Total length (mm)	Weight (kg)
1	878	3.1
2	1234	8.9
3	1518	17.2
4	1745	26.5
5	1927	36.2
6	2072	45.5
7	2189	54.0
8	2282	61.5
9	2357	68.1
10	2416	73.2

Pacific by Strasburg (1958), when combined with estimates of total length at age, yield Table 5.

Reproduction. According to Pratt (1979), the blue shark reaches maturity at approximately 2200 mm TL, which, according to our age estimates, is six or seven years of age. Thus blue sharks become reproductively mature at about 56% of their maximum reported size, and 83% of our estimated asymptotic length. This conforms to Holden's (1977) generalization that most elasmobranchs become mature at about 60% to 90% of their asymptotic lengths.

The blue shark is viviparous, with its embryos having a well-developed yolk sac placenta attached to the uterine wall of the mother (Pratt 1979). The number of pups in a litter is large for an elasmobranch—as many as 135 (Gubanov and Grigor'yev 1975). Gestation lasts from 9 to 12 months.

Migration. Blue sharks are highly migratory. A large number have been tagged in the Atlantic, and trans-Atlantic migrations have been reported (Casey 1979). Some sharks tagged off the northeastern coast of the United States have been recovered as far away as the eastern Atlantic and Mediterranean. One equatorial crossing has been reported. It is likely that the Pacific population also migrates considerable distances.

GENERAL DISCUSSION

Many problems arise in estimating age and growth patterns of large and mobile organisms. It is difficult to obtain sufficient samples of all size classes, because of high cost and the time involved. The size and activity of these fishes make them difficult to measure accurately. Because cleaned market fish are often used, a conversion from an available shorter dimension—such as the distance between origins of both dorsal fins—to our standard unit of measure (TL) may cause some errors in estimating size. However, the techniques we have developed and applied to delineate bands in centra of these three species have provided consistent results. The resultant growth curves are generally supported by size at birth and by asymptotic or maximum length information. A major objective is to understand the periodic nature of the band formation in shark centra. Even when tag-recapture length information is available, interpretations are often limited by the accuracy and precision of the measurements (Pratt and Casey, in press). There are promising techniques available, such as tetracycline marking, histology, centrum edge characteristics, and natural radioactive geochronologues (see Cailliet et al., in press b) which, applied to these species in more large-scale and comprehensive sampling programs, could increase our understanding of their growth processes.

Our preliminary findings on age and growth, coupled with the literature on size and reproductive characteristics, indicate that these three pelagic species, which often occur together in coastal areas around the world, differ in their life histories. The blue shark is generally smaller than the bonito or the common thresher shark. Because the upper lobe of the common thresher's tail constitutes almost half of its total length, it is more conservative to compare weight of these fishes. The common thresher and bonito sharks range up to about 454 kg maximum (Bigelow and Schroeder 1948; Applegate 1977), whereas the largest blue shark ever taken probably weighed about 181 kg (Bigelow and Schroeder 1948; Strasburg 1958). Considering tail length, size at birth exhibits a similar trend. Blue sharks range between 340 and 630 mm TL at birth; bonito sharks range between 705 and 900 mm TL; and common threshers range between 1386 and 1552 mm TL (Bigelow and Schroeder 1948; Garrick 1967; Gubanov 1978; Pratt 1979). Size at maturity, which varies considerably among individuals, appears similar for all three of these species. The blue shark ranges in length at maturity from 1800 to 2500 mm TL, common threshers from 2600 to 4267 mm TL, and bonitos from 1800 to 1828 mm TL (Bigelow and Schroeder 1948; Gubanov 1978; Pratt 1979). Relative to ultimate maximum size or age, the blue shark reaches maturity later than either the common thresher or bonito sharks.

There is an apparent trend for fecundity to be lower in the largest species among these, although information on their reproduction is relatively sparse. Blue shark fecundity estimates range from 23 to 135 per female (Tucker and Newnham 1957; Gubanov and Grigor'yev 1975; Gubanov 1978; Pratt 1979), whereas the best estimates for bonitos are between 2 and 16 (Bigelow and Schroeder 1948; Gubanov and Grigor'yev 1975; Gubanov 1978; Stevens 1983), and for common threshers between 2 and 4 (Bigelow and

Schroeder 1948; Strasburg 1958; Hixon 1979). There is very little information about the gestation period for pelagic elasmobranchs. Pratt (1979) estimated that blue shark embryos reach full term in 9 to 12 months. Our growth curve supports this contention. One of us (Bedford) estimates that gestation in the thresher sharks lasts about 9 months. Virtually nothing is known about the gestation period of the bonito shark.

In conclusion, our preliminary data and the available literature indicate that these three pelagic sharks attain large sizes and exhibit relatively slow growth rates, long life-spans, and relatively low but variable fecundities. Therefore, as first postulated by Holden (1973, 1974, 1977), it is quite possible that this combination of life-history traits could make these species susceptible to overfishing, depending upon their population abundance, distribution, and migration patterns. However, this conclusion may be countered by our estimate of a relatively early age of reproductive maturity. More extensive samples of all sizes over a wider geographical range, an equal representation of sexes, and more detailed demographic analyses including age, growth, and reproduction need to be conducted before definitive statements can be made about the life histories of these species. Then, perhaps, the fisheries can be predicted and satisfactorily managed.

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THE BILLFISH FISHERY RESOURCE OF THE CALIFORNIA CURRENT

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ABSTRACT

Two species of billfish—swordfish, *Xiphias gladius*, and striped marlin, *Tetrapturus audax*—contribute substantially to fisheries off southern California. Both are highly migratory, worldwide in distribution, and occur seasonally in southern California waters—the northern fringe of their range in the eastern Pacific. Catches are highly variable from year to year.

Since 1937, California has reserved striped marlin for the exclusive use of recreational fishermen, although the fish are commercially taken in most other areas of the Pacific including off Hawaii.

Swordfish are exploited primarily by commercial harpoon and drift gill net gear under a number of restrictive regulations. Management of the fishery is based primarily on social and economic considerations, which attempt an equitable allocation of fish to user groups. A Preliminary Fishery Management Plan for billfish was drafted for the Pacific Fishery Management Council in 1981; however, after review, the plan was not implemented, and management was retained by California.

RESUMEN

Dos especies de Xiphidae, *Xiphias gladius* (pez espada), y *Tetrapturus audax* (Marlín listado) contribuyen en proporción considerable a las pesquerías del Sur de California. Ambas especies se distribuyen por todos los océanos, realizan amplias migraciones, y aparecen en ciertas épocas del año en aguas del Sur de California, zona que constituye el límite septendrional de su distribución en el Pacífico oriental. Las capturas que se obtienen varían ampliamente de un año para otro.

En California, desde 1937 se ha seleccionado el Marlín listado para la pesca deportiva, aún cuando también se pesca comercialmente en otras áreas del Pacífico, incluyendo la región de Hawaii.

La pesca comercial captura pez espada con harpón y trasmallos, pero ajustándose a estrictas regulaciones. La administración de la pesquería se basa principalmente en consideraciones socials y económicas, que tratan de establecer una distribución equitativa entre los grupos interesados en esta pesquería. El plan prèliminar para la regulación de la pesca de los Xiphidos ha sido diseñado en 1981 por el Consejo para la regulación de las pesquerías del Pacífico. Sin embargo, después de su revisión, el plan no se ha adoptado, pero las regulaciones han sido mantenidas por California.

INTRODUCTION

Two species of billfish—swordfish, *Xiphias gladius*, and striped marlin, *Tetrapturus audax*—appear along the southern California coast during summer and fall and contribute substantially to local fisheries. Both are considered highly migratory. The swordfish is the only member of the family Xiphiidae. The striped marlin is a member of the family Istiophoridae, which includes spearfishes, sailfish, and black, white, and blue marlin. The stock structure of the swordfish and striped marlin in the Pacific is not clearly defined.

Swordfish are exploited by active and competitive commercial harpoon and drift gill net industries. Both species are esteemed by recreational game fishermen, although few swordfish are actually landed by recreational anglers. Since 1937, striped marlin in waters off California have been reserved exclusively for sportsmen.

SWORDFISH

Distribution

Swordfish are cosmopolitan in distribution, being found in tropical and temperate waters of all oceans. In the Pacific, statistics for the Japanese longline fishery indicate that swordfish are distributed between 50°N and 50°S latitudes. Distribution is not uniform: areas of apparent concentration are in the North Pacific (20°-45°N), in the eastern Pacific from California to Chile, and in the southwestern Pacific from Australia to New Zealand (Figure 1).

The stock structure of the Pacific swordfish population is not clearly understood. Two hypotheses are widely held: either the population consists of a single Pacific-wide stock, or it consists of three separate stocks with centers of concentration in the northwestern, southwestern, and eastern Pacific.

In the eastern Pacific, a coastwide movement of fish between Baja California and California is evidenced by limited tagging data and Japanese longline hooks in fish taken off southern California. This hypothesis is further supported by the seasonality of the Baja Cali-

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[Manuscript received February 14, 1983.]

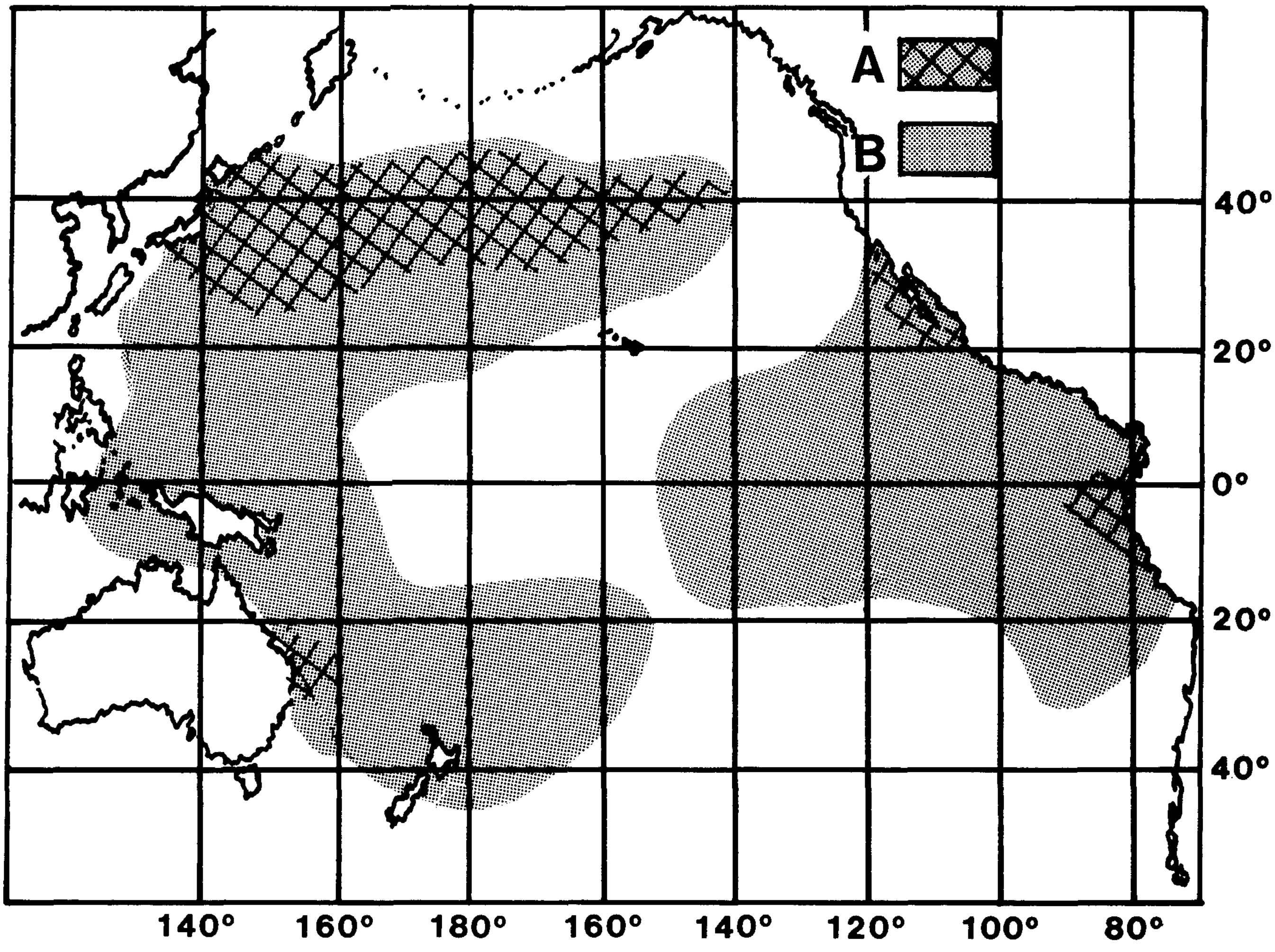

Figure 1. Distribution of swordfish determined from Japanese longline catch data: (*A*) high catch rate areas; (*B*) lower catch rate areas.

fornia and southern California fisheries. The Japanese longline fishery peaks off Baja California in December and January, followed by the southern California season, running from summer through fall.

Swordfish are found from the surface to at least 2,000 feet deep. They are caught by surface harpoon and rod-and-reel gear and at greater depths by gill nets and longlines.

Commercial Swordfish Fisheries in the North Pacific

In the North Pacific Ocean, the swordfish resource is exploited by several coastal and island nations. Japan, Taiwan, and Korea have large and mobile longline fleets and together account for most of the Pacific catch. Their combined longline fleets comprise over 2,000 vessels. In recent years, drift gill nets have accounted for 9%-10% of the swordfish taken by the Japanese fishery off Japan. The total annual Pacific catch of swordfish ranges from 10,000 MT to 19,000 MT and averages about 14,000 MT (Figure 2). A record of 24,286 MT of swordfish was caught in 1961. In the eastern Pacific (east of 150°W) off Mexico the annual catch of swordfish by foreign longline vessels averages about 4,700 MT a year (Figure 3).

The status of swordfish stocks in the Pacific was assessed by participants at the 1977 Billfish Stock Assessment Workshop (Shomura 1980). The participants concluded that, assuming a Pacific-wide stock, the resource is not overexploited and is in good condition. They further noted that catch per unit effort (CPUE) data from the Japanese longline fishery did not suggest overfishing of any of the hypothesized stocks.

California Commercial Swordfish Fisheries

Harpoon fishery. The swordfish harpoon fishery operates in the waters between Santa Barbara and the Mexican border (Figure 4).

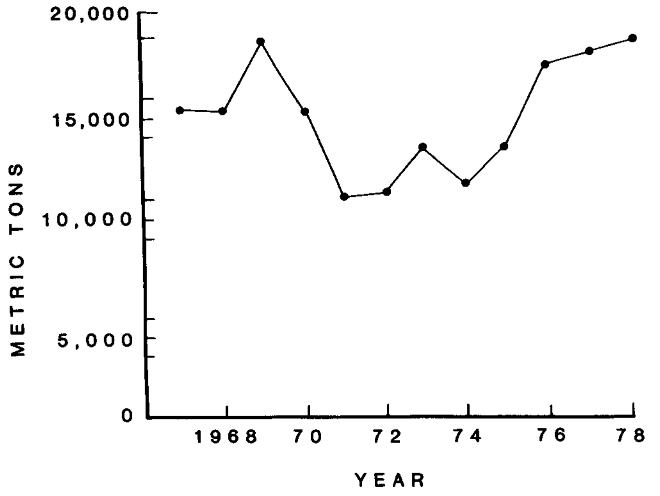

Figure 2. Catch of swordfish in the Pacific Ocean, 1967-78 (F.A.O.).

The fishery began sometime before 1908. In the early years catch records for swordfish and striped marlin were compiled as though these fish were the same species. Recognition of their separate status for the purpose of compiling fishery statistics first occurred in 1931 (Clark 1931).

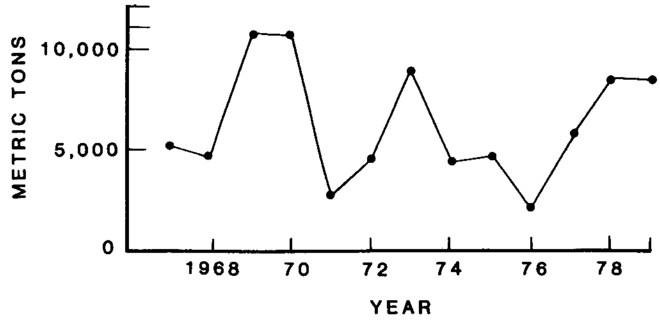

Figure 3. Estimated catch of swordfish in the eastern Pacific Ocean, east of 150°W longitude.

Prior to the mid-1920s there was very little demand for swordfish, and annual landings were low (Fitch 1960). Demand expanded in the second half of the 1920s as markets developed in the northeastern U.S. (Gillespie 1930; Fitch 1960). In response to this demand, California landings increased from about 10 MT in 1925 to over 58 MT in 1927. Between 1927 and

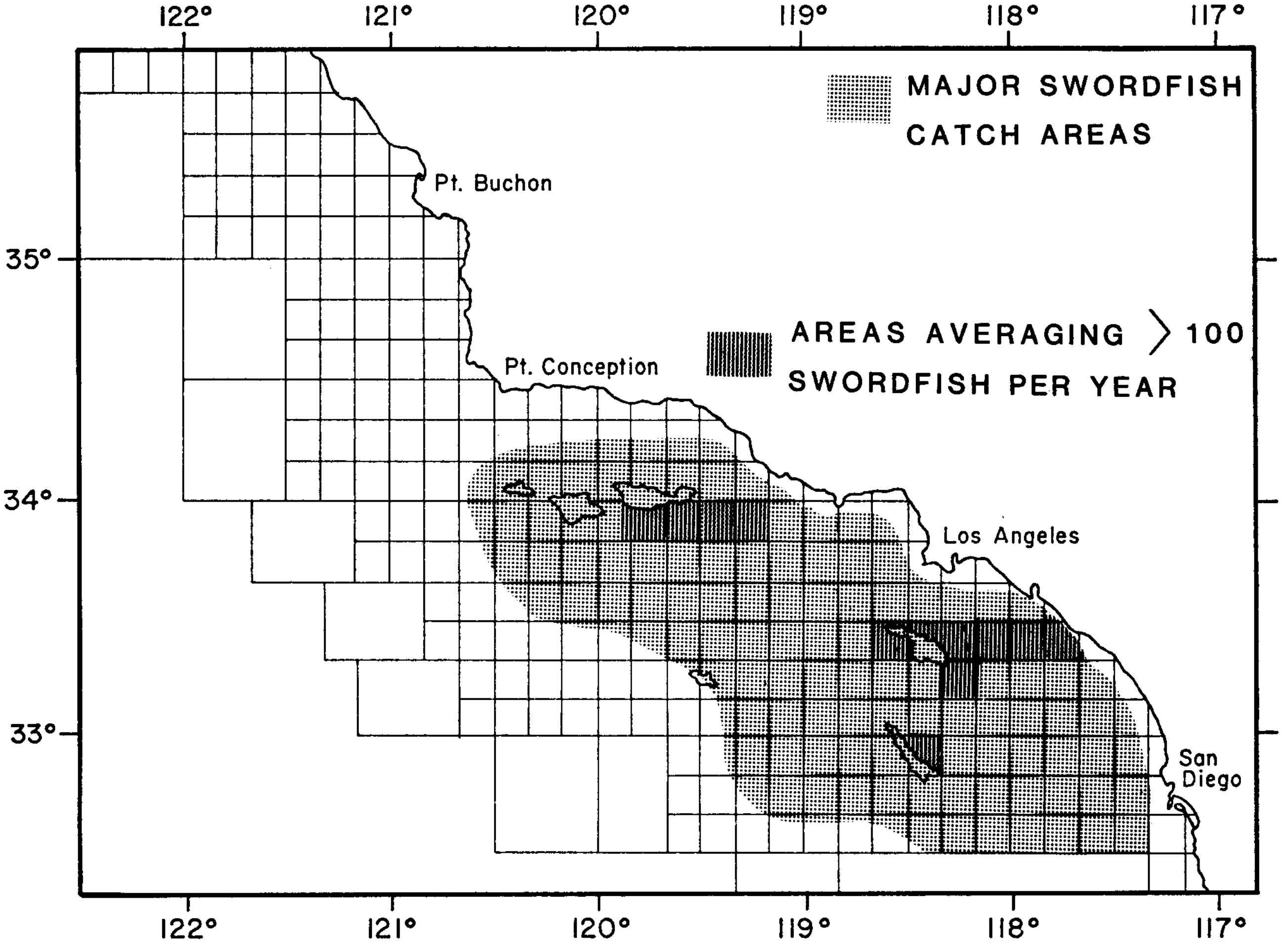

Figure 4. Area of operation, California harpoon fishery for swordfish, 1974-78.

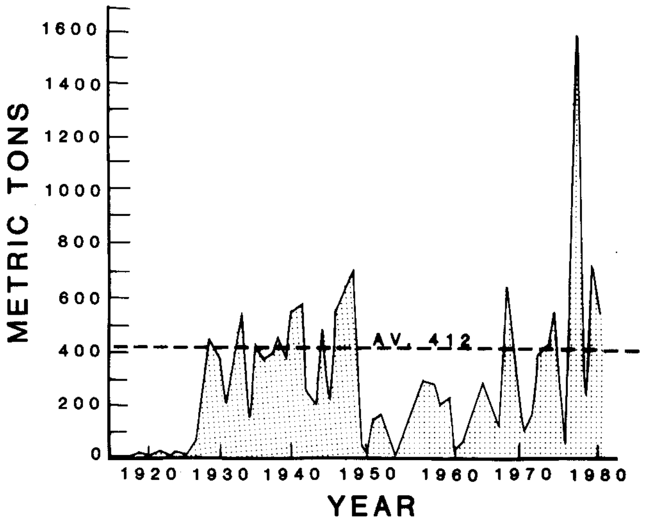

Figure 5. Swordfish landings in California, 1918-80, in metric tons adjusted to round weight (dressed weight plus 30%).

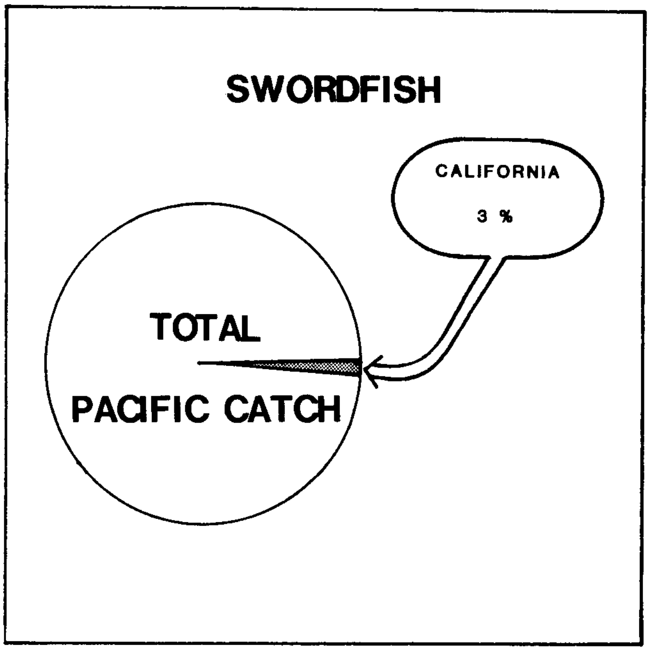

Figure 6. Average California swordfish landings are approximately 3% of the total average Pacific Ocean landings.

1948, landings fluctuated about a gradually increasing trend to a maximum of 622 MT in 1948. Landings declined to 16 MT in 1950, apparently because of a temporary shift in effort from swordfish to albacore. In 1951 the swordfish fishery resumed and has since fluctuated about a gradually increasing trend. In 1978 a maximum catch of 1,751 MT was recorded. The harpoon fishery has generally averaged a little over 400 MT per year since its beginning (Figure 5). This represents only 3% of the total Pacific-wide landings and 9% of the average eastern Pacific landings of swordfish (Figure 6).

Vessels engaged in swordfish harpooning are equipped with several items, some of which are unique to this fishery. Probably the most typical feature of a harpoon vessel is the *plank*. The plank is a scaffolding 20 to 30 feet long extending from the bow. The plank may be raised when the ship is traveling, particularly if seas are rough, or lowered into position when the vessel's crew is actively hunting swordfish. At the end of the plank is a small platform, termed the *pulpit*, on which the harpooner stands when the vessel is running a fish. Most of a fisherman's day is spent trying to see a fish at the water's surface. As an aid in locating fish, a second platform, or crow's nest, high on the vessel's mast is occupied during most of a fishing day. From the crow's nest a person can scan the nearby ocean surface for signs of finning. Binoculars are used to aid in the search. Once the fish is harpooned, line, buoys, and an attached marker-flag are thrown overboard, and the fish is allowed to tire while the vessel searches for more swordfish. It usually takes about 2 hours for a swordfish to become exhausted. Only then can the gear and fish be retrieved. Swordfish are dressed at sea and marketed with fins trimmed and the head removed back to the cleithrum.

The use of airplanes to locate swordfish began in the early 1970s. Between 1974 and 1975, the number of aircraft-assisted boats increased from 25 to 79. The number of planes engaged full-time in the harpoon fishery was approximately 20.[1]

Aircraft not only increase the searching area, but also make it possible to sight swordfish beneath the sea surface. The degree to which an aircraft can assist the searching operations is affected by weather and sea conditions (e.g., low stratus, haze and fog, heavy swell), and it is estimated that suitable conditions for the use of aircraft exist about 50% of the time. Aircraft tend to extend the fishing operation to include days of moderate chop, thereby extending the number of fishable days by an average of 25 per season. The catch per trip is greater for assisted than for unassisted vessels. Records for the 1974-75 season indicate that aircraft-assisted vessels landed about three times more swordfish than unassisted vessels.

The increased use of aircraft resulted in increased competition and conflict between commercial harpoon fishermen who did not use aircraft and those who did. Sportfishermen formed an alliance with harpoon fishermen who did not want the aircraft, and attempted to prohibit its use. In the 1973-74 session, the California legislature delegated the authority to man-

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[1] Hooker, C. W. Swordfish, *Xiphias gladius*, and the California fishery. Calif. Dept. Fish and Game. Long Beach, unpublished report. 29 p.

TABLE 1
History of Billfish Regulations

Year	Regulation
1931	Marlin and swordfish included in list of game fish. Sportfishing license required for species on list.
1933	Shipment of marlin meat out of state prohibited.
1935	Harpooning marlin prohibited. (Swordfish may be taken with harpoon and hook and line.)
1937	Selling marlin meat prohibited.
1951	Two swordfish per angler per day.
1971	One marlin per angler per day.
1973-74	Swordfish may be taken by permit only (commercial). Authority given to Fish and Game Commission to regulate commercial swordfish fishing.
1974	Fish and Game Commission adopts commercial swordfish fishing regulations. Logbook required. Notice given that aircraft could not be used after June 28, 1976.
1976	Fish and Game Commission permits use of aircraft for reconnaissance flights. Aircraft may not be used within 5-mile radius of swordfish boat operating aircraft.
1977	Radius extended to 10 miles from boat for aircraft operations.
1979	Swordfish taken incidental to shark gill net fishing may be sold.
1980	Shark gill netting under limited entry and permit system. Swordfish and marlin may be taken as incidental fish in shark drift gill nets. Marlin cannot be sold. Gill net take by quota system, based on harpooned swordfish and recreational catch of marlin. Onboard California Fish and Game observers required on vessels fishing under shark gill net and harpoon permits. (Kapiloff Bill—A.B. 2564).
1982	Permits the use of drift gill nets to take shark and swordfish, limits entry into the fishery, restricts the size and use of gear, closes specific areas for specified time periods to the use of drift gill nets for taking shark and swordfish, continues the additional privilege tax on thresher and bonito shark landings, and also continues the fees for the drift gill net shark/swordfish and harpoon permit. Also sets forth conditions under which the Department of Fish and Game must evaluate the resource. (Beverly Bill—S.B. 1573).

age the harpoon fishery to the California Fish and Game Commission. In 1974, the commission voted to prohibit use of the aircraft, effective June 28, 1976. In November 1976, the restriction was relaxed to allow aircraft to be used outside a 5-mile radius of the fishing boat. In 1977 the limit was increased to 10 miles (Table 1). This permits the use of aircraft to locate fish, but does not allow its use as an aid to harpooning.

The California harpoon fishery is essentially a summer/fall fishery, with the majority of effort expended between June and November. During the seasons when swordfish are not available or are available only in limited numbers, many of the full-time and some part-time swordfish fishermen shift their efforts towards other species or take shoreside jobs. Other species pursued include albacore, *Thunnus alalunga*, (0-120 days per season per boat); rockfish, *Sebastes* spp, (0-65 days per season per boat); and occasionally white sea bass, *Cynoscion nobilis;* halibut, *Paralichthys californicus;* and salmon, *Oncorhynchus* spp. The swordfish harpoon and albacore seasons are nearly coincidental. However, the former is primarily an inshore fishery, while the latter is offshore. Most swordfish fishermen prefer swordfish fishing to albacore fishing and will switch to albacore fishing only when swordfish are unavailable and albacore abundant (Clemens et al. 1965).

Estimates of effort in the California harpoon fishery are unavailable before 1974, at which time a mandatory swordfish permit and logbook system was instituted. There were 397 permits issued in 1974. The number increased 203% to 1,223 in 1979, then decreased in 1980. Of the individuals issued permits (1974-78), an average of 52% actually fished for swordfish, as evidenced by the submission of logbooks and market receipts. Approximately 34% of the individuals issued permits recorded catches of swordfish. The number of swordfish caught by individual permit holders varies considerably. An average of 12% of the active permit holders catch 50% of the swordfish (Table 2).

Drift gill net fishery. The southern California drift gill net fleet targets on pelagic sharks and swordfish in the deeper waters surrounding the California Channel Islands. The drift gill net fleet has undergone a rapid expansion from 15 participating vessels in 1977 to about 200 in 1982.

Drift net fishing operations are conducted during nighttime hours. Until 1982 fleet activities were con-

TABLE 2
Profile of the California Harpoon Swordfish Fishery, 1974-81

	Number by year							
Categories	1974	1975	1976	1977	1978	1979	1980	1981
Permits issued	397	473	387	442	802	1,223	*979 **408	428
Permit holders landing zero fish	236	312	313	274	502	—	220	
Permit holders landing 1-50 fish	135	139	73	149	200	—	648	194
Permit holders landing 51-100 fish	16	12	0	14	53	—	334	3
Permit holders landing >101 fish	10	10	1	5	47	—	13	1

*Prior to September 15
**After September 15 (institution of $150 permit fee)
—Data not available

ducted in the area south of Point Conception to the Mexican border. In the summer of 1982 drift gill net operation began to expand northward to Morro Bay. Currently a small number of vessels are fishing on an exploratory basis as far north as Monterey Bay. All drift gill net operations north of Point Conception are severely limited by sea conditions.

During the late summer and fall, large-mesh drift gill nets become an effective means for landing swordfish. In fact, this gear proved so effective that in October 1981, 3,121 swordfish were landed. This resulted in the closure of the drift gill net fishery, pursuant to California regulations permitting only an "incidentally" caught swordfish to be taken by drift gill net. During September 1982, new regulations were adopted to allow for use of drift gill nets to target on swordfish.

The basic gear for drift gill net operations includes a hydraulically driven spool, or drum, on which the net is rolled. The spool is most often located on the vessel's stern. Since the net is laid out and retrieved over the stern, there is a danger of wrapping the net around the prop. In order to avoid this, a guard railing constructed of some corrosion-resistant material such as galvanized steel tubing is lowered into the water during fishing operations.

The net is constructed of nylon twine usually size 18 or larger. No. 36 twine is sometimes used in the largest mesh nets. The mesh sizes of nets used in this fishery may range from 8 inches to 20 inches stretched. Mesh sizes of 14 and 16 inches seem to be favored. Most nets range from 10 to 20 fathoms in depth and may be as long as 1000 fathoms.

When in use, the drift gill net hangs vertically in the water column, stretched between a buoyant "cork line" on top and a "lead line" on the bottom. The entire net is suspended by a series of floats, attached at intervals of about 10 fathoms. The floats are attached to the cork line via extension lines, usually from 1 to 3 fathoms long. As a result, the net is suspended beneath the surface commensurate with the length of these extensions.

The boat remains attached to the net at one end. Attached to the opposite end of the net is a buoy, on which a strobe light and radar reflector are mounted. Occasionally, the crew may detach the boat from the net and switch to the opposite end. This is done in an effort to keep the drifting net in a straight line, because currents sometimes cause the net to wrap around itself.

California Sport Swordfish Fishery

Rod-and-reel fishermen consider swordfish one of the most desirable big game trophy fish. The Tuna Club (Avalon) has maintained records since 1898 and recorded the first swordfish taken with rod and reel in August 1913 (Tuna Club 1948). Prior to 1971 sportfishermen were permitted to take swordfish by both rod and reel and harpoon. In that year, the Fish and Game Commission declared that swordfish could be taken only by hook and line with a sportfishing license, and that harpoon fishing required a commercial license.

Club records indicate an average (1967-80) annual catch of swordfish by the rod-and-reel fishery of 29 fish, a negligible number compared to total Pacific, eastern Pacific, or commercial California catches. The peak catch (130 fish) was taken in 1978 (Figure 7).

The rod-and-reel fishery for swordfish in California operates between Santa Barbara in the north and 60-Mile Bank (32° 02′N, 118° 12′W) in the south. Within this range most rod-and-reel catches are made in the same areas as harpoon catches. The fishery extends from May through December.

STRIPED MARLIN

Distribution

Striped marlin are distributed throughout the Pacific and Atlantic oceans between 45°N and 45°S latitude. CPUE statistics for the Japanese longline fishery suggest a horseshoe-shaped pattern of high population density in the Pacific (Figure 8). The greatest hook rates in the Pacific are recorded from the area off the southern tip of Baja California, Mexico. High catch rates are also recorded from the central North Pacific and the eastern South Pacific (DeSylva 1974). The center of the high catch rate area off Mexico remains in the same position throughout the year, but expands and contracts seasonally. Its most expanded state

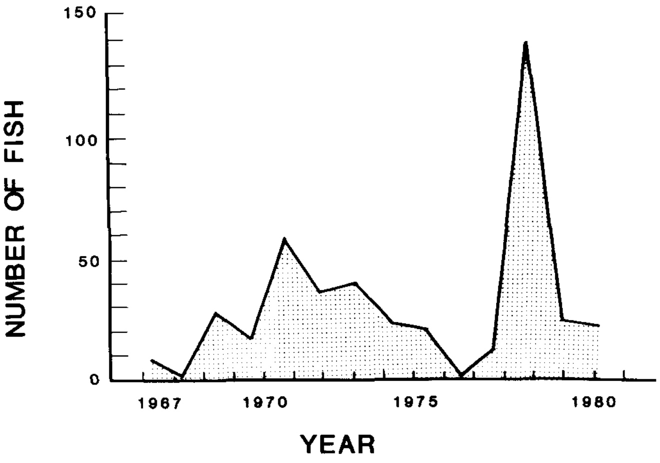

Figure 7. Annual catches of swordfish by the recreational rod-and-reel fishery off California, 1967-80 (PFMC 1981).

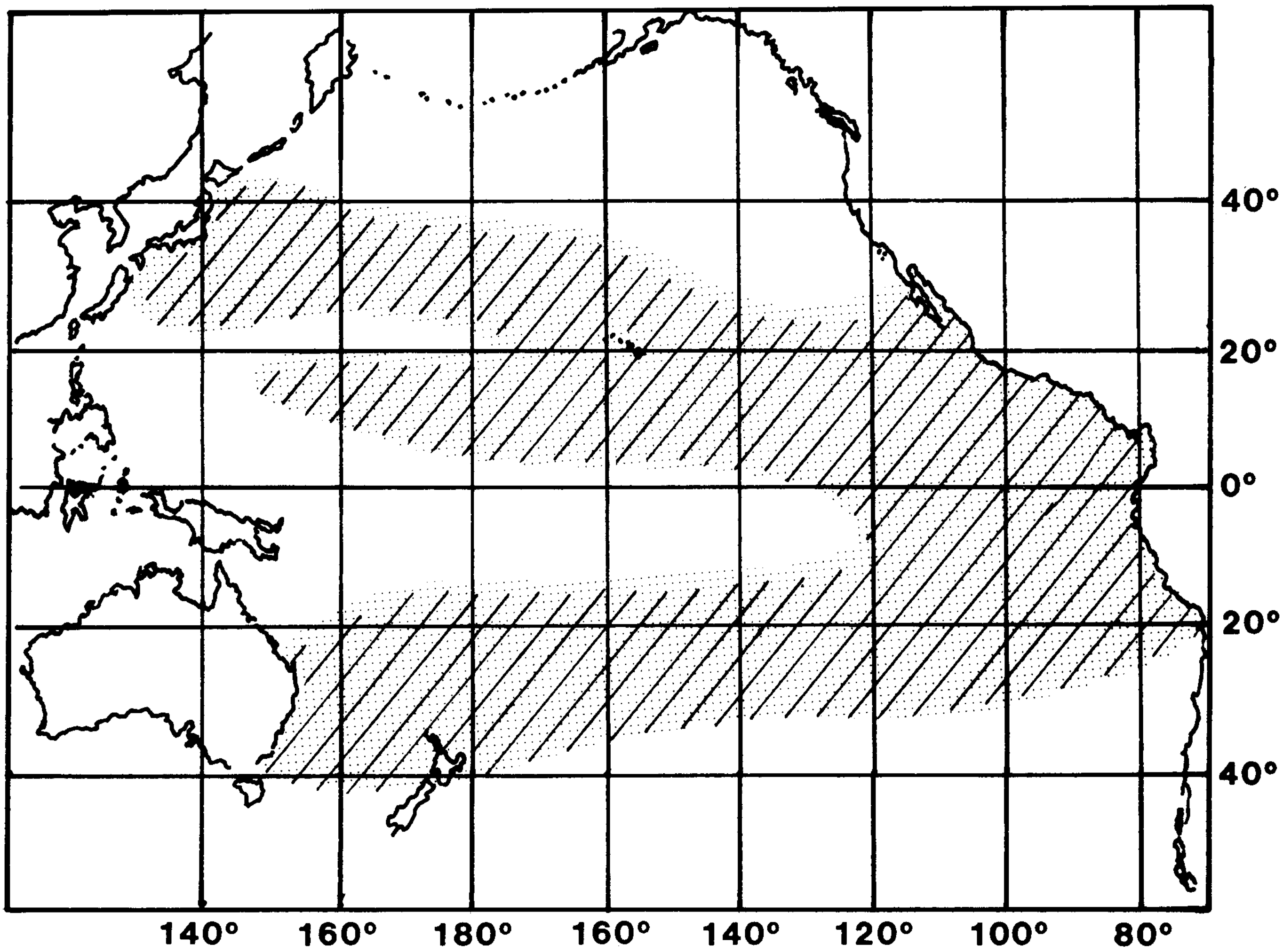

Figure 8. Distribution of high catch rate areas for striped marlin in the Pacific Ocean (Joseph et al. 1974).

occurs during the third quarter of the year, its least in the first quarter (Squire 1974).

Two recoveries of fish tagged off California suggest the possibility of long-range, transoceanic migration by striped marlin in the Pacific Ocean. One tag was recovered 1,500 miles west and one 2,400 miles south of the tagging area. Although these recoveries do not indicate particular migration routes, they do support the hypothesis that the striped marlin is highly migratory. Within the eastern Pacific, limited tag returns also suggest a northward migration along the west coast of Baja California, possibly to waters off California (Squire 1978).

Little is known of the vertical distribution of striped marlin. They are caught near the surface by trolled lines, harpoons, gill nets, and perhaps deeper by longlines. Striped marlin have been caught as deep as 289 m on experimental, vertical longline gear (Saito and Sasaki 1974).

The evidence is insufficient to delineate a particular stock structure for striped marlin in the Pacific. Participants at the 1977 Billfish Stock Assessment Workshop concluded that striped marlin in the Pacific are probably either (1) a single Pacific-wide stock or (2) one of two stocks separated roughly at the equator. Workshop participants concluded that on a Pacific-wide basis the resource is not overexploited and is in good condition. Considering the two-stock theory, participants concluded that the outlook is good for increased yields in the north Pacific stock with modest increases in fishing pressure.

Landings

Striped marlin, together with other billfishes and tunas, are exploited in the Pacific by the longline fleets of Japan, Korea, and Taiwan. In the eastern Pacific, the fishery is primarily a Japanese operation, with some participation by Koreans and Taiwanese in recent years. Pacific-wide landings of striped marlin have ranged from 14,000 MT to 27,000 MT and rep-

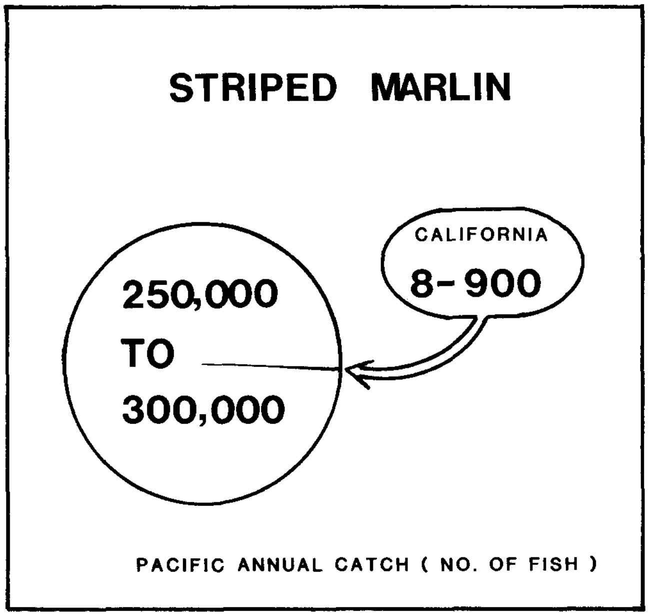

Figure 9. Comparison of the annual average California catch vs annual average Pacific Ocean catch.

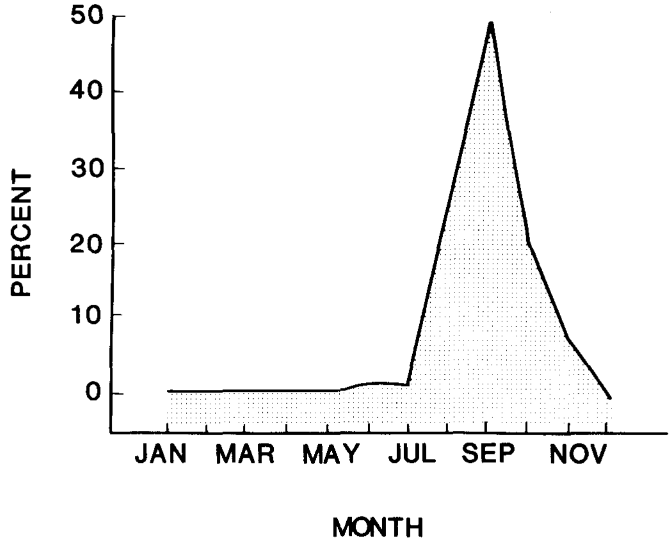

Figure 10. Average monthly distribution of the California catch of striped marlin (1963-79) by the recreational rod-and-reel fishery (PFMC 1981).

resent from 250,000 to 300,000 fish taken annually (Figure 9). The estimated annual landings in the eastern Pacific, east of 150°W longitude, average about 9,000 MT a year, or about 128,000 fish.

California Marlin Sport Fishery

The rod-and-reel fishery is seasonal and extends from July to November. The largest single monthly catches are usually made in September (Figure 10). Since 1941, most sport-caught marlin have been weighed at the docks of three major billfishing clubs: The Tuna Club, Avalon; The Balboa Angling Club, Newport; and The Marlin Club, San Diego. An estimated 90% of the total catch is weighed at these clubs. There is some duplication, because a member of one club may weigh his catch at another club's dock, nearer where the catch was made; subsequently, the catch may be listed by both clubs.

Club records indicate considerable fluctuation in annual catch, with an average (1941-80) of 751 striped marlin per year (Figure 11). In addition, a number of striped marlin are tagged and released, or released without tagging.

An average (1963-67) 11% of striped marlin landed in California by the rod-and-reel fleet was taken from Mexican waters. An average of 44% of the marlin landed at San Diego, and less than 1% of those landed at Los Angeles, were taken from Mexican waters.

The major portion of the marlin rod-and-reel fleet in southern California is berthed in the greater Los

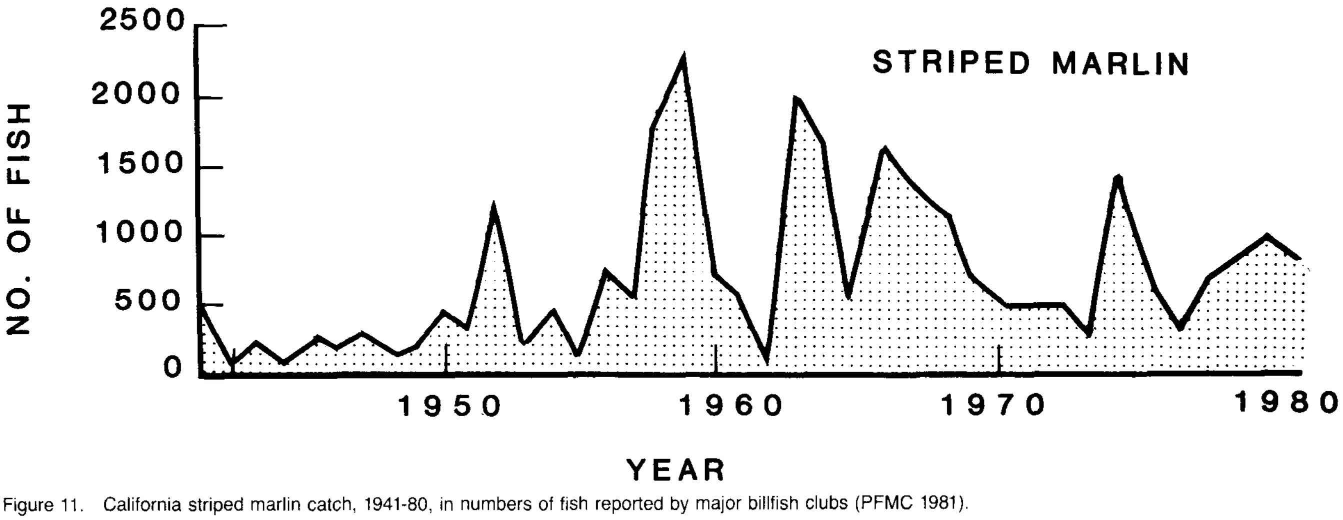

Figure 11. California striped marlin catch, 1941-80, in numbers of fish reported by major billfish clubs (PFMC 1981).

Angeles area (Dana Point to Marina del Rey, California) and at San Diego. Catches are made in waters between the northern Channel Islands off California and the Coronado Islands, Mexico. In some years the catch is uniformly distributed over the area. In other years the catch may be centered either off San Diego in the south, or near Catalina Island in the Catalina Channel to the north. Club records indicate that rod-and-reel vessels tend to fish water nearest to their home ports.

HISTORY OF MANAGEMENT

Management of California's swordfish resource has never involved population concepts such as maximum sustainable yield. The state's commercial swordfish fleet has never ventured beyond the protected nearshore waters off southern California. As a result, the limited activities of this fleet pose no threat to the stability of a cosmopolitan high-seas stock like swordfish or striped marlin.

But management involves more than population statistics. Mediation of local conflicts between user groups, based on social or economic considerations, may dominate the development of any management regime. Such has been the history of billfish management in California. The state's management policies have historically reflected adjustments for the transfer and allocation of fish from one user group to another. The latest management legislation is no exception (Table 1).

Regulatory control over the sport fishery for striped marlin and the commercial harpoon fishery for swordfish is currently under the California Fish and Game Commission, a body appointed by the governor. Regulatory control over the use of drift gill nets to take swordfish remains in the state legislature. The Department of Fish and Game serves as a research and enforcement arm under the executive branch of state government. Its function is to collect information needed by the regulatory bodies to enable them to make management decisions. The needed information includes biological, social, and economic concerns. The department makes recommendations concerning management to the regulatory bodies.

In response to requirements of the U.S. Magnuson Fishery Conservation and Management Act of 1976, the Pacific Fishery Management Council initiated the development of a Fishery Management Plan (FMP) in 1979 for billfish and oceanic sharks within the West Coast Fishery Conservation Zone, 3-200 miles offshore. In late 1981 the council's Plan Development Team presented a draft FMP for the billfish and oceanic sharks for council review and action. The FMP presented background material on the history, biology, and socioeconomic factors influencing the fisheries, and offered a number of management options for consideration. The council noted that only a small percentage of the total Pacific billfish harvest was taken in waters under the council's jurisdiction and that only a fraction of the stock biomass occurred in the U.S. Fishery Conservation Zone. It further noted that, because of the highly migratory, transboundary nature of the billfish, stock management can only be accomplished through international cooperation. Additionally, the council noted that all participants in this fishery were California residents. Consequently, the council elected to delay further development of a federal plan at this time.

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WHITE SEABASS, *ATRACTOSCION NOBILIS*, IN CALIFORNIA-MEXICAN WATERS: STATUS OF THE FISHERY

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ABSTRACT

Past efforts to restore and enhance the white seabass resource in California waters have been unsuccessful. A review of the history of the fishery, catches, and management indicates that the resource continues to decline. Information on early life history, fecundity, and migration are definitely needed, as is an assessment of recent management regulations.

RESUMEN

Los esfuerzos para restaurar y mejorar las poblaciones de corvina (*Atractoscion nobilis*) en aguas de California no han tenido éxito. Una revisión de la historia de la pesquería, capturas y reglamentación, indican que este recurso pesquero continúa disminuyendo. Se precisa obtener más información sobre el ciclo de vida, larvas, fecundidad y migraciones, así como un análisis y estimación de las regulaciones que se han establecido recientemente en esta pesquería.

INTRODUCTION

White seabass (*Atractoscion nobilis*) has long been an important sport and commercial fish in southern California because it is an excellent food fish and an angling challenge.

The total commercial catch has decreased slowly since the early 1900s (Skogsberg 1939), and the sport catch has declined since its peak in 1949 (Thomas 1968). The fish were once abundant as far north as San Francisco, but few are now caught north of Point Conception. This indicates that a constriction of range has taken place.

Various management regimes designed to enhance the white seabass resource have been established since 1931, when declining catches of this desirable species were first noted. This synopsis of the white seabass fishery in California provides a background for future management considerations. Information from Department of Fish and Game catch statistics, white seabass fishing logbooks, current literature, and personal communications were used in this analysis.

THE FISH

The white seabass is the largest of the croaker family (Sciaenidae) on the U.S. Pacific coast. The largest recorded weight is 37.7 kg (83 lbs), but few attain weights of over 27 kg (60 lbs) (Thomas 1968). They have a recorded range from Magdalena Bay, Baja California, to Juneau, Alaska. Today the economic range is from Point Conception to Punta Abreojos, Baja California. White seabass are found in schools and also occur as solitary individuals (Skogsberg 1939; Squire 1972).

Market samples indicate that white seabass spawn between the months of March and July, with peak spawning from April to June (Skogsberg 1925). There is some question about the age at which they mature. Clark (1930) found that 50% of the males over 60 cm in length (TL) were mature, but that 50% of the females had not yet matured at 70 cm (TL). Her conclusion was that all white seabass are mature at 80 cm (TL). The eggs are pelagic, and juveniles are believed to rely on kelp canopy for cover (Feder et al. 1974). The fish are carnivorous, feeding on anchovies, herring, sardines, squid, and pelagic crabs. Migration or fish movement has not been proven, but has been deduced from the appearance and disappearance of the white seabass at various locations along the coast in different seasons.

THE SPORT FISHERY

Sportfishermen have been using hook and line to catch white seabass from piers, jetties, private boats, and commercial passenger fishing vessels (CPFVs) for over 100 years. A variety of baited and nonbaited lures have also been used successfully. Catch records from the CPFV fleet collected by the Department of Fish and Game from 1947 to the present provide an index of the recreational take. This catch peaked in 1949, with 64,000 fish being caught, and has steadily declined (Figure 1). The CPFV catch for California in 1978 hit a record low of 284 fish. The relative angler success (RAS)[1] for that same fishery shows an identical decline (Figure 2) from a high of 0.13 fish/angler

[Manuscript received February 2, 1983.]

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[1] Relative angler success (RAS), the ratio of total white seabass caught to the total number of anglers, is a less rigid measure of CPUE, since white seabass is rarely a target species.

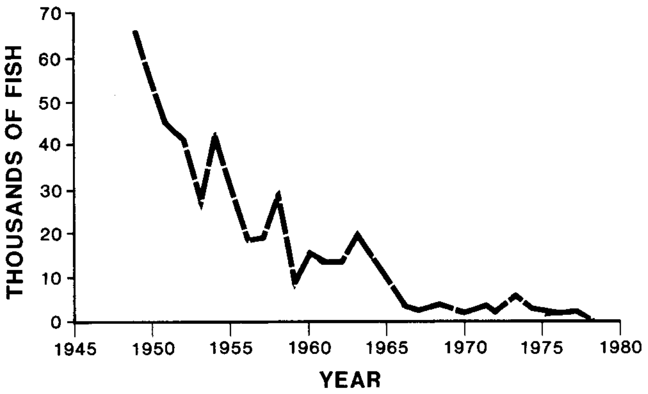

Figure 1. White seabass catch (in thousands of fish) from commercial passenger fishing vessels in California waters from 1949 to 1978. (The 1978 value is 284 fish).

TABLE 1
Estimated White Seabass Catches and Angler Success from the Private Trailerable Boat Survey

Year	Estimated catch	Actual # sampled	% legal	Angler success
1976-77	2,649	473	6.6	0.0087
1977-78	1,977	497	11.2	0.0074
1981	1,750	394	16.0	0.0052

The survey was not conducted in 1979 and 1980.

in 1949 to less than 0.001 fish/angler in 1978. Since 1965 the angler success has been below 0.01 fish/angler.

Data from a survey of private-boat fishermen (Wine 1978, 1979, 1982) shows that the number of white seabass caught by anglers fishing from private, trailerable boats has declined since 1976, as has the angler success (Table 1). The survey also found that the vast majority of fish taken from this fishery were smaller than the minimum legal size, 71 cm (28 in). The survey in 1976 revealed that only 6.6% of the white seabass sampled were of legal size or above. However, the percentage of legal fish slowly increased to 16% by the end of 1981. A 1978 angler survey indicated that many recreational fishermen could not separate juvenile white seabass from a number of other commonly caught croakers (Hartmann 1980). This fact, coupled with a widespread ignorance of regulations applying to white seabass, may account for the high percentage of undersized fish being kept. The fact that the percentage of legal fish has slowly increased may indicate better compliance with regulations and some success in educating the angler in species identification. It is unlikely that more legal-sized fish have become available to the anglers on private boats, because the total number of white seabass caught by all sectors of the fishery has continued to decline.

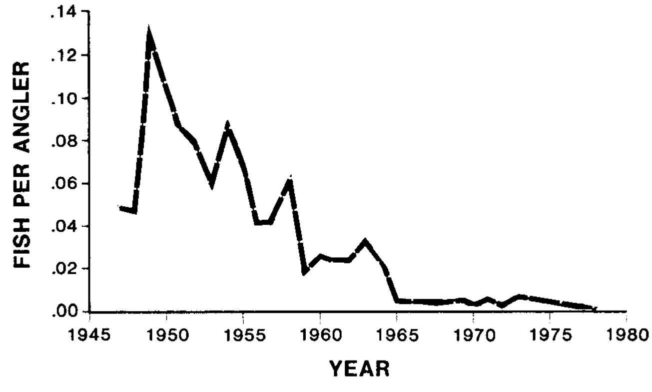

Figure 2. Catch of white seabass per angler in the California commercial passenger fishing vessel fishery from 1947 to 1978.

THE COMMERCIAL FISHERY

Nets have always been the most important gear in the commercial white seabass fishery. In the early 1920s gill nets were fished from 8-9-meter (25-30-ft) boats (Whitehead 1930). Purse seines were also used on schooling fish until the late 1920s, when catches began to decline, and use of this gear became uneconomical. Today in California waters white seabass are caught almost exclusively with set gill nets. The nets are now fished with a mechanized reel and are approximately three times longer than those used 50 years ago. The size of boat (9-12 m) in today's fishery has not changed significantly. The nets are generally constructed of multifilament nylon webbing, although monofilament nylon webbing is gaining acceptance.

Drift gill nets were used in the U.S. fishery in Mexican waters, although some set nets were also employed. Historically, this fishery involved between 12 and 20 southern California vessels that entered Mexican waters (with authorization) to harvest white seabass. The fish were off-loaded in California ports and have always been included in the California catch records. Between the early 1950s and 1981 the percentage of California white seabass landings taken in Mexican waters increased substantially (Figure 3). However, in January 1982 Mexico began denying permits to U.S. commercial fishermen. This action has cut the total U.S. commercial catch by more than 80% and entirely eliminated catches by U.S. vessels in Mexican waters.

The number of boats landing white seabass each year in the California fishery has remained fairly constant, but both the kg/landing and total catch have declined (Figure 4). Commercial landings were under 45 MT (100,000 lbs) in 1981, the lowest level on record.

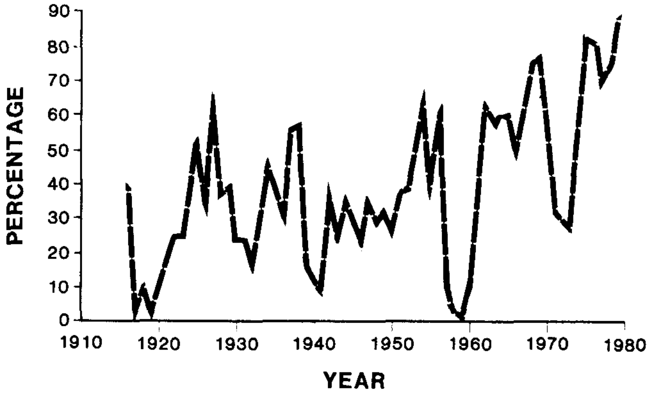

Figure 3. The percentage of California commercial white seabass landings taken in Mexican waters from 1916 to 1979.

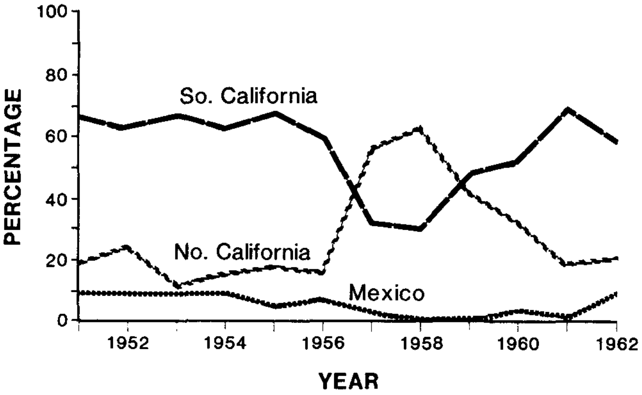

Figure 5. The percentage of the California commercial white seabass fishing fleet landing white seabass from north of Point Conception, southern California, and Mexico from 1951 to 1962.

FISHERY ANALYSIS

An analysis of catch trends for the U.S. commercial catch and recreational white seabass fisheries from 1951-72 indicated that sport angler success had declined, while the commercial success rate had remained relatively stable (MacCall et al. 1976). However, this analysis combined U.S. commercial catches from California and Mexican waters. Reanalysis of the California recreational and commercial catches for 1951 to 1981, excluding fish from Mexico, indicates a significant decline in both fisheries except during the years 1957-61 (Figure 4). It has been postulated that increased catches during these years resulted from white seabass moving up the coast with the unusually warm water from areas farther south (Radovich 1961). From 1957-61, the number of boats landing white seabass increased, and a shift in fishing areas occurred (Figure 5). Fish caught in Mexico by the U.S. fleet contributed only 3% of the total catch, while landings from waters north of Point Conception represented as much as 36% in 1960. When the ocean water temperatures returned to normal levels, so did the catch figures from north of Point Conception. Presently, landings from this area contribute approximately 1% of the total U.S. catch.

Gill nets are commonly set near rocky headlands to target on white seabass, but catches are more typical of an incidental fishery. Of the 131 boats landing white seabass from California waters in 1981, only 20 (15%) landed more than 455 kg (1000 lbs). Generally, white seabass constituted considerably less than 17% by weight of the total 1981 catch of all species by these boats.

Comparison of the size-frequency distribution of white seabass caught from CPFVs and by commercial boats shows the two groups harvesting different age groups of the stock (Figure 6). Recreational fishermen typically catch juveniles, especially in and around kelp beds. Commercial gill nets set in the same areas capture larger adult fish. Although the net mesh size can select for larger fish, if the larger fish are present in the area they should also be available to sportfishermen. Adult white seabass may be nocturnal feeders

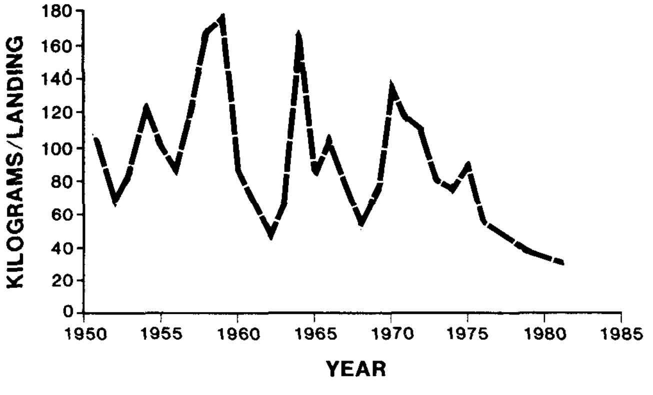

Figure 4. Average kilograms of white seabass per landing by the California commercial fleet from 1951 to 1981.

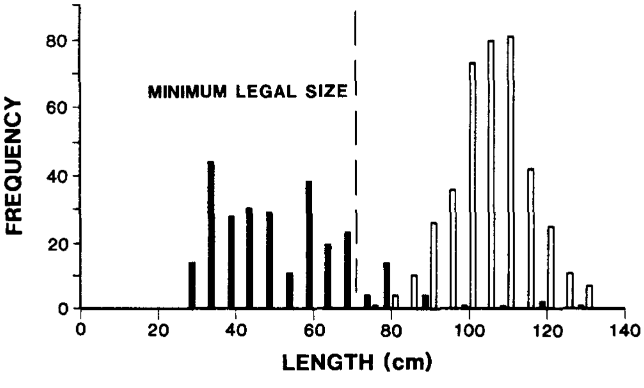

Figure 6. White seabass length frequencies from the California commercial passenger fishing vessels catch (solid bars), $N = 254$, and the California commercial catch (open bars), $N = 396$, from 1975 to 1976.

(or spawners), coming inshore only at night when commercial nets are fishing and most sportsmen are home asleep. It may be that white seabass prefer live squid, which are seldom available to sportsmen. The factors responsible for the size difference between recreationally caught and commercially caught fish are not yet understood.

Various factors may be contributing to the decline of the white seabass fishery off California. Thomas (1968) calculated the instantaneous total mortality (*Z*) to be 0.89 in 1958, with fishing mortality (*F*) to be 0.59. Therefore, white seabass have, at times, been heavily exploited, and overfishing has probably contributed to the decline of the population. The large number of juvenile fish in the sport take also reduces recruitment. If, as Parrish, Nelson, and Bakun (1981) hypothesize, surface currents act to entrain larvae nearshore, then environmental degradation caused by human activities may have impacted reproductive success in the Southern California Bight. Unfavorable oceanographic conditions and changes in the availability of forage species may also influence the distribution of this species.

REGULATIONS

Since 1931, white seabass regulations have been enacted and frequently changed. These attempts at management have included various licenses, permits, bag limits, seasonal and gear restrictions, and size limits (Table 2). Regulations in effect as of January 1, 1983, include a strict 71-cm TL size limit for both sport and commercially caught white seabass. There is a three-fish-per-day bag limit for the recreational fisherman. A permit and logbook reporting system are still in effect for those commercial fishermen employing a gill or trammel net to capture white seabass. A closed season also exists from March 15 to June 15 south of Point Conception.

Two management options that have been considered, but are not yet employed, are an 81-cm (32 in) TL size limit for all sectors of the fishery, and a complete moratorium on white seabass fishing in Califor-

TABLE 2
Summary of White Seabass Regulations from 1931 to the Present

Date (lic. req.)	Season length	Size limit	Bag limit	Gear and area restrictions	Special conditions
1931-33 (commercial lic. req.)	July 1-Apr. 30	≥28″	None	No nets within 4-mile radius of San Juan Pt. in Orange County; bait nets only in Santa Monica Bay.	5 fish any size with hook and line, but may not be sold.
1933-35 (same)	Hook & line all year	Same	May 1-June 30 (5 per day—hook & line)	Same	After Oct. 25, 1933, no fish may be sold from May 1-June 30. Rest of reg. same as above.
1935-37 (same)	Same as above. No net fishing May 1-Aug. 31.	Same	May 1-Aug. 31: 500 lbs/person; 2500 lbs/boat.	No nets in any Orange County waters (later rescinded)	Same
1937-39 (sportfishing lic. req.)	Same	Same	Sportfishing limit (15/day) for anyone on sportfish boat.	Same	Sport-caught fish may not be sold.
1939-41 (same)	Net fishing permitted year round.	Same	Same	No purse seines in Calif. Gill net mesh ≥3½″	Same
1941-49 (same)	Same	Same	Same	Same	Same
1949-53 (same)	Same	Sportfish bag not more than 5 fish, <28″	Sportfish: 10/day	Same	Same
1953-57 (same)	Same	Same	Commercial: 1000 lbs/person/day; 5000 lbs/boat/day.	Same	Same
1957-71 (same)	Same	Sportfish: 2 of 10/day under 28″	Same	Same	Same
1971-73 (same)	Same	No fish <28″	Same	Same	Same
1973-78 (same)	Same	One fish <28″	Same	Same	Same
1978 (same)	Same	No fish <28″	Same	Same	Same
1980-81 (same)	Season closed Mar. 15-June 15	Same	Sportfish: 3/day/person.	Same	Logs required. Permits required.
1982 (same)	Same	Same	Same	Certain area closures for nets with mesh less than 6″.	Permits no longer required.

nia. Either of these options would need to be in effect for at least five years before an assessment of their impact could be made. There is no guarantee, of course, that either regimen would achieve the desired effect of enhancing the white seabass population.

RECENT STUDIES

In 1975 the Department of Fish and Game initiated a study of white seabass to provide information concerning fecundity, fish movement, and stock definition. The project failed to produce any answers because of the lack of specimens (Maxwell 1977).

Recently, the National Marine Fisheries Service successfully induced spawning in captive white seabass (press release dated April 21, 1982, U.S. National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). Continued research in this endeavor may produce much-needed fecundity and early-life-history information. Obtaining this information is critical, considering the depressed status of the white seabass fishery in California.

SUMMARY

Despite various management actions, the white seabass fishery in California waters continues to decline. Many factors may be responsible for this decline. Isolating the actual causes, however, is becoming increasingly difficult because fewer and fewer specimens are available for study. Perhaps with persistent efforts to utilize the limited material available, additional information on fecundity, movement, and reproductive requirements may be obtained and may lead to a management regime that facilitates the recovery of white seabass off California.

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YELLOWTAIL, *SERIOLA LALANDEI* VALENCIENNES

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ABSTRACT

Yellowtail are highly prized by anglers. They are slow-growing fish that mature sexually by age three. Studies on food habits indicate they are opportunistic feeders, with adults consuming primarily small fish. Yellowtail migrate north as the ocean warms in the spring and return south when it cools. Recent data collected from partyboats operating off Mexico indicate a decrease in the yellowtail population.

RESUMEN

Seriola lalandei (pez de limón) es muy apreciado por los pescadores de caña. Estos peces crecen con lentitud y tardan tres años en alcanzar la madurez sexual. Estudios sobre el pez de limón indican, que se alimenta de lo que encuentra, y los adultos consumen principalmente peces pequeños. *Seriola lalandei* emigra hacia el norte en la primavera, según va aumentando la temperatura oceánica, retornando hacia el sur cuando sobreviene el enfriamiento de las aguas. Datos obtenidos durante las operaciones de los barcos de pesca deportiva navegando en aguas mexicanas, indican un descenso notable en las poblaciones de *Seriola lalandei.*

INTRODUCTION

The yellowtail is one of the most highly prized gamefishes found off southern California. It is the largest member of the family Carangidae found in the state, although the Pacific amberjack, *Seriola dumerili,* grows to a larger size off Baja California. The fish ranges from Chile on the south to southern Washington on the north (Miller and Lea 1972). Within this range, yellowtail occur in fishable quantities from Cape San Lucas, Baja California, to Los Angeles County.

LIFE HISTORY

Yellowtail begin their lives during the summer months, June through September. During this period, adults that are about to spawn move offshore, generally to an area of shoals or islands that may be as far as 113 to 161 km (70 to 100 mi) from the mainland. The fish form spawning aggregations and broadcast their eggs and milt into the water (Walford 1937). Some two-year-olds may spawn; all fish three years and over definitely are capable of spawning. Young fish spawn once during the season, but those over seven years of age apparently are capable of multiple spawnings.

Age and growth studies conducted on yellowtail have indicated that the fish are relatively slow growing. They gain approximately 1.36 to 1.82 kg (3 to 4 lb) a year during most of their lives, although very large individuals may gain only 0.45 to 0.90 kg (1 to 2 lb) per year (Table 1). Growth can vary considerably from year to year and also between and within geographical areas. Because of this, only a moderately good fit can be obtained when using a von Bertalanffy growth equation (Beverton and Holt 1957).

Limited knowledge exists about the food habits of yellowtail. Studies conducted during the 1950s indicated that adult fish were highly piscivorous. At that time jack mackerel *(Trachurus symmetricus),* northern anchovies *(Engraulis mordax),* and sardines *(Sardinops sagax)* were the most frequently encountered items in yellowtail stomachs. Notes on the time of day yellowtail were caught for stomach analysis suggested that they fed primarily during daylight hours: amorphous material was usually present in fish taken at night, whereas fish captured during the day contained a large percentage of undigested or partially digested food. The regular presence of amorphous material in stomachs of fish taken at night indicates that yellowtail have a rapid rate of digestion, since food was surely ingested no earlier than the previous morning.

During the early 1950s, the California Department of Fish and Game tagged over 14,000 yellowtail (Collyer 1954). Two-thirds of the fish were tagged during 1955, two years prior to a warm-water event lasting from 1957 to 1959. The distribution of these fish during the warm-water years was quite revealing, since elevated ocean temperatures accentuated their movements (Radovich 1961).

Results of the tagging study indicate that there are two groups of yellowtail off Baja California (Baxter 1960). One group occurs south of Cedros Island, while the second group occupies the area from Cedros Island northward (Figure 1). There is some interchange of fish between the two groups, but it usually takes place around Cedros Island. No fish tagged south of San Hipolito Bay were ever recovered off southern California, although a

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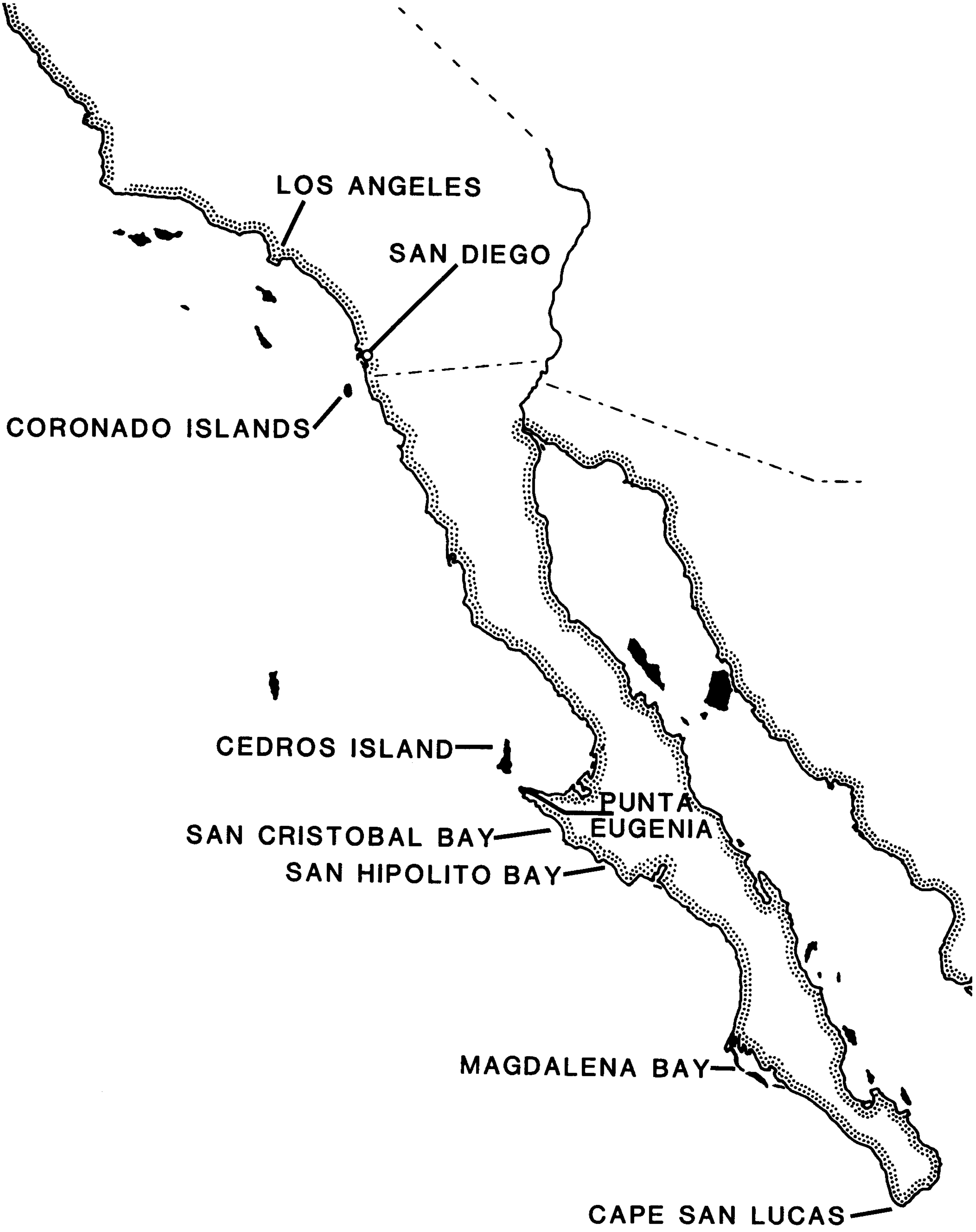

Figure 1. Outline map of southern California and Baja California.

TABLE 1
Observed Age, Length, and Weights of Yellowtail

Age	Observed length	Observed weights	
	TL (mm)	Kg	Lbs
1	510	1.72	3.8
2	640	3.36	7.4
3	710	4.50	9.9
4	780	6.00	13.2
5	830	7.23	15.9
10	1035	12.36	27.2
12	1125	15.90	35.0

few were taken in the mixing area around Cedros Island. Few fish were tagged off southern California or northern Baja California, and none of those recovered were taken farther south than San Cristobal Bay. This indicates that the fishery off southern California is dependent on yellowtail from the northern group.

The tagging study also helped to determine the timing of coastal migrations. Generally, tagging showed that the fish moved northward as the water warmed in the spring. During the summer they left the nearshore areas to spawn offshore, and returned in the fall. Eventually the fish moved south as the water cooled late in the year. During years when the water remained several degrees above normal through the winter, yellowtail remained in northern waters year round.

CATCH ANALYSIS

Yellowtail fishing off southern California is highly dependent on fish moving into the area. Because of this, catches have varied considerably. During warm-water periods like 1957-59, commercial passenger fishing vessel (CPFV) catches have approached 450,000 fish per year for southern California and the Coronado islands. In years when the water is cool, catches are rare. The most recent "good" year for yellowtail fishing off southern California occurred in 1973. During that year, the water temperature was several degrees above normal throughout the spring, and over 230,000 fish were landed. The catch was dominated by two-year-old fish (1971 year class), a departure from the historic norm of four- and five-year-olds dominating. During 1981, a year in which spring water temperatures were elevated, the local yellowtail catch for CPFVs was a little over 10,000 fish. Very young fish dominated the fishery with one- and two-year-olds making up a large percentage of the catch.

Data collected from CPFVs working off Mexico may explain why yellowtail landings have declined off southern California. The data from these vessels indicate that six- to nine-year-old fish dominated the catch between 1974 and 1979 (Figure 2). The boats occasionally caught smaller fish, but usually avoided them. Beginning in

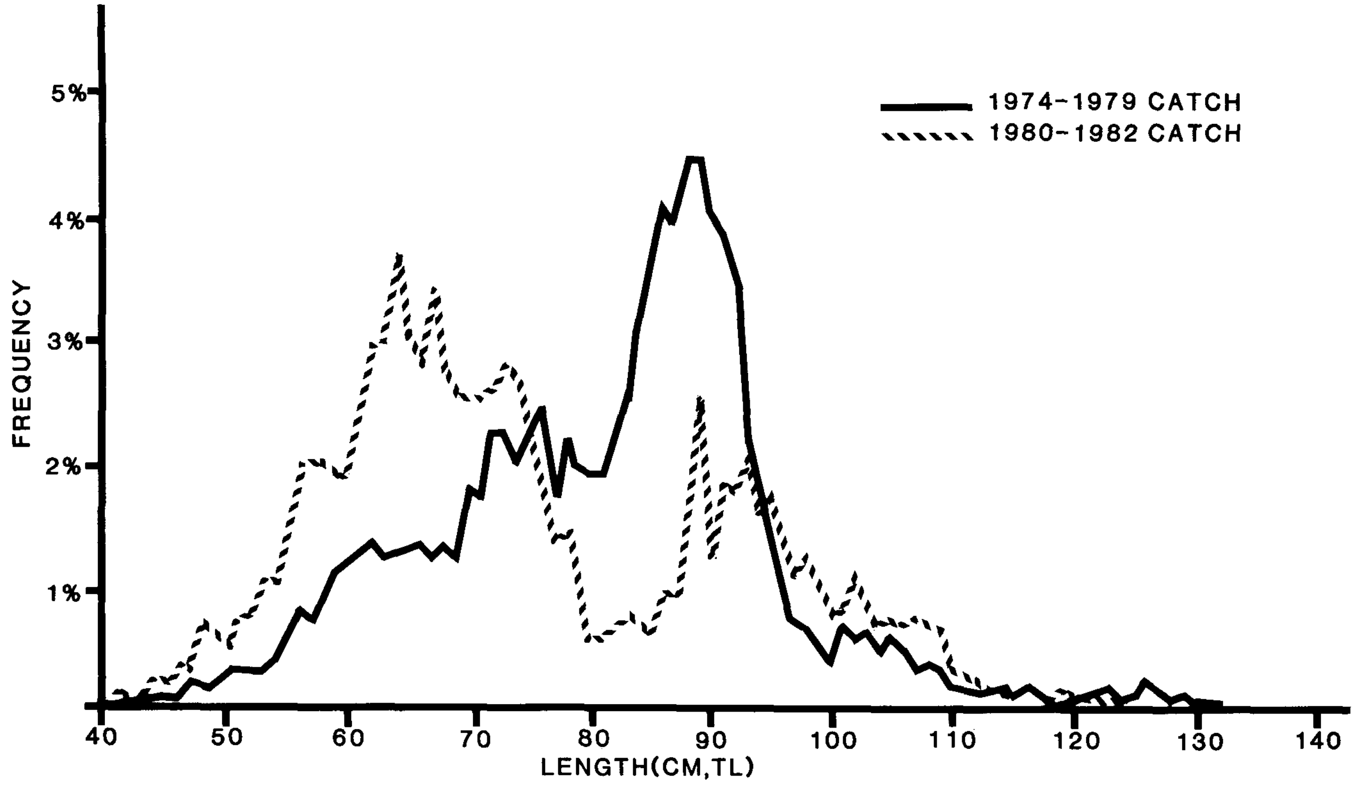

Figure 2. Length composition of the long-range partyboat yellowtail catch from Baja California, 1974-82.

1980 and continuing through 1982, large yellowtail were difficult to find, with two- and three-year-old fish making up the majority of the catch. The change in age structure of the catch was dramatic in 1980, suggesting that something had happened or was happening to the yellowtail population off Baja California. Age compositions indicate that there were a number of year-class failures starting in 1975 and continuing through 1978. Recruitment of the 1979 and 1980 year classes was relatively good, as evidenced by their recent dominance of the fishery. Why the 1975-78 year classes failed is unknown. However, their failure has had a significant effect on CPFVs operating off Baja California, and should explain why yellowtail fishing off southern California has declined rapidly in recent years. A decline in the size of yellowtail, barring an increase in abundance caused by an unusually large year class, implies a decrease in the population off Baja California. This apparently has manifested itself as a decrease in the availability of fish off southern California.

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CALIFORNIA BARRACUDA LIFE HISTORY, FISHERIES, AND MANAGEMENT

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ABSTRACT

Despite efforts to manage it, the California barracuda, *Sphyraena argentea,* has markedly declined in abundance from levels exhibited prior to 1950. This paper presents a history of the California barracuda fisheries, a summary of the fish's life history and population dynamics, an evaluation of the resource under current management practices, and recommendations for improvements in current management.

Evaluation of the current status of the resource indicates its abundance off southern California is low but slowly improving, with a marked improvement in size composition. Management recommendations, when adopted, should help increase the rate of recovery.

RESUMEN

La abundancia de *Sphyraena argentea* (espetón o barracuda) ha venido disminuyendo desde antes de 1950, a pesar de los esfuerzos encaminados a regular la pesquería. En este trabajo se presenta la historia de la pesquería del espetón, un resumen de su ciclo de vida y dinámica de poblaciones, así como una evaluación de las reservas que existen, considerando las reglamentaciones actuales y las recomendaciones necesarias para mejorar las existencias.

La evaluación del estado actual de las poblaciones de *Sphyraena argentea* indica que escasean frente a la parte meridional de California, aunque van aumentando con lentitud, presentando una mejoría notable en la estructuración de las tallas. Las regulaciones que se recomiendan, una vez adoptadas, ayudarían a que las poblaciones incrementasen en notable cuantía.

LIFE HISTORY

The California barracuda *(Sphyraena argentea)* is the only member of the barracuda family found off the west coast of the United States; it also occurs along northern Baja California, Mexico.

The fish's reported range is Cape San Lucas, Baja California (Berdegue 1956), north to Prince William Sound, Alaska (Pinkas 1966); however, they are seldom observed north of Point Conception, California, except in years when ocean waters off California are exceptionally warm.

California barracuda are nearshore, pelagic-schooling predators, which feed upon a variety of smaller species including anchovies *(Engraulis mordax),* sardines *(Sardinops sagax caeruleus),* young Pacific mackerel *(Scomber japonicus),* young jack mackerel *(Trachurus symmetricus),* and grunion *(Leuresthes tenuis).* Market squid *(Loligo opalescens)* are eaten when offered as bait, but have not been observed in stomachs examined for food items. Barracuda, in turn, are known to be fed upon by giant sea bass *(Stereolepis gigas),* California sea lions *(Zalophus californianus),* harbor seals *(Phoca vitulina),* and porpoise (Frey 1971).

An annual northward migration of California barracuda along the northern Baja California and southern California coast during late spring and early summer has been well documented through tag-recapture investigations (Pinkas 1966). This northward movement coincides with seasonal warming of nearshore coastal waters. Good correlations between average sea-surface temperatures off southern California from January through June and the numbers of barracuda captured by sport fishermen aboard commercial passenger fishing vessels during the year indicate that the strength of migration also is related to temperature (Figure 1) (Pinkas 1966; Schultze 1981). An annual southward migration along the coast during late summer, fall, or early winter is not as apparent as the northward spring-summer migration. Judging from the diffused pattern of catches made from late summer to early winter, the southward return migration appears more prolonged and less coherent than the northward migration.

California barracuda reach a maximum size of about 120 cm (48 in) in total length, 7.3 kg (16 lb) in weight, and 12 + years of age. Specimens larger than 90 cm (35 in), 2.7 kg (6 lb), and 10 years of age, however, are now seldom seen in either commercial or sport catches. California barracuda grow rapidly during their first 4 years, reaching 65 to 70 cm in length; then growth slows to about 5 cm per year (Walford 1932). Younger fish tend to remain near shore, while older fish are more common over shallow banks farther from shore and at offshore islands.

California barracuda begin maturing during their second year of life (Walford 1932). Males typically

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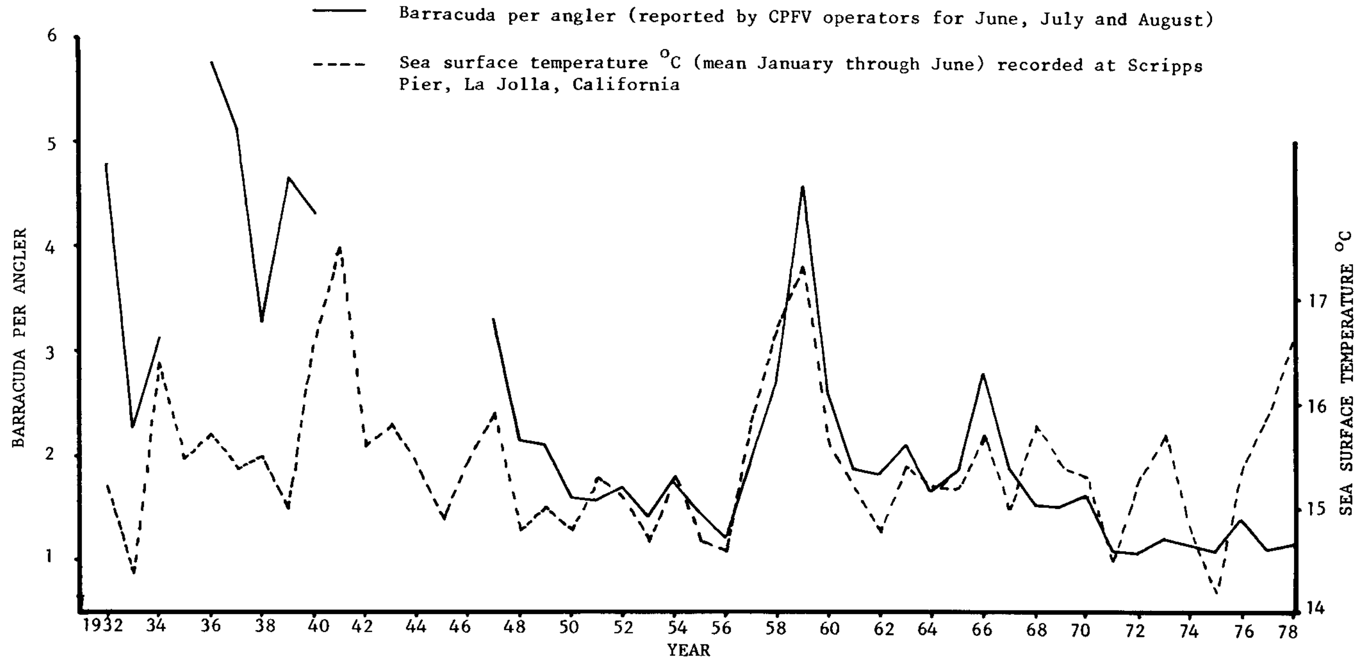

Figure 1. Reported barracuda per angler and sea-surface temperatures off southern California from 1932 through 1978.

mature earlier than females. Although 100% of the males are capable of spawning in their second year, only about 75% of the females are mature in their second year. All of the females are mature in the third year. Spawning occurs primarily during May, June, and July in nearshore waters of Baja California and southern California. Female barracuda, six to seven years of age, were estimated to produce between 300,000 and 400,000 mature eggs for one spawning, and spawning may occur more than once each season (Walford 1932).

FISHERIES

California barracuda are unusual among the world's species of barracuda in having supported relatively large commercial and sport fisheries. Demand for barracuda as a food fish was historically high, and interest in barracuda as a sport-angling species has traditionally been high. Despite a variety of regulations enacted over the years to conserve and manage this resource, landings by both commercial and sport fishermen have declined (Tables 1 and 2, Figures 2 and 3).

Commercial Fishery

The California commercial barracuda fishery began in the 1800s. The fishery developed rapidly following World War I with the introduction of purse seine vessels and the concurrent expansion and development of California fisheries for white seabass *(Atractoscion*

TABLE 1
Yearly Commercial Landings of California Barracuda in Metric Tons

Year	California waters	South of state	Total metric tons
1889	—	—	227
1890	—	—	232
1891	—	—	316
1892	—	—	148
1895	—	—	445
1899	—	—	541
1904	—	—	981
1908	—	—	1,455
1915	—	—	1,632
1916	1,011	209	1,220
1917	1,347	43	1,390
1918	1,765	432	2,197
1919	1,834	811	2,645
1920	2,082	1,642	3,724
1921	2,084	1,379	3,463
1922	2,144	694	2,838
1923	2,332	938	3,270
1924	2,150	1,087	3,237
1925	2,714	936	3,650
1926	1,337	944	2,281
1927	1,978	837	2,816
1928	1,991	939	2,930
1929	1,783	592	2,370
1930	1,596	567	2,163
1931	1,515	382	1,897
1932	1,138	191	1,329
1933	1,323	73	1,396
1934	818	173	991
1935	910	279	1,189

Continued on next page

TABLE 1 (continued)
Yearly Commercial Landings of California Barracuda in Metric Tons

Year	California waters	South of state	Total metric tons
1936	1,021	331	1,352
1937	817	517	1,334
1938	573	576	1,149
1939	1,348	510	1,858
1940	1,156	531	1,687
1941	1,349	559	1,908
1942	1,019	550	1,569
1943	1,082	633	1,715
1944	1,052	605	1,657
1945	792	967	1,759
1946	744	667	1,411
1947	770	441	1,211
1948	500	465	965
1949	410	706	1,116
1950	404	621	1,026
1951	304	653	957
1952	340	612	951
1953	257	396	653
1954	221	489	710
1955	147	371	518
1956	23	319	342
1957	176	134	310
1958	342	74	416
1959	504	19	523
1960	521	37	558
1961	217	105	322
1962	237	102	339
1963	158	14	172
1964	114	38	152
1965	124	40	164
1966	106	39	145
1967	128	14	142
1968	52	12	64
1969	32	2	34
1970	10	1	11
1971	8	<1	8
1972	6	0	6
1973	17	0	17
1974	17	0	17
1975	27	.1	27
1976	74	.2	74
1977	34.8	.2	35
1978	22	.3	22
1979	16.5	.5	17
1980	Unavailable		
1981	30	0	30

TABLE 2
Number of California Barracuda Reported Landed by Southern California Commercial Passenger Fishing Vessel Operators

Year	Barracuda
1936	595,062
1937	742,849
1938	374,109
1939	732,878
1940	704,520
1946	598,000*
1947	677,499
1948	383,757
1949	366,423
1950	242,380
1951	269,418
1952	336,562
1953	166,478
1954	281,049
1955	154,939
1956	87,218
1957	577,060
1958	782,226
1959	1,195,579
1960	755,360
1961	391,853
1962	335,507
1963	483,699
1964	303,070
1965	443,304
1966	892,697
1967	470,480
1968	372,246
1969	358,518
1970	373,801
1971	50,474
1972	38,243
1973	92,483
1974	55,284
1975	26,289
1976	107,557
1977	48,701
1978	73,174
1979	69,434
1980	27,909
1981	65,960*

*Figures incomplete

nobilis), yellowtail *(Seriola lalandei),* Pacific mackerel *(Scomber japonicus),* and bluefin tuna *(Thunnus thynnus)* (Skogsberg 1925). Commercially landed barracuda have traditionally been landed fresh or on ice, and sold fresh.

Peak annual commercial landings of over 3,700 MT were made in the 1920s. During this period, gill net and trolling vessels fished barracuda in California waters. Purse seine vessels pursued barracuda in late fall and winter off Baja California, as well as participating in the spring-summer fishery off California. This effectively represented a year-round commercial fishery for barracuda over much of its range. Seasonal exploitation of barracuda by different segments of the

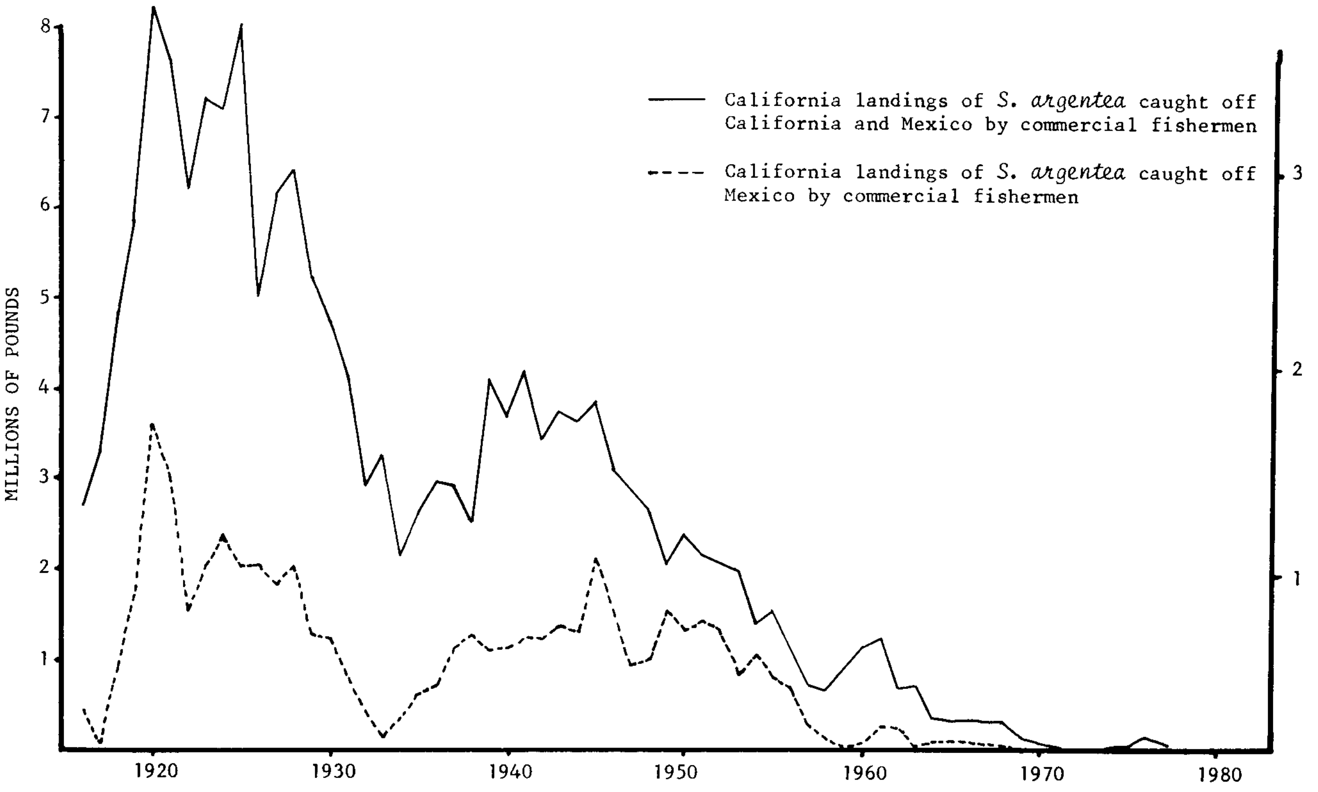

Figure 2. California commercial landings of California barracuda from California and Mexico, and just Mexico.

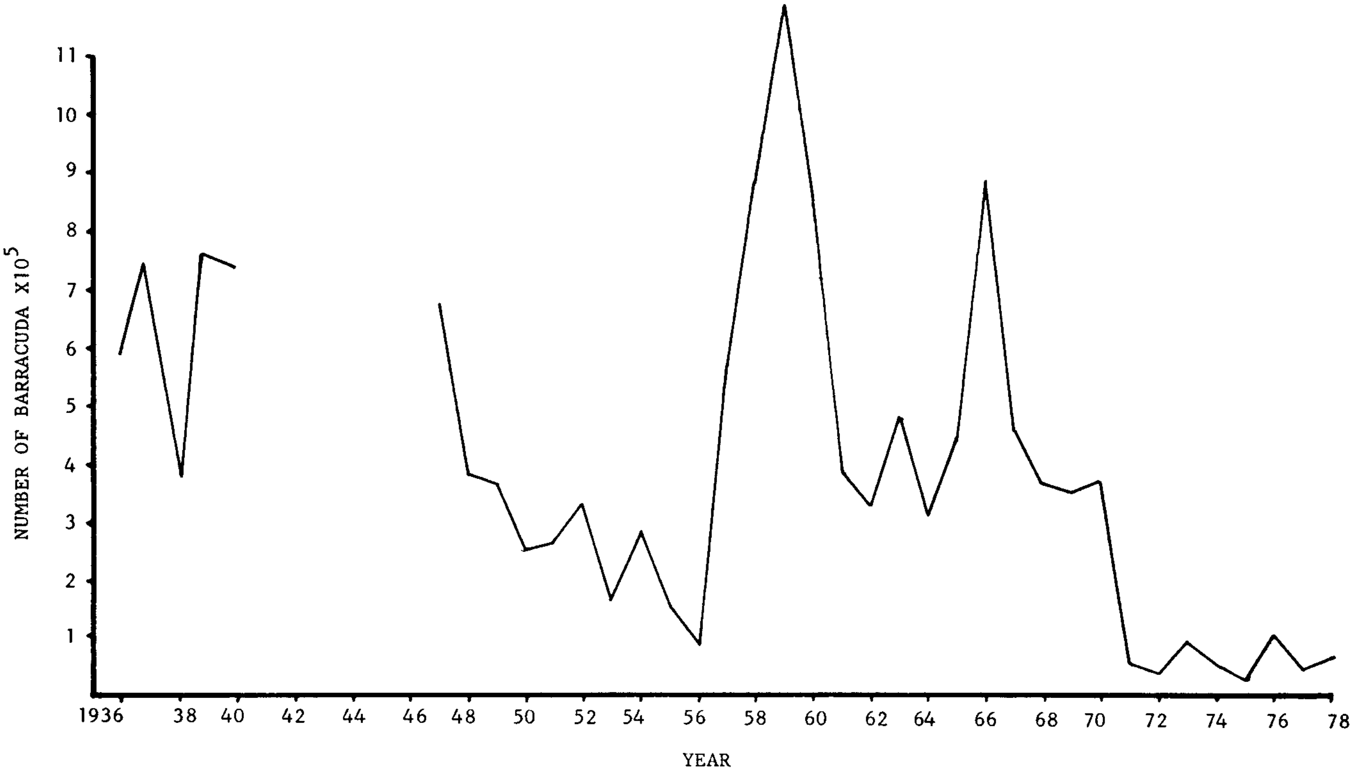

Figure 3. Landings of California barracuda reported by California commercial passenger fishing vessel operators.

commercial fishery off Mexico and southern California continued through the 1940s.

The decline in commercial landings noted during the 1930s is thought to have been primarily a result of (1) a decline in fishing pressure caused by new regulations, (2) the economic difficulties faced by the fishing industry during the depression years, and (3) a suspected but unconfirmed decline in barracuda stock abundance caused by intense exploitation (Janssen 1937; MacCall, et al. 1976). The increase in commercial landings of barracuda during the 1940s appears to have resulted from a combination of good local availability off southern California from 1939 through 1941 because of abnormally warm ocean waters off our coast and increased effort for barracuda as a result of the wartime demand for protein.

Commercial barracuda landings steadily declined following the Second World War. Barracuda appears to have lost some of its marketability following the war, and purse seine captains found it increasingly difficult to (1) locate schools of barracuda off Mexico, (2) obtain orders for barracuda, and (3) make profitable trips with rising operating costs and the moderate-to-low prices paid for barracuda. Purse seine fishing of barracuda off Mexico had virtually ceased by 1956 and has not revived since. A nine-year cooling trend of ocean waters off California from 1948 through 1956 reduced annual northward barracuda migrations, and landings by local gill net and troll fishermen declined as well. A moderate increase in commercial landings occurred during 1957-59, when exceptionally warm ocean waters off the west coasts of California and Mexico resulted in large numbers of barracuda migrating north into southern California coastal waters (Pinkas 1966). Landings by the local gill net fleet declined again during the 1960s, following a return to more normal ocean water temperatures.

The commercial fishery was nearly extinct by 1969, as gill net fishermen found it increasingly difficult to locate commercial quantities of legal-sized barracuda. Commercial landings during the 1970s and 1980s have been small and made almost entirely by a few gill net vessels fishing local waters during May and June. Although increases in the commercial pounds-per-landing of barracuda have occurred in recent years, the market demand for barracuda at this time is relatively low, and less incentive exists now than in past years to pursue barracuda commercially (Schultze 1981).

Sport Fishery

The sport fishery for California barracuda is made up of the partyboat or commercial passenger fishing vessel fleet (CPFVs), from which paying customers fish for a fee; privately owned boats used for recreational fishing; and anglers fishing from piers, the shoreline, jetties, and breakwaters. By far the most important component of the sport fishery, and the one for which the greatest amount of historic information is available, is the CPFV fishery, which developed in the late 1920s and 1930s. The CPFV fleet was capturing roughly the same number of barracuda during the latter half of the 1930s as the commercial fishery was, or about 400,000 to 700,000 fish per year (Pinkas 1966). However, relatively greater numbers of young barracuda were landed by sport fishermen than by commercial fishermen. The sport fishery declined sharply during World War II, reducing fishing pressure on younger age groups for a period of about five years.

From 1946 through the present, the CPFV sport fishery has accounted for most of the barracuda being landed by both sport and commercial fisheries. The number of barracuda landed by CPFV anglers from 1948 through 1956 declined steadily to a low of 87,000 fish in 1956. With the warming of ocean waters off California from 1957 through 1959, landings of barracuda by CPFV anglers rebounded to record high levels. When ocean waters cooled to more average temperatures following 1959, landings declined to between 300,000 and 400,000 fish per year during the 1960s. By the late 1960s, however, it became apparent that catches were being sustained mainly by young barracuda less than 4 years of age (Schultze 1973). Heavy exploitation of young barracuda during these and previous years undoubtedly accelerated the decline in numbers, and by 1970 it became apparent that the population was seriously depleted.

Numbers of barracuda landed by CPFV anglers during the 1970s averaged less than 100,000 each year. This substantial decline from earlier 1960s CPFV landings is largely a result of a minimum size limit adopted in 1971. Many undersized barracuda are, therefore, returned to the water following capture and are not reported with the legal catch, thereby substantially reducing the reported landings during the 1970s.

MANAGEMENT EFFORTS

The principal regulatory measures undertaken to manage and conserve the California barracuda resource since the rapid expansion of the fishery in the post-World War I era are summarized in Table 3. The 1917 three-pound minimum size regulation on barracuda landed commercially corresponded closely with today's size limit of 28 inches (71.1 cm). However, this size limit, expressed in weight, proved impractical because of difficulty in estimating weights of fish aboard vessels at sea. Enforcement officers also ex-

TABLE 3
Regulations

Year	Regulation
1915	No barracuda less than 18 inches may be bought or sold. Barracuda designated a game fish requiring a sport license to take.
1917	No barracuda less than 3 pounds may be bought or sold.
1927	Unlawful for purse seine or other roundhaul to take or possess barracuda from May 15 through July 31.
1932	Unlawful for purse seine or other roundhaul to take or. possess barracuda from May 1 through July 31.
1934	No barracuda may be sold between May 1 and June 30. No more than 5 barracuda weighing less than 3 pounds each may be possessed each day; they are not to be sold or purchased.
1935	Barracuda not less than 3 pounds may be taken with hook and line. No nets may be used to take barracuda between May 1 and August 31. Between May 1 and August 31 a limit of 500 pounds of barracuda per man or 2,500 pounds per boat.
1939	Daily marine sport bag limit of 15 game fish in aggregate (no more than 15 barracuda if only barracuda caught).
1940	No purse seine or roundhaul may be used to take barracuda north of the international boundary with Mexico. Barracuda gill net mesh must be no less than 3½ inches stretched mesh.
1941	May not sell any sportfish taken under the authority of a sportfishing license. Repeal restriction on 500 pounds of barracuda per person and 2,500 pounds of barracuda per boat.
1947	Weight limit of 3 pounds changed to length limit of 28 inches for sport and commercial. Not more than 5 barracuda less than 28 inches per day in sport bag.
1949	Daily sport bag limit no more than 10 of one species and 15 in aggregate of species.
1957	No more than 2 barracuda shorter than 28 inches allowed in the daily bag limit. Daily bag limit of 10 game fish in aggregate.
1971	No barracuda less than 28 inches allowed in daily bag limit.

perienced difficulty in rapidly identifying sublegal-sized barracuda when moderate-to-large numbers of barracuda were landed. The three-pound limit was changed to 28 inches in 1947.

From 1925 through 1929, California Department of Fish and Game biologists conducted life-history studies on size and age at maturity, fecundity and length-weight relationship, and observed the fishery in an attempt to estimate what portion of the stock should be protected to conserve the resource and maintain landings under the intense fishing pressure of that time (Walford 1932). The observed size and age composition of barracuda in sampled commercial landings during the height of the 1920s commercial fishery was broad, encompassing fish from 2 through 12 years of age. Although large, older barracuda were abundant at that time, samples from the commercial fishery indicated that a large proportion of landings was composed of barracuda smaller than the allowable three-pound minimum (Walford 1932). Observations of actual fishing practices also revealed that significant quantities of undersized barracuda were wasted when schools of 2-, 3-, and 4-year-old barracuda were captured (primarily by purse seiners but also by gill nets and lampara vessels) and then dumped overboard after discovery that they were undersized (Skogsberg 1925). Most of these discarded barracuda did not survive.

During the 1930s, regulations affecting the use of nets to take barracuda were changed at almost every session of the legislature, with emphasis on prohibiting netting of barracuda during the major spawning months of May and June. Controversy surrounding the excessive destructiveness of purse seines on barracuda raged until 1939, when purse seines were finally banned in state waters; however, their use in waters off Mexico was unregulated and continued until the mid-1950s. Under current California state law, barracuda captured in purse seines off Mexico may be landed in California.

Gill nets used to capture barracuda must, by law, have a minimum stretched mesh of 3½ inches (8.9 cm). This regulation was instituted in 1940, without full evaluation of its ability to protect barracuda less than 28 inches (71.1 cm) TL. Recent investigation suggests that a small increase in mesh size of one-quarter inch should substantially increase protection for barracuda shorter than 28 inches without affecting the legal take of barracuda.

Sport-fishing regulations pertaining to barracuda up until 1971 were permissive, at best. In June 1941 it became illegal to sell sport fish caught under authority of an angling license. A three-pound barracuda size limit until 1947, and a 28-inch size limit imposed after 1947 were liberally tempered by allowing each angler to keep an allowance of undersized barracuda in each daily bag limit. These regulations appear to have been largely ineffective in conserving the California barracuda resource because the allowance essentially cancelled the effectiveness of the size limit. The commercial barracuda fishery was virtually extinct by the late 1960s; sport fishermen were landing fewer and predominantly young barracuda. A 1966 Department of Fish and Game recommendation for a strict 28-inch (71 cm) size limit was finally enacted in 1971 and remains in effect today.

The major efforts at barracuda management since 1971 have centered upon monitoring the catches and population to assess the effects of this strict size limit upon the stock and the fisheries. Monitoring size composition of sport and commercial samples since 1971 has shown a progressive and sustained increase in the number of age classes available to fishermen (Figures 4, 5, and 6) (Schultze 1981; Wine 1979a, b, c, d, and

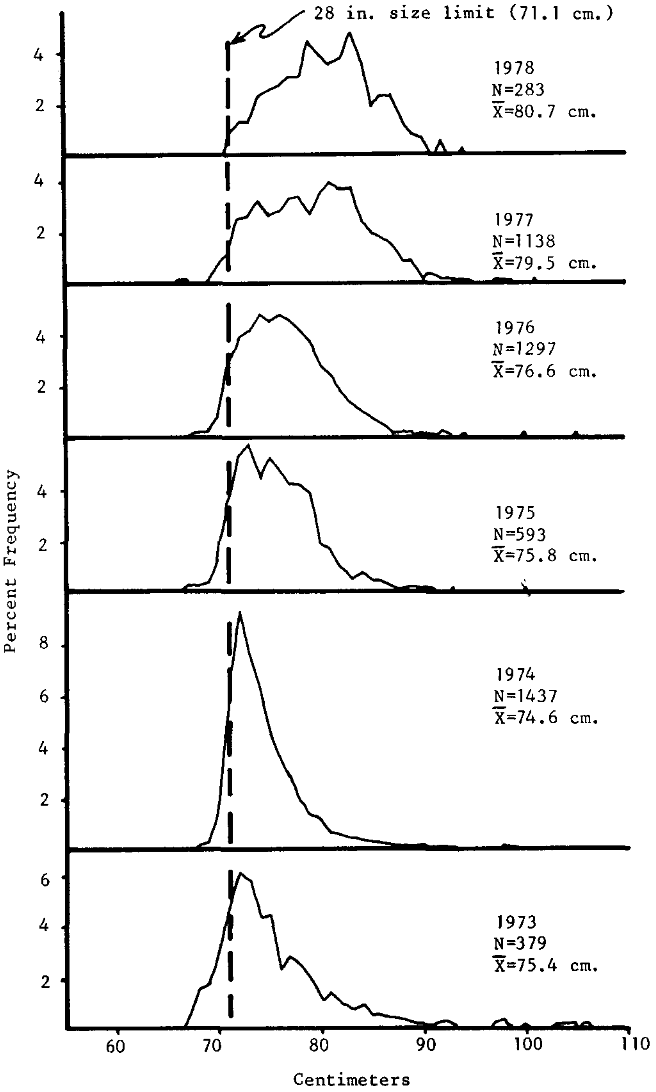

Figure 4. Size composition of commercial landings of California barracuda measured at the San Pedro fresh-fish markets.

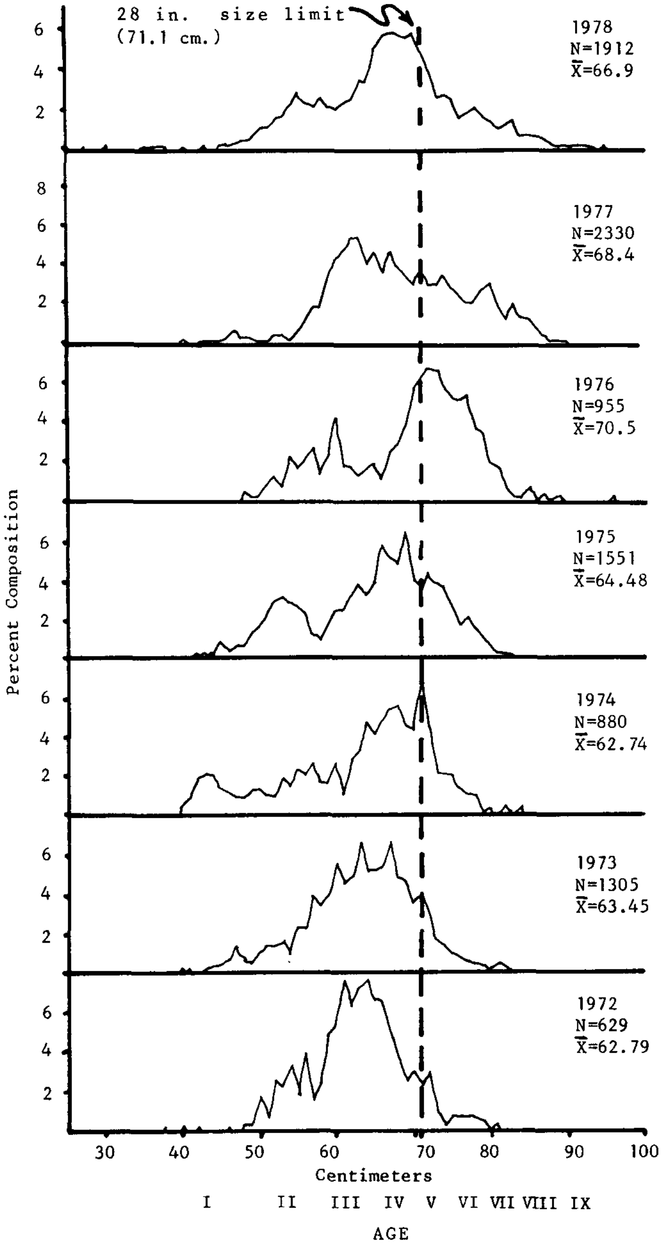

Figure 5. Size and age composition of California barracuda measured aboard southern California commercial passenger fishing vessels from 1972 through 1978. Sampled barracuda shorter than 28 inches were returned to the water.

pers. comm.). I assume this increase in availability of older fish has resulted from increased survival of barracuda due to reduced fishing mortality on young fish. The gradual reappearance of 7-, 8-, and 9-year-old barracuda in both sport and commercial catches, and their continued and relatively stable presence as components of these catches for five and six years is encouraging. This provides a broader and therefore more stable reservoir of spawning stock from which, presumably, larger year classes can be produced, given oceanographic conditions favorable to spawning and survival.

Identifying real increases in stock abundance (number of barracuda in the population each year) as a result of the strict 28-inch size regulation has been more difficult. As indicated above, there appears to have been some improvement in commercial catch per unit of effort for the mid-1970s, yet numbers of sport fish being landed remain between 50,000 and 100,000 fish per year. One of the major difficulties in estimating changes in barracuda abundance is that we are collecting data on an unknown portion of the stock each year.

RECOMMENDATIONS

It is uncertain how long recovery of the stock might take. Management action should continue to concentrate on ensuring the maximum survival of barracuda

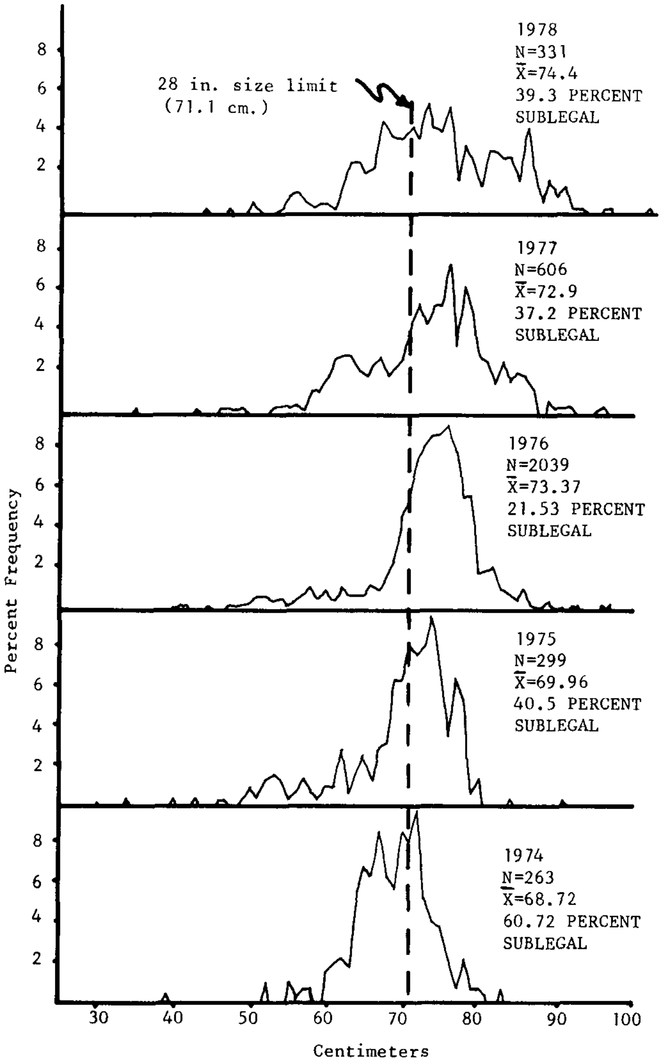

Figure 6. Size composition of California barracuda landed by southern California independent private boat fishermen. Sampled barracuda shorter than 28 inches (71.1 cm) total length were retained by these anglers.

through at least three spawning seasons. The present minimum size limit of 28 inches (71.1 cm) is believed necessary to increase the population and to maintain it at optimum levels under continued exploitation. Although the California barracuda resource shows signs of slow recovery since the late 1960s and early 1970s, there is no assurance that recovery will continue if there is an uncontrolled increase in exploitation.

I believe the following recommendations represent the most effective measures that can be implemented now to restore and maintain the California barracuda resource:

1. Maintaining, monitoring, and enforcing the existing 71.1-cm size limit is the foremost recommendation. Although strict compliance with this regulation has not yet been fully achieved in California waters, observed compliance by CPFV anglers has been good. Skippers and crew members of these vessels are able to inform anglers of, and urge compliance with, fishing regulations, thereby improving the probability of compliance and increasing the effectiveness of the regulation.

   Private boat anglers, on the other hand, appear unwilling to adhere to the regulations, or so the size composition of barracuda sampled from private boats reflects. Although private boat catches at this time make up a relatively small portion of barracuda landings (10-15% of total sport catch) continued noncompliance with the law will retard recovery of the fishery.

2. California barracuda should be considered in discussions with Mexico concerning cooperative management of marine resources. The California barracuda resource has historically proven itself vulnerable to overexploitation; although it appears that Mexico has applied relatively light commercial fishing pressure, its sport fishery claims large numbers of young, maturing barracuda each year. The barracuda stock could benefit substantially from a strict 28-inch size limit on all barracuda caught and landed in Mexico.

   If the barracuda resource is to recover to a level of maximum sustainable harvest, then Mexico can be expected to play a key role in how effectively this resource is managed. Data pertinent to management should be made available to Mexico. Heavy fishing effort off Mexico would undoubtedly reduce the availability of barracuda off California. However, historical catch data indicate that if the stock is restored to, and maintained at, moderate-to-large size, successful and sustainable catches should be possible in both southern California and Baja California waters.

3. Allowable minimum gill net mesh size for barracuda should be increased to 3.75 inches. This would bring the size of barracuda caught in gill nets more into line with present size restrictions on other fishermen and allow more 3- and 4-year-old barracuda to escape and spawn. In 1976 an estimated minimum of 5,300 additional undersized barracuda might have escaped to spawn if 3.75-inch mesh had been used. With an increased mesh size, fishermen would expend less effort removing and measuring undersized barracuda from their nets, and the markets would receive fewer sublegal ones.

A change in mesh size will require the construction of new nets, and conversion time should be allowed. Barracuda gill nets tend to last longer than some other nets because of their limited contact with abrasive surfaces and limited exposure to light. Allowing three to five years to convert to 3.75-inch mesh should reduce the financial impact of converting to new nets.

The number of commercial vessels landing barracuda is now the smallest since before World War I, and a change in nets will have less economic impact now than in the future, should the barracuda fishery expand.

4. Limit the depth of the gill nets to 170 meshes or 11.4 meters (6.25 fms). This would reduce their effectiveness if unlawfully used as encircling nets for barracuda, without significantly affecting legal operations. In addition, prohibit any barracuda aboard vessels carrying gill nets of less than 3.75-inch mesh. This should reduce the temptation to fish for undersized barracuda with small-mesh nets, and it will expedite law enforcement by eliminating the need to apprehend fishermen in the act of capturing undersized barracuda with illegal mesh.

5. Apply present size and gear restrictions to all California barracuda landed or imported regardless of origin. This is directed primarily at the roundhaul nets that may still capture California barracuda in Mexican waters. Restriction against roundhaul nets would have no impact upon the current fishery, but it would eliminate future exploitation by this gear. Size restrictions upon imported barracuda would aid law enforcement and encourage conservative practices by Mexican fishermen.

6. Remove the allowance of undersized barracuda for all commercial fishermen with the exception of five per boat per day for gill net fishermen for their personal use (not to be sold). An allowance for other than gill net fishermen is unnecessary because undersized barracuda caught by rod and reel or trolling (the only other fishing methods, other than roundhaul nets) are easily released alive.

7. Increase efforts to educate recreational fishermen about regulations, species recognition, and release techniques. A reduction in the large numbers of undersized barracuda destroyed by anglers would contribute much towards the recovery of the resource. Simplified aids to fish identification and the reasons for regulations must be made available to all anglers. Newspapers and magazines should be more fully used to distribute this information.

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BLUEFIN TUNA IN THE EASTERN NORTH PACIFIC OCEAN

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ABSTRACT

Northern bluefin tuna caught in the eastern North Pacific are spawned in the western Pacific and are taken with a variety of fishing gears throughout their life cycle. Total annual catches and catch per unit effort for surface and subsurface fisheries have been declining since the mid-1960s. Stock structure suggests the need for international management.

RESUMEN

Los atunes *(Thunnus thynnus)* que se capturan en la zona nordeste del Pacífico, han nacido en el Pacífico occidental, y se pescan a lo largo de su ciclo vital mediante diversos artes y redes. Las capturas anuales y por unidad de esfuerzo, tanto en las pesquerías de aguas superficiales, como en aguas más profundas, han ido disminuyendo desde mediados de la década de 1960. La estructura de las existencias sugiere que se precisa una cooperación internacional para regular esta pesquería.

INTRODUCTION

The Northern bluefin tuna was once plentiful and is still highly prized by sport and commercial fishers. One subspecies *(Thunnus thynnus thynnus)* is caught in the Atlantic Ocean; a second subspecies *(T. t. orientalis)* is caught in the Pacific. Total catches have drastically declined in both oceans, prompting management measures in the Atlantic, but not in the Pacific. Northern blue fin range throughout the Pacific, with surface fisheries near Japan and North America, and subsurface longline fisheries throughout much of the range.

STOCK STRUCTURE

Northern bluefin tuna spawn in the Philippine and South China seas from April to July (Yabe et al. 1966; Nishikawa et al. 1978). The larvae drift with the Kuroshio current towards Japan, where age 0+ (20-60 cm) bluefin are caught by the troll and bait fisheries. Many of the young fish remain in the vicinity of Japan, but a large number migrate across the Pacific and arrive off Baja California in April or May as 60-80-cm fish. Returns from tagged fish have shown these migrant bluefin to remain off the coast of North America for up to three years (Hanan 1983), whereas aging studies have shown fish as old as 6+ in the commercial catch from the eastern North Pacific (Schultze and Collins 1977). A few very large bluefin have been taken in the eastern Pacific, confirming the existence of older fish (Dotson and Graves in press); however, since no larvae have been found in the eastern North Pacific, it is hypothesized that migrant bluefin return to the western Pacific to spawn.

BIOLOGY

Northern bluefin tuna raised in captivity mature at about 3+ years, and females may carry as many as ten million eggs. Northern bluefin in the Pacific have been aged to 9+ years; large adults have only man and killer whales *(Orcinus orca)* as known predators. Hanan (1983) estimates a fishing mortality of 0.7/yr from the purse seine fishery in the eastern Pacific. Food studies in the eastern Pacific (Pinkas 1971) suggest that bluefin consume anchovy *(Engraulis mordax)*, red crab *(Pleuroncodes planipes)*, pacific saury *(Cololabis saira)*, squid *(Loligo opalescens)*, and hake *(Merluccius productus)*, in order of relative contribution to the diet. Bluefin tend to school by size in the 40-80-kg size classes, although mixed catches by size and species occur.

FISHERIES

The reluctance of northern bluefin to take a baited hook has generated a challenging sport fishery and a commercial fishery composed almost entirely of purse seiners. From 1900 to 1930, the Tuna Club of Santa Catalina Island, California, averaged 40 bluefin over 45 kg (100 pounds) annually in the sport catch. Since 1930 a *total* of only ten bluefin over 45 kg has been reported, and the average sport-caught bluefin is about 11 kg. In 1981 a commercial gill net boat caught a 237-kg bluefin near Anacapa Island, California (Dotson and Graves in press). That fish measured approximately 200 cm and would have been much older than the oldest bluefin aged from this area. In 1982 a skin diver speared a record 180-kg bluefin at Gaudalupe Island, Baja California, showing that a few large bluefin are still in the eastern Pacific.

Commercially, bluefin were first fished by purse seine about 1914; the first large catches were made in 1918 (Whitehead 1931). From 1918 to 1930, bluefin were fished almost exclusively in the Southern California Bight by the purse seine fleet out of San Pedro,

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[Manuscript received January 31, 1983.]

California, and in 1930 the fishing range extended to Guadalupe Island, Baja California. In the late 1950s the high-seas bait-boat fleet began converting to purse seine gear, subsequently fishing bluefin and extending the fishing range to the tip of Baja California. From 1957 to 1969 approximately 70% of the commercial catch was made by U.S. purse seine vessels of 100-300-ton carrying capacity. With the recent increase in drift gill netting, some bluefin are now being caught in the eastern Pacific with this gear.

Northern bluefin contributes about 1% of the world tuna catch and is worth about $10 million annually. In California, bluefin is canned for an ex-vessel value just under $1200 per short ton, but its real value is in the fresh-fish market, where it is sold primarily for sashimi at an ex-vessel price of about $2000 per short ton.

Normally bluefin are available from May to October, with the first catches occurring off Baja California. The largest catches shift from the south towards the north as the season progresses (Hanan 1983); although since the 1950s most of the bluefin has been caught off Baja California.

The long-term catch histories for both the sport and commercial fisheries show decreasing trends (Table 1), and even though Mexico has had a 200-mile territorial limit for some time, they have enforced it only in the last few years, which would not account for the long-term decline in total catches. Catch per unit effort (CPUE) analysis for the eastern Pacific surface fishery and the Japanese longline fishery also shows declining trends (Hanan 1983). Although these two indicators signal caution, another method—length-frequency analysis—shows little change over time. Because of a lack of sufficient fishing-effort information from the western Pacific, and since northern bluefin is considered a single Pacific-wide stock, no further analysis of stock status has been attempted.

These disturbing trends in catch and CPUE suggest that the nations fishing northern bluefin tuna should establish the necessary data collections to determine the status of the entire stock. It may be that some preliminary management measures by the Inter-American Tropical Tuna Commission are in order.

TABLE 1

Annual Total Bluefin Tuna Landings in the Eastern North Pacific Ocean by Commercial and Sport Fisheries

Year	Commercial (MT)	Sport (#fish)	Year	Commercial (MT)	Sport (#fish)
1918	2722	*	1951	1752	7142
1919	6800	*	1952	2076	145
1920	4776	*	1953	4433	4276
1921	894	*	1954	9537	966
1922	1275	*	1955	6173	8179
1923	1460	*	1956	5727	34187
1924	1470	*	1957	9215	6428
1925	1725	*	1958	13934	884
1926	2960	*	1959	6914	1330
1927	2222	*	1960	5422	27
1928	6215	*	1961	9603	2268
1929	3414	*	1962	14651	2453
1930	9943	*	1963	14189	737
1931	1603	*	1964	10642	693
1932	486	*	1965	7556	92
1933	254	*	1966	16846	1998
1934	8327	*	1967	6601	3166
1935	11418	*	1968	6063	1231
1936	8585	2920	1969	7172	1470
1937	5758	4020	1970	4024	1833
1938	8041	11927	1971	8415	749
1939	5369	9909	1972	13390	1470
1940	9058	6878	1973	10576	5347
1941	4318	*	1974	5748	5765
1942	5826	*	1975	9578	3348
1943	4617	*	1976	10561	2040
1944	9228	*	1977	5151	1838
1945	9341	*	1978	5903	479
1946	9993	528	1979	6743	1087
1947	9452	2194	1980	3128	729
1948	2961	104	1981	1016	*
1949	1991	1841	1982	2860	*
1950	1242	27			

*No data available

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THE NORTH PACIFIC ALBACORE—AN IMPORTANT VISITOR TO CALIFORNIA CURRENT WATERS

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ABSTRACT

The North Pacific albacore, *Thunnus alalunga,* is a highly migratory species, valuable to domestic and foreign fisheries. Albacore are found off the west coast of North America from about central Baja California to British Columbia, Canada, from late spring through fall. U.S. fishermen traditionally harvested the resource with surface gear within a few hundred miles of the shore until the mid-1970s, when an increasing number of West Coast- and Hawaiian-based jig vessels began operating from slightly west of the date line eastward across the North Pacific. A U.S. longline subsurface fishery also appears to be developing during winter beyond 1200 miles off southern California. The albacore is also highly sought after along the U.S. west coast by a large number of sportfishermen.

At the present time none of the North Pacific albacore fisheries is under management. Statistics and analysis currently available indicate that the resource is healthy. Recent estimates of MSY range from about 92,000 MT to 166,000 MT. Since the early 1960s, total catches for all fisheries harvesting albacore in the North Pacific have fluctuated; during the past decade they have ranged from about 70,000 MT to 124,000 MT.

Results from recent tagging studies suggest (1) that there are at least two substocks of fish constituting the North Pacific albacore population and (2) that these substocks have different migratory patterns. Off North America the separation in the proposed substocks occurs at Cape Mendocino, California, near 40°N. The proposed northern substock of fish makes trans-Pacific migrations between the eastern and western North Pacific, resulting in an exchange of fish between the northern area of the U.S. fishery and the Japanese livebait and gill net fisheries, and the longline fishery west of 180°. The proposed southern group of fish appear to enter the U.S. fishery south of about 40°N and are also fished by the longline fisheries east of 180°.

The migration, distribution, availability, and vulnerability of albacore are markedly influenced by oceanographic conditions in the North Pacific, notably by oceanic fronts. Recent research using acoustic telemetry methods to determine the location and swimming depth of free-swimming albacore, in conjunction with oceanographic observations made by ship and satellite suggests that water clarity's effect on the tuna's ability to see its prey is an important mechanism underlying the aggregation of tuna in the vicinity of oceanic fronts.

RESUMEN

Thunnus alalunga, albacora del Pacífico Norte, es una especie que efectúa amplias migraciones, manteniendo pesquerías nacionales y extranjeras de elevado valor económico. *T. alalunga* se encuentra desde finales de primavera hasta finales del otoño en aguas de las costas occidentales de Norte América, aproximadamente desde la parte central de Baja California (México) hasta la Columbia Británica (Canadá). Los pescadores de los Estados Unidos utilizan artes que operan en aguas de superficie, abarcando una zona que se extiende varios cientos de millas mar afuera; pero desde mediados de la década de 1970-1980, aumentaron los barcos al curricán en la costa del oeste y los de base en Hawaii, y así esta pesquería va avanzando en el Pacífico progresivamente hacia el este desde los 180° de longitud. Los Estados Unidos pescan con palangre durante el invierno, abarcando aguas más profundas, extendiéndose a más de 1200 millas del Sur de California. El albacora es también muy apreciado en la pesca deportiva, que opera a lo largo de las costas occidentales de los Estados Unidos.

Hasta ahora ninguna de las pesquerías de albacora ha sido sometida a regulaciones. Las estadísticas y análisis de los datos parecen indicar que esta pesquería logra mantenerse en buenas condiciones. Estimaciones recientes indican que las reservas de estas poblaciones alcanzan de las 92,000 a las 166,000 Toneladas métricas. Desde principios de la década de 1960-1970, las capturas totales, incluyendo todas las pesquerías de albacora en el Pacífico septentrional, han fluctuado oscilando durante la década pasada entre 70,000 hasta 124,000 Toneladas métricas.

Los resultados obtenidos mediante marcado de peces sugieren que en el Pacífico Norte hay dos poblaciones de albacora, las cuales presentan distintas rutas migratorias. La separación de estas propuestas pobla-

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[Manuscript received May 13, 1983.]

ciones en la zona de América del Norte, se presenta en las inmediaciones de Cabo Mendocino, California, aproximadamente a los 40°N. Los peces de la propuesta población nórdica efectuan migraciones transoceánicas entre el Pacífico oriental y occidental, resultando así un intercambio de peces entre la pesquería del norte de los Estados Unidos y las pesquerías japonesas con cebo vivo y trasmallos y la pesquería con palangre al oeste de 180°. El propuesto grupo meridional de peces entran al parecer la pesquería de los Estados Unidos al sur de los 40°N, y también se pescan con palangre al este de los 180°.

La migración, distribución, presencia y vulnerabilidad del albacora se ven influidas notablemente por las condiciones oceanográficas del Pacífico Norte, principalmente por los frentes oceánicos. Investigaciones recientes utilizando métodos telemétricos acústicos para determinar la distribución y localización en profundidad del albacora, en conjunción con observaciones oceanográficas efectuadas desde barcos y satélites, revelan que el comportamiento de agrupación de estos peces en las inmediaciones de los frentes oceánicos está condicionada más por el alimento que por los mecanismos termo-fisiológicos.

INTRODUCTION

Albacore tuna, *Thunnus alalunga* (Bonneterre), is a highly migratory tuna that supports important U.S. commercial and recreational fisheries and several foreign fisheries in the North Pacific. Over the past decade fisheries operating on North Pacific albacore have expanded, and research has yielded new information about this valuable resource. The purpose of this paper is to give an overview of the catch, effort, and catch-per-unit-effort trends of fisheries harvesting the North Pacific albacore and to provide information on the condition of the stock. Also, results from selected research investigations dealing with albacore oceanography and biology will be given.

FISHERIES HARVESTING NORTH PACIFIC ALBACORE

Japan and the U.S. account for the majority of the catches of North Pacific albacore—approximately 70% and 28%, respectively, from 1961 through 1978. Canada, Korea, and Taiwan each land about 0.5% to 1% of the total catch.

Historically, the Japanese have had two distinct fisheries harvesting albacore—a pole-and-line surface fishery operating during spring and summer and a longline subsurface fishery operating during winter. In 1978 a third Japanese fishery gained importance with the dramatic expansion of summer gill net fishing targeted on albacore.

For several decades the pole-and-line fishery extended eastward from near the coast of Japan to about 150°E; however, in the early 1970s it was expanded to east of the date line. The Japanese longline fishery is executed across much of the North Pacific, and by 1981 gill net operations had spread almost entirely across the North Pacific to within several hundred miles of the North American coast.

The U.S. fishery for albacore, which began in the early 1900s, uses surface trolling and pole-and-line fishing gears (Dotson 1980). The fishing takes place during summer and autumn in waters within a few hundred miles of the coast between central Baja California and British Columbia. Major geographical variations in the location of the fishing occur; during some periods it is centered in waters off the Pacific Northwest, during others, off southern-central California (Laurs et al. 1976). These geographical shifts in the location of the fishing have been linked to variations in environmental conditions (Clark et al. 1975). In 1975 the U.S. troll fleet began a broad extension of its operating range (Laurs and Nishimoto 1977). In recent years 75 to 100 vessels have started to fish near the date line about May, and to operate eastward across the mid-North Pacific to end the season in autumn off the coast of the U.S.

Recently, the U.S. albacore industry conducted a series of exploratory fishing operations to evaluate the feasibility of a winter U.S. longline fishery for albacore in the eastern Pacific (Laurs et al. 1981). The results of the experiments are encouraging, and a number of vessels have indicated a desire to participate in this new albacore fishery for the U.S.

CATCH, EFFORT, AND CATCH-PER-UNIT-EFFORT TRENDS

Catch Trends

Estimated annual catches of North Pacific albacore by country and gear type are given in Figure 1 for years 1961-79 (Bartoo and Kume 1982a) and in Table 1 for years 1962-81 (Bartoo and Kume 1982b). Since the early 1960s, total catches of North Pacific albacore fluctuated annually, but showed an increasing trend until 1976, when a peak of nearly 124,000 MT was recorded. During the early and middle 1970s, the increased catches reflected a rapid development of the Japanese pole-and-line fishery. In 1977, the catch declined by 40% compared to the average of the preceding 6 years; the decline was due primarily to the sharply reduced Japanese pole-and-line catch. Catches in 1978 recovered to the 1974-77 average of 97,000 MT, but in 1979 the catch again declined, mainly because the U.S. catch fell to its lowest point in nearly 40

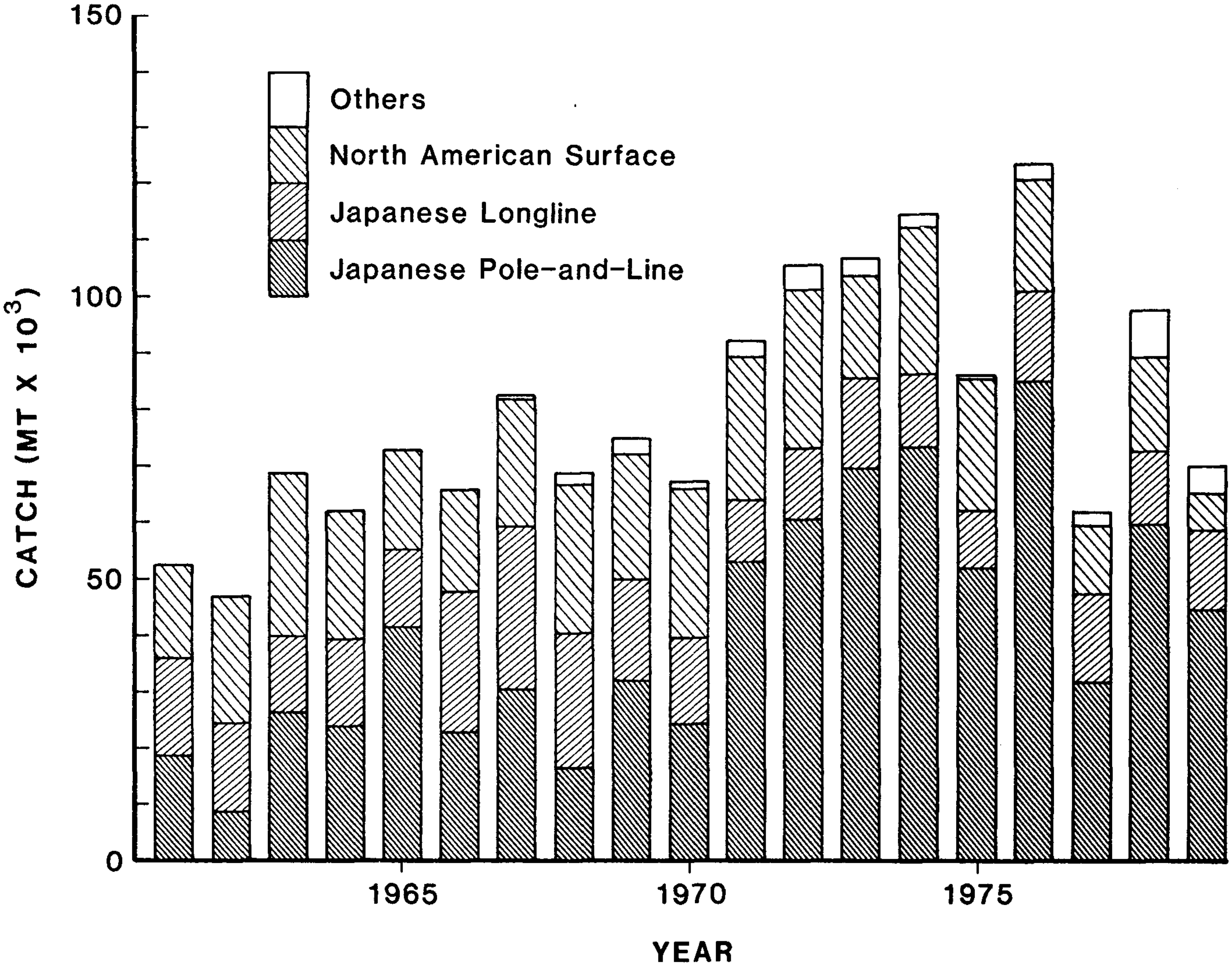

Figure 1. Annual catches of North Pacific albacore in the Japanese pole-and-line, Japanese longline, and North American surface fisheries, 1961-79 (Bartoo and Kume 1982a).

years—a little more than 7,000 MT. In 1980, the total catch increased to over 74,000 MT. It appears that the 1981 total catch was about 76,000 MT. The 1981 Japanese pole-and-line catch of albacore declined to about 26,000 MT, its lowest level since 1970, but this was offset by a dramatic increase in the Japanese drift gill net catch to nearly 20,000 MT.

Effort Trends

Effort trends within the U.S. troll fishery and the Japanese pole-and-line and longline fisheries are shown in Table 2 (Bartoo and Kume 1982b). The U.S. troll effort has remained rather stable except for 1972 and 1979 when the amounts of effort exerted were high and low, respectively. Effort by the Japanese longline fishery, the longest historical series available, shows considerable variability, but is relatively constant in the late 1970s at a level corresponding to about 75% of that in the 1960s and about 150% of that in the early 1970s. The Japanese pole-and-line effort increased substantially in the 1970s—primarily as the result of larger vessels entering the fishery—to levels almost triple those of the 1960s. In recent years the number of vessels in the 100 to 200 gross ton class, which account for more than 80% of the Japanese pole-and-line albacore catch, has declined (Bartoo and Kume 1982b). However, the number of large (greater than 100 gross tons) drift gill net vessels has been increasing, and the gill net fishery has expanded its operations farther eastward, with some fishing as far east as 135°W[1].

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[1] Bartoo, N. 1982. United States albacore surface fishery catch distribution determined from logbook records. Seventh North Pacific Albacore Workshop. Working Paper NPAL/82/12, 26 p.

TABLE 1

Catches for North Pacific Albacore in Metric Tons, 1952-81

	Japan					Taiwan & Korea	United States				Canada	
Year	Pole-and-line	Long-line	Gill net	Other gear	Total	Longline	Baitboat	Jigboat	Sport	Total	Jigboat	Grand Total
1952	41,386	26,687		237	68,710			23,843	1,373	25,216	71	93,997
1953	32,921	27,777		132	60,830			15,740	171	15,911	5	76,746
1954	28,069	20,958		38	49,065			12,246	147	12,393	—	61,458
1955	24,236	16,277		136	40,649			13,264	577	13,841	—	54,490
1956	42,810	14,341		57	57,208			18,751	482	19,233	17	76,458
1957	49,500	21,053		151	70,704			21,165	304	21,469	8	92,181
1958	22,175	18,452		124	40,731			14,855	48	14,903	74	55,708
1959	14,252	15,502		67	30,121			20,990	—	20,990	212	51,323
1960	23,156	17,369		76	42,601			20,100	557	20,657	5	63,263
1961	18,636	17,437		268	36,341		2,837	12,054	1,355	16,246	4	52,591
1962	8,729	15,764		191	24,684		1,085	19,753	1,681	22,519	1	47,204
1963	26,420	13,464		218	40,102		2,432	25,142	1,161	28,735	5	68,812
1964	23,858	15,458		319	39,635	26	3,411	18,389	824	22,624	3	62,283
1965	41,491	13,701		121	55,313	16	417	16,461	731	17,609	15	72,953
1966	22,830	25,050		585	48,465	16	1,600	15,169	588	17,357	44	65,882
1967	30,481	28,869		520	59,870	17	4,113	17,814	707	22,634	161	82,682
1968	16,597	23,961		1,109	41,667	15	4,906	20,441	951	26,298	1,028	69,008
1969	32,107	18,006		1,480	51,593	21	2,996	18,826	358	22,180	1,365	75,157
1970	24,376	15,372		956	40,704	23	4,416	21,039	822	26,277	354	67,358
1971	53,198	11,035		1,262	65,495	24	2,071	22,496	1,175	25,442	1,587	92,548
1972	60,762	12,649	1	921	74,333	25	3,750	23,600	637	27,987	3,558	105,903
1973	69,811	16,059	39	1,883	87,792	35	2,236	15,652	88	17,976	1,270	107,073
1974	73,576	13,053	224	1,065	87,918	40	4,777	20,177	739	25,693	1,207	114,858
1975	52,157	10,060	166	402	62,785	28	3,243	18,926	1,243	23,412	101	86,326
1976	85,336	15,896	1,070	1,394	103,696	37	2,700	16,314	766	19,780	252	123,765
1977	31,934	15,737	688	1,039	49,398	561	1,497	10,012	619	12,128	53	62,140
1978	59,877	13,061	4,029	3,209	80,176	53	950	15,700	871	17,512	23	97,773
1979	44,662	14,249	2,856	1,280	63,047	81	303	6,253	75	6,631	289	70,050
1980	46,743	14,660	2,986	1,516	65,988	—	382	7,599	174	8,155	212	—
1981	26,000	—	20,000	—	—	—	—	—	—	15,838	200	—

Remarks:

1. Figures for 1979-81 are preliminary.
2. Japanese longline catches for 1952-60 exclude minor amounts taken by vessels under 20 gross tons. Longline catches in weight are estimated by multiplying annual number of fish caught by average weight statistics.
3. Japanese pole-and-line catches include catches by research vessels.
4. United States jigboat catches include minor amounts taken by baitboats not submitting logbooks.
5. Jigboat catches for years 1952-60 include baitboat catches.
6. United States sport catch is a minimum estimate based on partial coverage.
7. Grand totals omit unknown but minor catches by longline and pole-and-line vessels of the Republic of Korea.

Catch Rate Trends (CPUE)

Nominal catch-per-unit-effort (CPUE) data for the U.S. troll fleet for 1961-70 are given in Laurs et al. (1976), and CPUE statistics for the major North Pacific albacore fisheries for 1961-81 are shown in Table 3 (Bartoo and Kume 1982b) and for 1961-79 in Figure 2 (Bartoo and Kume 1982a). CPUE within the U.S. troll fishery showed no apparent upward or downward trend from 1961-70, but declined from 1971-80. CPUEs in 1979 and 1980 were the lowest observed since records began. However, in 1981, CPUE increased to more than double the value for 1980. The catch rates over the long term have varied, being highest in the late 1960s when effort was unusually variable.

CPUE within the Japanese longline fishery showed a steady decline from the early 1950s through 1960, increased substantially through 1966, and then declined through 1971. Since then the trend in catch rate has been stable.

CPUE of the Japanese pole-and-line fishery showed a slight decreasing trend from 1962-80, except for relatively high values from 1970-76. A peak catch rate of 8 MT/fishing day was reported in 1974. The catch rate reached a low of about 3 MT/fishing day in 1977, then increased slightly before dropping to about 3 MT/fishing day again in 1981.

Condition of the Stock

In 1974 the Southwest Fisheries Center and the Far Seas Fisheries Research Laboratory in Shimizu, Japan, informally agreed to exchange research results

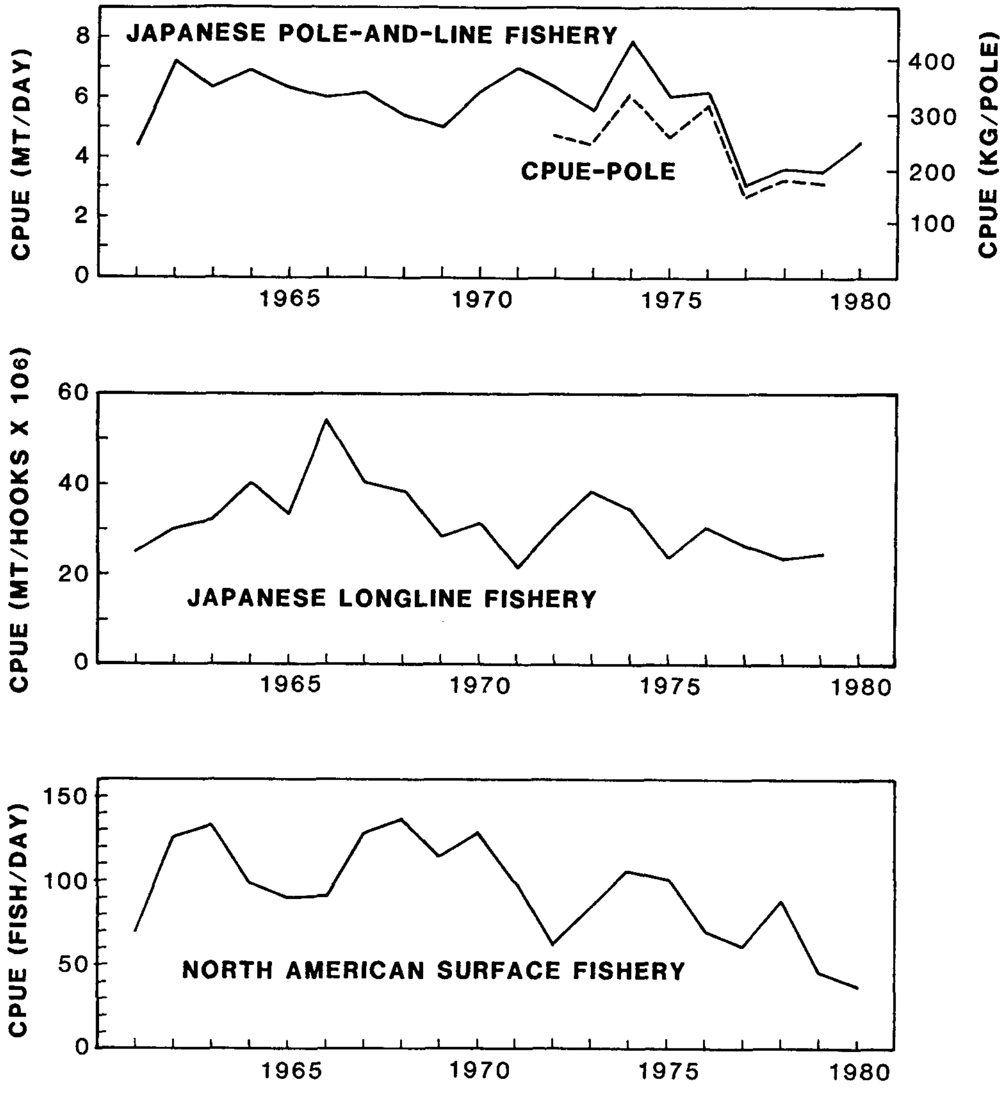

Figure 2. Annual catch rates of North Pacific albacore in the Japanese pole-and-line, Japanese longline, and North American surface fisheries, 1961-80 (Bartoo and Kume 1982a).

concerning the North Pacific albacore resource. In 1982 this agreement was extended to include the Pacific Biological Station at Nanaimo, Canada. There have been seven North Pacific Albacore Workshops held with scientists from the U.S. and Japan; in some cases scientists from Canada, Taiwan, and Korea participated. One of the objectives of the workshops is to share information for appraising the condition of the North Pacific albacore resource.

At the 1982 workshop a paper was presented on results of production model analyses based on updated abundance indices and effective effort statistics, and assuming a single stock[2]. The estimates of MSY ranged from 92,000 MT to 166,000 MT, depending largely on the assumed shape of the equilibrium yield-effort relationship. This range of estimates is consistent with results presented at past workshops. Participants at the workshop cautioned that critical assumptions underlying production model analyses may be difficult to satisfy when applied to albacore.

According to the report of the Seventh North Pacific Albacore Workshop (Bartoo and Kume 1982b),

> "Based on statistics and analyses currently available, the stock appears to be healthy. However, close monitoring is required, especially in view of increased effort in the drift gill net fishery, about which very little is known, and because of the declining catch-per-unit-effort in the major fisheries. Reliable assessment of the North Pacific albacore stocks remains a crucial task, beset by numerous problems. In particular, the measurement of effective effort is necessary, but is exceedingly difficult in the surface fisheries,

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[2] Kume, S. 1982. An approach to evaluate the stock status of North Pacific albacore by production model analysis. Seventh North Pacific Albacore Workshop. Working Paper NPAL/82/11, 6 p.

TABLE 2
Estimated Effective Effort by Fishery for North Pacific Albacore, 1961-81

Year	Japan longline (hooks x 10^6)	Japan[1] pole-and-line (days)	Japan[1] pole-and-line (poles x 10^3)	U.S.[1] effort (days)
1952	283.0			
1953	311.1			
1954	409.6			
1955	395.3			
1956	389.1			
1957	346.4			
1958	384.3			
1959	373.7			
1960	455.5			
1961	432.0	4,235		25,255
1962	309.0	1,209		27,464
1963	259.0	4,200		31,456
1964	232.4	3,478		30,355
1965	242.7	6,628		24,945
1966	276.8	3,843		25,756
1967	434.8	5,005		26,453
1968	355.8	3,108		29,175
1969	361.2	6,447		28,528
1970	253.2	3,958		20,165
1971	255.2	7,631		44,015
1972	186.7	9,695	227.8	67,319
1973	173.5	12,685	287.8	32,031
1974	153.8	9,421	226.4	39,748
1975	158.1	8,766	204.5	35,449
1976	227.2	13,921	278.9	38,445
1977	256.2	10,609	203.4	32,292
1978	252.8	16,725	321.9	32,111
1979	278.7	12,761	252.3	17,924
1980	203.0	*	*	28,418
1981	*	*	*	20,945

[1] Japanese pole-and-line days are not the same as U.S. effort days.
*Data not available.

where oceanographic processes and weather conditions strongly influence fish availability and catchability. Further, stock recruitment processes are not understood, and many questions about stock structure remain unanswered. As pointed out in past workshops, these subjects should be placed high on the research agenda of the participating laboratories. In the meantime, sensitivity analyses are needed to better define the robustness of current assessment procedures and the direction and magnitude of possible biases.''

STOCK STRUCTURE AND MIGRATION PATTERNS

There is a growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs and Wetherall 1981) that North Pacific albacore are not as homogeneous as usually assumed (Clemens 1961; Otsu and Uchida 1963). Results from recent tagging studies (Table 4) suggest that at least two substocks constitute the North Pacific albacore population and that these substocks have different migratory patterns (Laurs and Nishimoto 1979). Fish belonging to a proposed northern substock migrate between the eastern and western North Pacific, causing an exchange of fish between the U.S. fishery north of about 40°N, the Japanese livebait and gill net fisheries, and the foreign longline fisheries west of 180°. The proposed southern group of fish has a different migration scheme from that of the northern group, and appears to enter the U.S. fishery south of about 40°N, and the longline fisheries east of 180°. Only a very small proportion of the southern group of fish appears to migrate between the eastern and western Pacific and enter the Japanese pole-and-line or gill net fisheries. Also, during a given fishing season there is virtually no exchange of fish in the U.S. fishery between the northern and southern groups, although there is a small amount of interannual exchange.

Laurs and Wetherall (1981) found that the growth rate of North Pacific albacore recaptured either off the coast of North America north of 40°N or in the western North Pacific off Japan was significantly lower than that for tagged fish recovered off North America south of 40°N during 1972-78. The differences in growth rate are consistent with differences in length frequencies of albacore caught off North America north and south of 38°N during the period when most recoveries were made (Laurs and Lynn 1977) and during earlier years (Brock 1943). Thus a variety of types of information including tag and recapture data, growth-rate analyses, and differences in size composition of fish caught in the U.S. fishery support the hypothesis that the North Pacific albacore is not a homogeneous population, but rather that there are at least two substocks.

DETERMINATION OF ABSOLUTE AGE

A major void in our understanding of albacore biology is an understanding of true size and age structure. The daily ring increment method for aging fishes (Pannella 1971) offers great promise for determining absolute age and growth rates for albacore. Results from an experiment with tetracycline injection at time of tagging and release have verified that daily rings are laid down on the otolith of the albacore (Laurs and Nishimoto 1981). The method is being applied to albacore otoliths, and valid data on absolute age and size structure will be available in the near future. Preliminary results indicate that the length at first birthday is about 35 to 40 cm FL.

INFLUENCE OF OCEANOGRAPHIC CONDITIONS ON ALBACORE

There is ample evidence that the migration routes and small-scale movements of albacore are markedly influenced by oceanographic conditions. For example, albacore fishing grounds in the western Pacific have been linked to oceanic fronts (Uda 1973). Also, the

TABLE 3
CPUE[1] Statistics for Major North Pacific Albacore Fisheres, 1961-80

Year	Japan Pole-and-line		United States	Japan longline		
	Fishing days	Poles	jig	"Young" area[2]	"Main spawning" area[3]	Entire area[4]
1961	4.40		69.17	0.55	0.14	0.25
1962	7.22		124.59	0.67	0.14	0.30
1963	6.29		132.09	0.68	0.19	0.32
1964	6.86		97.61	0.90	0.19	0.40
1965	6.26		89.07	0.70	0.25	0.33
1966	5.94		90.45	1.20	0.27	0.54
1967	6.09	259	126.83	0.88	0.29	0.40
1968	5.34	227	135.23	0.84	0.29	0.38
1969	4.95	211	112.57	0.60	0.31	0.28
1970	6.13	261	127.39	0.66	0.27	0.31
1971	6.94	295	96.68	0.43	0.22	0.21
1972	6.25	266	61.08	0.63	0.30	0.30
1973	5.49	242	82.89	0.85	0.30	0.38
1974	7.81	325	105.17	0.64	0.30	0.34
1975	5.98	255	99.81	0.46	0.21	0.23
1976	6.13	306	69.22	0.66	0.21	0.30
1977	3.01	157	59.90	0.60	0.14	0.26
1978	3.58	186	86.80	0.52	0.17	0.23
1979	3.50	187	45.41	0.53	0.21	0.24
1980	4.44	268	36.78	0.72	0.26	0.33
1981	3.05	—	80.11	—	—	—

[1] Unit: MT/vessel-day and kg/pole-day for Japan pole-and-line; fish/vessel-day for United States jig; fish/100 hooks for Japan longline
[2] "Young" area is 25°-45°N from October to March and 30°-45°N from April to September.
[3] "Main spawning" area: 10°-25°N
[4] Entire area: 0°-45°N

seasonal migration of albacore into North American coastal waters has been found to be associated with the Transition zone and its frontal boundaries (Laurs and Lynn 1977). In addition, oceanographic conditions play an important role in the local concentrations and movements of albacore in U.S. coastal waters. Using concurrent ultrasonic tracking of free-swimming fish and oceanographic sampling, Laurs et al. (1977) found that albacore tend to aggregate in the vicinity of coastal upwelling fronts, presumably to feed, and to move away from the area when upwelling ceases and the front is no longer present.

TABLE 4
Summary of Where Tagged Albacore Were Recovered Relative to Area of Release

Area of Recovery	Area of release Inshore south 40°N	Inshore north 40°N	Offshore 130°W
Inshore south 40°N	78%	7% (0.8)*	31%
Inshore north 40°N	5% (0.4)*	32%	30%
Japanese livebait	4.5%	48%	21%
Japanese longline			
East of 180°	2%	0%	0.5%
West of 180°	0%	2.5%	1.5%
Unknown			
U.S. fishery	11.5%	9.5%	16%
Japanese fishery	0%	1%	0%

*Percentage recovered same year of release.

Very little has been published concerning relationships between oceanographic conditions and the vertical distribution of albacore. However, Clemens (1961) hypothesized that the thermocline acts as a barrier to albacore and that variations in albacore availability in waters off the U.S. are related to variations in the topography of the 14°C (58°F) isotherm.

Laurs et al. (1980) examined the vertical distribution of free-swimming albacore, measured by acoustic telemetry, in relation to ocean vertical thermal structure, measured concurrently with expendable bathythermographs (XBTs). We found that tracked fish spend little time in the upper layer, where it has been generally believed immature albacore (< about 6 years old) are distributed. The fish spent much of their time in the thermocline and were often well below the thermocline. Fish were found in waters 2° to 5°C (4° to 10°F) below what has been thought to be the optimal temperature range for albacore (Clemens 1961). Also, in some instances the tracked fish underwent changes in depth distribution resulting in temperature changes of as much as 5°C (10°F) within 10- to 30-minute periods.

Recently Laurs and Austin (unpublished results) investigated the small-scale migration patterns of albacore in relation to oceanic frontal boundaries using ocean color and infrared satellite data collected contemporaneously with observations made from ships at sea. NIMBUS-7 Coastal Zone Color Scanner (CZCS) and NOAA 6 satellite AVHRR infrared data were collected in conjunction with field experiments where acoustic telemetering methods were used to track the horizontal and vertical movements of free-swimming albacore, and XBT observations were made to determine subsurface ocean thermal structure. Three albacore were tracked for approximately 24 hours and one for about 15 hours. The results showed that (1) total distances tracked ranged from about 40 to 60 km, with all fish remaining in the same parcel of warm water that was separated from waters to the north, south, and inshore by about a 2°C (4°F) temperature gradient as shown by infrared thermal imagery; (2) tracked fish spent most of the time in waters within and below the thermocline, and only small amounts of time in the upper mixed layer; (3) the fish exhibited marked vertical excursions in depth, with the range being larger during the day than at night; (4) the fish spent most time in waters with temperatures considerably lower than what has been generally believed to be the preferred temperature range for albacore; and (5) when changing depth, the fish, frequently within a 20-minute period, passed through a vertical gradient of temperature amounting to 6° to 7°C (12° to 15°F), or about 3+ times greater than the horizontal temperature gradient at the surface indicated by ship measurements and the infrared thermal imagery.

These findings indicate that the reasons that tunas aggregate on the warm side of surface temperature fronts—an economically significant phenomenon that has been observed on scientific cruises and is well known by fishermen—may not be related to thermal-physiological mechanisms (Neill 1976). Instead, Laurs and Austin speculate that one or more behavioral mechanisms related to feeding may be responsible. Ocean color measurements made by the CZCS in conjunction with the tracking study and with catches made by commercial fishing vessels[3] provide data that support this hypothesis.

The diffuse attenuation coefficient (k), a measure of water clarity measured by the CZCS, showed a gradient nearly coincident with the sea-surface temperature gradient pattern, with lower values of k in the warm waters and higher values in the cooler waters. The distribution of color boundaries indicated by the ratio of blue:green color bands measured by the CZCS was also similar to the gradient pattern observed in the diffuse attenuation coefficient (k).

The results show that the albacore remained in water that had higher clarity than adjacent waters. This suggests that water clarity's effect on the tuna's ability to see its prey may play a key role in the mechanisms underlying the aggregation of tunas on the warm, clear side of ocean surface thermal fronts.

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Part III

SCIENTIFIC CONTRIBUTIONS

ICHTHYOPLANKTON AND ZOOPLANKTON ABUNDANCE PATTERNS IN THE CALIFORNIA CURRENT AREA, 1975

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ABSTRACT

The 1975 CalCOFI data were analyzed to provide a description of regional and seasonal zooplankton and ichthyoplankton abundance patterns. Zooplankton and ichthyoplankton abundances were found to be independent of each other on all scales examined. Zooplankton abundance decreased from north to south and inshore to offshore and appeared to be related to distribution of surface nutrient levels. Greatest ichthyoplankton abundance occurred off southern California and northern Baja California and was due to large spawning stocks of migratory species (anchovy, hake, and jack mackerel); the other ichthyoplankton fraction had complex abundance patterns because of its multispecies composition. Seasonal zooplankton abundance fluctuations along the coast (from Punta Eugenia northward) appeared to follow the northward seasonal progression of coastal upwelling. Maximum ichthyoplankton abundance was associated with periods of relatively stable water conditions prior to the onset of intense coastal upwelling. Persistent high-intensity zooplankton patchiness found off northern Baja California is associated with a zone of surface-layer convergence extending to the coast from offshore areas. This convergence zone may mark a separation of southern California and central-southern Baja California coastal biological regimes.

RESUMEN

Se analizaron los datos obtenidos en 1975 durante el programa CalCOFI, con objeto de obtener información sobre la abundancia regional del zooplancton e ictioplancton a lo largo de las estaciones del año. La abundancia de zooplancton no mantenía relación con la abundancia de ictioplancton, a todas las escalas analizadas. La abundancia de zooplancton decrecía de norte a sur y de la zona costera a la oceánica, y aparecía en cierto modo relacionada con la distribución de los nutrientes en las aguas de superficie. La mayor abundancia de ictioplancton se presentaba frente a la parte meridional de California y la zona norte de Baja California, constituyendo el resultado de las grandes concentraciones de poblaciones de especies migratorias (*Engraulis mordax*, *Merluccius productus* y *Trachurus symmetricus*), mientras que la otra porción de ictioplancton presentaba un patrón complejo debido a su composición multiespecífica. Las fluctuaciones en la abundancia del zooplancton a lo largo de las estaciones del año en la zona costera, al norte de Punta Eugenia, siguen al parecer con el avance de la estación, la progresión hacia el norte de las surgencias costeras. La máxima abundancia de ictioplancton aparecía asociada con períodos de estabilidad relativa de las aguas, antes de desencadenarse las intensas surgencias costeras.

Agregaciones persistentes de zooplancton de elevada cuantía se observaron frente a la parte norte de Baja California, asociadas con una zona de convergencia en superficie, extendiéndose desde la costa hasta mar afuera. Esta zona de convergencia pudiera marcar una separación en los regímenes biológicos costeros del sur de California y la parte centro-meridional de Baja California.

INTRODUCTION

Patterns and processes of oceanic life are sketchily known because of the vastness of oceanic regions, the diversity of oceanic biota, and costs of sustained oceanic study. The importance of abundance variations among certain commercially important oceanic fishes led to the field program of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). This program has provided description of hydrographic conditions in coastal waters and the California Current system (Reid et al. 1958) and has collected a vast amount of information on zooplankton and ichthyoplankton abundances in these waters since 1951.

The CalCOFI zooplankton data have been treated by a variety of researchers, and abundance fluctuations of the entire assemblage as well as its major taxa have been related to both short- and long-term physical processes within the California Current system (Reid et al. 1958; Colebrook 1977; Bernal 1980; Chelton 1981, 1982). The ichthyoplankton data have received comparatively little attention. Although abundance fluctuations among a few commercially important species have been examined in detail, the distribution, abundance, and composition of other ichthyoplankton elements have virtually been ignored.

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Never before have the zooplankton and ichthyoplankton elements been considered together.

Zooplankton and ichthyoplankton are fundamentally different fractions of pelagic communities. Zooplankton individuals spend their entire life cycle as plankton; their distribution and abundance are greatly affected by advective processes within oceanic regions. Larval fishes are the temporary planktonic stages of individuals that are for the most part nektonic and to a large extent zooplanktivorous; ichthyoplankton abundances reflect spawning locales and suitability of conditions for larval survival and recruitment to adult populations. Conditions affecting zooplankton and ichthyoplankton distribution and abundance may be quite different.

Our purpose in this paper is to use the 1975 CalCOFI survey data of zooplankton and ichthyoplankton abundances to identify major seasonal and regional features within the California Current system. Zooplankton and ichthyoplankton abundance patterns are compared to each other and related to physical processes within the current system.

METHODS

The 1975 ichthyoplankton and zooplankton data were derived from standard CalCOFI oblique plankton tows taken with a 1-m diameter net (mesh size, 505 μm) fished from 0 to 210 m. Samples were collected according to the basic CalCOFI station plan (Figure 1), with increased numbers of inshore sampling locations (Lasker 1978). All larval fishes were sorted out, identified, and counted. The larvae of five commercially important pelagic schooling species (anchovy, hake, sardine, jack mackerel, and Pacific mackerel) were sorted and treated separately from the 200+ other larval fish taxa collected. The five species are herein grouped together and referred to as the "PL" ("pelagic" larvae); the remaining taxa are considered together as the "OL" ("other" larvae). Ichthyoplankton abundances used are "total larvae" (all species lumped), the five combined PL species, and the OL fraction. The PL and OL fractions are treated separately because abundances of the PL (especially anchovy and hake) mask abundance relations of the OL. Data on individual PL species are included in tables, figures, and the Appendix, but receive only cursory treatment here; absolute and relative abundances of individual taxa are considered in Loeb et al., 1983a, b. Larval fish abundances are expressed as numbers of larvae per 10 m^2 sea-surface area; macrozooplankton (≥ 5 μm) abundance is wet displacement volume (cc per 1,000 m^3) (Kramer et al. 1972).

Absolute regional abundance estimates are mean numbers of larvae per m^2 sea surface multiplied by sea-surface area of the region. These are summed to provide the total estimated larval fish abundance within the CalCOFI survey area by cruise and for all six 1-month cruises (Appendix).

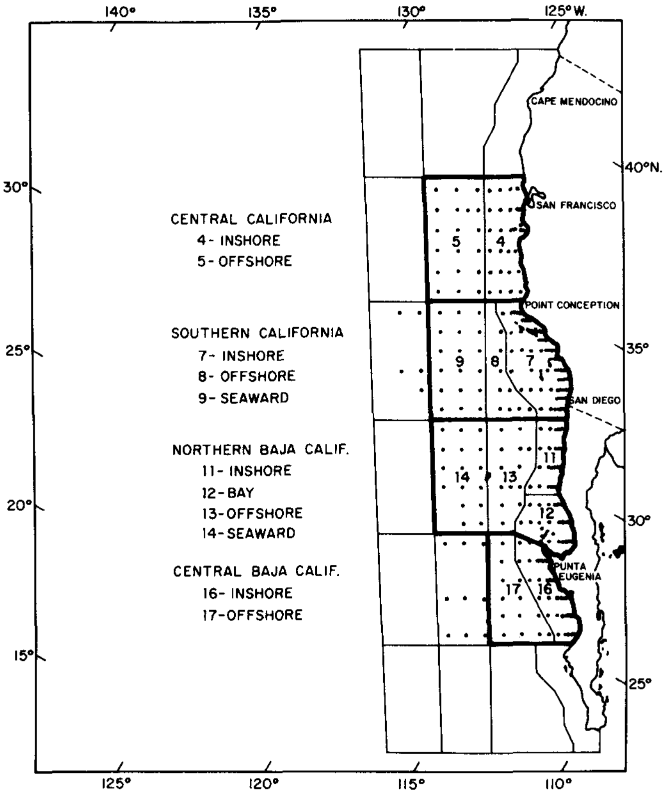

Figure 1. CalCOFI stations, regions, and areas sampled during the 1975 survey.

Data from 1,504 samples were formatted by cruise and standard CalCOFI regions. Thirteen regions were sampled (Figure 1); however, two of these (regions 10 and 18) received relatively less intensive coverage (< 10 samples per region; Table 1) and are not included in the analysis. The 11 regions considered were sampled during at least six 1-month cruises, and most were represented by ≥ 10 samples per cruise (Table 1). Most regions were sampled in December, January, March, May, July, and October; central California regions 4 and 5 were sampled in November rather than October. November data for southern California regions 7, 8, and 9 were used rather than October data, because larger numbers of samples were available (Table 1). For overviews of abundance and diversity patterns, regional data were combined into four latitudinal areas (central and southern California, northern and central Baja California; Figure 1) and into inshore, offshore, and seaward areas.

Larval fish diversity is expressed in two ways: as the mean number of fish taxa per tow, and as the total number of fish taxa taken in 60 randomly selected

TABLE 1
Regional Sampling Effort, 1975 CalCOFI Survey

		Cruise/month							
Area	Region	7412 Dec.	7501 Jan.	7503 Mar.	7505 May	7507 July	7510 Oct.	7511 Nov.	Total no. samples
Central	4	26	26	23	13	24	—	25	137
California	5	10	4	18	9	12	—	11	64
Southern	7	80	81	81	79	77	7	74	479
California	8	10	8	9	9	9	4	4	53
	9	18	18	16	18	18	—	14	102
	10	2	2	—	—	—	—	—	4
Northern	11	26	26	19	27	26	28	—	152
Baja	12	28	28	18	28	28	29	—	159
California	13	13	13	10	13	13	12	—	74
	14	4	12	4	12	15	15	—	62
Central	16	38	38	18	2	37	37	—	170
Baja	17	13	12	4	1	13	13	—	56
California	18	—	2	1	2	2	2	—	9

samples (10 samples/cruise) from each region. Regions 8 and 17 were represented by 53 and 56 samples, and those diversities may be underestimated.

Sample variability due to patchiness within each region is described by an index of dispersion based on variance to mean ratios ($S^2/\bar{x}$) and compared to an expected chi-square distribution (Pielou 1977). Here chi-square $P \leqslant 0.05$ implies aggregation, $0.05 < P < 0.95$ implies no significant departure from randomness, and $P \geqslant 0.95$ implies regularity of distribution. Extremely large index-of-dispersion values reflect high-intensity patchiness (Haury et al. 1978). Index-of-dispersion values for zooplankton abundances are based on biomass, and those of larval fishes are based on numbers of individuals per 10 m^2; consequently, comparisons cannot be made between these values.

Day-night abundance comparisons are based on day (1 hour before sunrise to 1 hour after sunset) and night samples. Differences of these (and other) mean abundances are tested with a 2-tailed Z test (Dixon and Massey 1969).

Comparisons of zooplankton and ichthyoplankton geographical and seasonal abundance patterns are made using Kendall's tau and concordance tests (Tate and Clelland 1957) on ranked regional and cruise abundances. Kendall's tau provides a correlation coefficient that is a measure of the similarity between the order of rankings within two data sets (e.g., between zooplankton and ichthyoplankton ranked regional abundances within a cruise or ranked cruise abundances within a region). The concordance test is a nonparametric analysis of variance performed on several sets of rankings; it is used here to test for similarity of zooplankton, PL, and OL seasonal abundances rankings within areas.

Kolmogorov-Smirnov (K-S) tests (Conover 1971) are based on the maximum differences between cumulative percent curves for two sets of data. They are used here to identify significant differences in the timing of the zooplankton and ichthyoplankton abundance increases.

TAXONOMIC PROBLEMS

The 1,504 samples yielded 104 species, and 100 higher taxa (50 generic, 45 familial, and 5 ordinal). Many abundant larvae (especially the Myctophidae and Bathylagidae) are identified to species, but identification of many coastal larvae, especially *Sebastes* spp (Scorpaenidae) and subtropical forms, is difficult. These identification problems limit analyses, especially the interpretation of diversity indices where inclusion of multispecies groupings certainly underrepresents the actual species richness of a region. This is a major problem only in nearshore and southern regions, but suggests caution in between-region comparisons of diversity.

RESULTS

Abundance and Diversity Estimates

Tables 2 and 3 and the Appendix present 1975 zooplankton and ichthyoplankton abundances by cruise and for all cruises combined for each region. The zooplankton, total larvae, and OL categories all exhibit large sample variances; standard deviations range from 0.3-2.3 times the mean values. Index of dispersion values for zooplankton biomass (Table 4A) and for numbers of total larvae and OL (Table 4B) by region and cruise predominantly indicate extreme aggregations of these categories (X^2 probabilities

≤ 0.05 for 77% of zooplankton, 94% of total larvae, and 85% of OL indices of dispersion). Because of tow-to-tow sample variability caused by patchiness, only large differences in abundance within and between regions can be detected as significant with standard statistical tests.

TABLE 2

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise		Region										
7412		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	260.7	176.2	85.2	93.4	132.7	85.1	56.6	83.0	53.2	44.5	50.8
	σ	117.0	108.0	49.1	64.1	131.0	70.9	30.6	42.6	11.6	28.9	40.2
Total larvae	χ	132.4	75.7	213.8	83.4	53.2	177.3	93.4	128.1	106.5	679.2	70.4
	σ	247.0	68.9	201.0	100.0	33.7	236.0	119.0	58.4	127.0	884.0	87.1
Anchovy	χ	2.2	8.5	123.2	9.4	—	88.4	62.0	4.5	—	597.6	—
	σ	4.6	18.4	154.0	18.3	—	180.0	112.0	9.0	—	878.0	—
Hake	χ	0.9	—	1.8	—	—	—	—	—	—	0.6	—
	σ	3.1	—	0.8	—	—	—	—	—	—	1.8	—
Sardine	χ	—	—	—	—	—	—	—	—	—	7.5	—
	σ	—	—	—	—	—	—	—	—	—	20.8	—
Other larvae	χ	129.3	67.2	88.8	74.0	53.2	88.9	31.4	123.6	106.5	73.5	70.4
	σ	247.0	53.6	135.0	84.7	33.7	80.6	34.8	61.7	127.0	64.7	87.1
No. tows		26	10	80	10	18	26	28	13	4	38	13
Cruise		Region										
7501		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	206.6	117.5	104.8	89.1	84.2	159.5	130.3	62.2	68.7	51.4	42.8
	σ	152.0	40.0	55.2	35.5	58.4	174.0	83.3	20.7	31.6	41.0	23.4
Total larvae	χ	425.0	127.5	1943.3	4628.4	1886.9	2183.2	2539.1	2133.1	193.8	625.3	201.8
	σ	344.0	122.0	2155.0	2730.0	4248.0	4341.0	4293.0	3096.0	92.5	1443.0	296.0
Anchovy	χ	11.8	—	1463.5	4027.0	189.9	1997.1	2374.5	2059.5	24.2	554.6	109.1
	σ	24.5	—	2123.0	3123.0	584.0	4320.0	4166.0	3097.0	35.9	1438.0	272.0
Hake	χ	28.9	—	89.0	449.2	1593.0	25.9	1.3	5.5	—	5.6	1.0
	σ	55.6	—	370.0	833.0	4120.0	50.7	5.1	14.0	—	10.5	3.5
Jack mackerel	χ	—	—	0.2	—	—	—	—	—	—	—	—
	σ	—	—	1.4	—	—	—	—	—	—	—	—
Sardine	χ	—	—	—	—	—	—	7.5	—	—	8.7	—
	σ	—	—	—	—	—	—	17.2	—	—	39.3	—
Other larvae	χ	384.3	127.5	390.7	152.1	104.0	160.2	155.8	68.2	169.6	56.6	91.7
	σ	328.0	122.0	433.0	119.0	60.8	134.0	152.0	34.8	96.2	69.8	73.5
No. tows		26	4	81	8	18	26	28	13	12	38	12
Cruise		Region										
7503		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	187.1	143.6	284.1	145.4	115.4	346.3	488.7	94.9	63.8	252.9	97.0
	σ	80.5	121.0	208.0	61.0	61.6	454.0	389.0	45.8	39.1	198.0	24.0
Total larvae	χ	311.1	151.0	2494.4	2721.4	659.9	2857.9	2112.8	941.9	876.2	1656.2	1307.3
	σ	203.0	102.0	2405.0	2665.0	1113.0	1931.0	3845.0	1036.0	1056.0	1911.0	1263.0
Anchovy	χ	1.9	0.4	2047.4	1973.4	15.3	2054.0	1883.6	313.2	2.5	1569.1	1068.5
	σ	5.1	1.9	2344.0	2178.0	40.1	1768.0	3755.0	688.0	3.3	1882.0	1345.0
Hake	χ	2.0	1.1	82.8	548.3	525.0	617.0	36.3	529.1	297.8	5.7	1.8
	σ	4.0	3.1	269.0	978.0	1053.0	957.0	58.5	921.0	541.0	8.4	3.5
Jack mackerel	χ	—	0.2	—	—	8.3	4.6	1.3	22.0	333.5	2.4	13.5
	σ	—	0.7	—	—	21.7	13.2	3.9	19.0	414.0	6.0	20.3
Sardine	χ	—	—	0.7	—	—	—	—	—	—	—	—
	σ	—	—	0.7	—	—	—	—	—	—	—	—
Other larvae	χ	307.1	149.3	364.1	199.7	111.3	182.4	191.6	77.6	242.5	79.1	223.5
	σ	203.0	101.0	318.0	182.0	97.8	106.0	335.0	43.3	276.0	69.5	226.0
No. tows		23	18	81	9	16	19	18	10	4	18	4

Continued on next page

TABLE 2 (Cont.)

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise						Region						
7505		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	338.7	258.8	322.9	512.0	203.1	486.9	196.4	172.2	88.9	177.0	—
	σ	397.0	174.0	463.0	568.0	160.0	618.0	124.0	91.3	28.0	42.4	—
Total larvae	χ	103.2	119.1	293.8	76.4	97.3	1396.1	1510.8	248.0	221.2	1319.5	400.0
	σ	83.4	75.7	410.0	57.0	69.3	2527.0	3549.0	195.0	126.0	251.0	—
Anchovy	χ	2.9	—	243.0	2.7	—	1324.3	1210.1	60.1	0.5	1186.0	—
	σ	10.5	—	404.0	5.7	—	2504.0	3067.0	161.0	1.7	124.0	—
Hake	χ	2.7	11.2	0.04	—	1.6	0.4	—	1.0	—	—	—
	σ	4.6	17.6	0.34	—	3.1	2.1	—	3.6	—	—	—
Jack mackerel	χ	—	—	—	—	—	5.3	0.3	76.0	10.8	—	—
	σ	—	—	—	—	—	9.9	1.7	112.0	9.6	—	—
Sardine	χ	—	—	—	—	—	—	6.9	—	—	—	—
	σ	—	—	—	—	—	—	36.5	—	—	—	—
Other larvae	χ	97.6	107.9	50.8	73.8	95.7	66.2	293.5	110.9	210.0	133.5	400.0
	σ	78.3	61.6	49.0	59.0	68.0	60.7	530.0	60.7	124.0	127.0	—
No. tows		13	9	79	9	18	27	28	13	12	2	1

Cruise						Region						
7507		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	276.9	292.8	165.3	179.4	197.6	179.3	169.1	78.8	50.5	118.5	64.3
	σ	194.0	259.0	199.0	124.0	123.0	292.0	166.0	35.7	19.5	121.0	67.3
Total larvae	χ	62.4	56.1	198.9	119.2	79.9	331.9	641.0	228.9	343.5	284.5	343.7
	σ	44.0	43.0	281.0	124.0	59.1	621.0	996.0	298.0	233.0	341.0	293.0
Anchovy	χ	1.5	—	163.6	3.7	0.2	263.2	160.2	17.4	0.1	68.0	34.0
	σ	5.0	—	277.0	9.9	0.7	580.0	216.0	25.8	0.5	175.0	121.0
Hake	χ	—	—	—	—	—	—	1.7	—	0.2	0.1	—
	σ	—	—	—	—	—	—	4.0	—	0.8	0.6	—
Jack mackerel	χ	—	1.2	0.7	49.3	18.3	2.7	—	12.6	17.5	1.1	0.2
	σ	—	4.3	4.1	127.0	19.9	6.4	—	11.9	13.5	3.9	0.6
Sardine	χ	—	—	—	—	—	—	0.2	—	—	20.3	—
	σ	—	—	—	—	—	—	0.9	—	—	71.5	—
Other larvae	χ	61.0	54.8	34.6	66.2	61.4	66.0	478.9	198.9	325.7	194.9	309.4
	σ	42.7	41.7	34.1	28.6	50.5	64.2	864.0	300.0	238.0	261.0	248.0
No. tows		24	12	77	9	18	26	28	13	15	37	13

Cruise						Region						
7510		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	—	—	139.7	40.2	—	126.0	118.1	45.6	43.8	112.4	105.9
	σ	—	—	86.4	34.5	—	211.0	132.0	23.2	27.6	93.5	108.0
Total larvae	χ	—	—	684.9	53.5	—	101.5	357.1	79.9	182.4	334.8	182.7
	σ	—	—	448.0	61.0	—	88.9	463.0	33.4	140.0	376.0	202.0
Anchovy	χ	—	—	293.1	30.8	—	23.0	136.3	—	0.8	104.9	27.7
	σ	—	—	219.0	61.5	—	44.7	297.0	—	2.6	229.0	96.6
Hake	χ	—	—	—	—	—	—	0.2	0.2	—	—	—
	σ	—	—	—	—	—	—	0.9	0.9	—	—	—
Jack mackerel	χ	—	—	—	1.2	—	0.5	0.1	—	—	—	—
	σ	—	—	—	2.5	—	1.5	0.4	—	—	—	—
Sardine	χ	—	—	—	—	—	0.7	17.5	—	—	5.0	—
	σ	—	—	—	—	—	2.8	27.1	—	—	13.3	—
Pacific mackerel	χ	—	—	—	—	—	—	1.2	—	—	1.5	—
	σ	—	—	—	—	—	—	4.5	—	—	5.2	—
Other larvae	χ	—	—	391.7	21.5	—	77.4	201.9	79.7	181.6	223.3	154.9
	σ	—	—	311.0	13.2	—	66.3	304.0	33.6	138.0	223.0	189.0
No. tows		—	—	7	4	—	28	29	12	15	37	13

Continued on next page

TABLE 2 (Cont.)
Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise 7511		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	254.2	105.4	107.6	74.2	91.6						
	σ	252.0	59.0	96.5	44.1	88.3						
Total larvae	χ	78.8	32.1	337.5	63.0	68.0						
	σ	55.5	15.8	339.0	35.1	64.8						
Anchovy	χ	0.1	—	292.7	—	1.5						
	σ	0.4	—	335.0	—	2.8						
Hake	χ	—	—	1.6	—	—						
	σ	—	—	4.8	—	—						
Jack mackerel	χ	—	—	0.03	—	—						
	σ	—	—	0.23	—	—						
Sardine	χ	—	—	0.04	—	—						
	σ	—	—	0.35	—	—						
Other larvae	χ	78.8	32.1	43.1	63.0	66.5						
	σ	55.5	15.8	34.6	35.1	64.7						
No. tows		25	11	74	4	14						

Ichthyoplankton abundances given for total larvae, 5 species constituting the PL, and other larvae (OL).

TABLE 3
Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10m^2 sea-surface area) for All Samples Taken Within Each of 11 CalCOFI Regions (6 Cruises Total) during 1975

		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	247.2	184.7	179.1	183.6	139.7	225.5	174.1	89.8	60.9	100.6	70.0
	σ	203.0	164.0	245.0	282.0	119.0	372.0	207.0	63.2	30.6	116.0	68.9
Total larvae	χ	193.1	95.0	932.3	1241.2	486.5	1084.5	1146.8	621.3	271.1	617.3	282.3
	σ	246.0	85.7	1653.0	2290.0	1922.0	2404.0	2816.0	1515.0	329.0	1102.0	457.0
Anchovy	χ	3.5	1.4	736.6	966.4	363.8	898.0	908.5	418.5	5.2	475.3	117.6
	σ	12.2	7.6	1528.0	2089.0	1840.0	2310.0	2638.0	1494.0	18.0	1096.0	437.0
Hake	χ	6.3	1.9	30.0	164.0	4.5	81.6	4.7	72.7	19.3	2.0	0.3
	σ	26.4	7.5	193.0	550.0	13.7	388.0	22.5	371.0	141.0	6.2	1.8
Jack mackerel	χ	—	0.3	0.1	8.6	—	2.0	0.2	18.5	27.8	0.5	1.0
	σ	—	1.9	1.8	53.6	—	7.0	1.5	53.9	123.0	2.7	5.9
Sardine	χ	—	—	0.02	—	—	0.13	5.8	—	—	9.1	—
	σ	—	—	0.31	—	—	1.19	21.2	—	—	40.0	—
Pacific mackerel	χ	—	—	—	—	—	—	0.21	—	—	0.34	—
	σ	—	—	—	—	—	—	1.95	—	—	2.45	—
PL	χ	9.8	3.6	766.8	1139.0	404.4	981.8	919.3	509.7	52.3	487.2	119.0
	σ	32.3	10.7	1563.0	2265.5	1904.0	2372.0	2640.0	1522.0	259.0	1098.0	439.0
OL	χ	183.3	91.4	165.5	102.1	82.1	102.7	227.5	111.5	218.7	130.0	163.3
	σ	235.0	82.1	277.0	111.0	67.0	97.3	478.0	137.0	176.0	181.0	188.0
No. tows		137	64	472	53	102	152	159	74	62	170	56
							Ranked regional abundance					
Total larvae		10	11	4	1	7	3	2	5	9	6	8
PL		10	11	4	1	7	2	3	5	9	6	8
OL		3	10	4	9	11	8	1	7	2	6	5

Ichthyoplankton abundances given for total larvae, 5 species constituting the PL, and other larvae (OL). Regional ranks provided for total, PL, and OL abundances.

TABLE 4
Index of Dispersion Values for (A) Zooplankton Biomass and (B) Total Larval Fish (TL) and OL Abundances Within 11 CalCOFI Regions by Cruise

		Region										
		Central California			Southern California			Northern Baja California			Central Baja California	
		4	5	7	8	9	11	12	13	14	16	17
A. Zooplankton												
Cruise												
7412		52.5	66.2	(28.3)	44.0	129.3	59.1	16.5	21.6	(2.5)	(18.8)	31.8
7501		111.8	13.6	(29.1)	14.1	40.5	189.8	53.2	(6.9)	(14.5)	(32.7)	(12.8)
7503		34.6	102.0	152.3	25.6	32.9	595.2	309.6	22.1	24.0	155.0	(5.9)
7505		465.3	117.0	663.9	630.1	126.0	784.4	78.3	48.4	(8.8)	10.2	—
7507		135.9	229.1	239.6	85.7	76.6	475.5	169.9	(16.2)	(7.5)	123.6	70.4
7510 (11)		249.8	33.0	(86.5)	26.2	85.1	353.3	147.5	(11.8)	(17.4)	77.8	110.1
B. Total larvae and OL												
Cruise												
7412	TL	460.8	62.9	189.0	119.9	(21.3)	314.1	151.6	26.6	151.4	1150.5	107.8
	OL	471.8	42.8	205.2	96.9	(21.3)	73.1	(38.6)	30.8	151.4	57.0	107.8
7501	TL	278.4	116.7	2389.8	1610.2	9563.6	8631.5	7258.4	4493.6	44.1	3330.0	434.2
	OL	280.0	116.7	479.9	93.1	35.5	112.1	148.3	(17.8)	54.6	86.1	58.9
7503	TL	132.5	68.9	2318.8	2609.8	1877.2	1304.7	6638.1	1139.5	1272.7	2205.0	1220.2
	OL	134.2	68.3	277.7	165.9	85.9	61.6	585.7	24.2	314.1	61.0	228.5
7505	TL	67.4	48.1	572.2	42.5	49.4	4574.0	8336.9	153.3	71.8	47.7	—
	OL	62.8	35.2	(47.3)	47.2	48.3	55.7	957.1	33.2	73.2	120.8	—
7507	TL	(31.0)	32.9	397.0	129.0	43.7	1161.9	1547.6	389.9	158.0	408.7	249.8
	OL	(29.9)	31.7	(33.6)	(12.4)	41.5	62.4	1558.8	452.5	173.9	349.5	198.8
7510(11)	TL	39.1	(7.8)	340.5	19.6	61.8	77.9	600.3	(14.0)	107.5	422.3	223.3
	OL	39.1	(7.8)	(27.8)	19.6	62.9	56.8	457.7	(14.2)	104.9	222.7	230.6

Values within parentheses indicate nonsignificant departures ($P > 0.05$) from random distribution.

Larval fish diversity is presented in Table 5 as (A) mean numbers of taxa per tow and (B) total numbers of taxa in 60 tows within each region. Mean numbers of larval fish taxa per tow varied much less than larval abundance values (standard deviations 0.3-0.7 times mean values) and reflect relatively constant regional diversities within each cruise. Between-cruise mean diversity values generally varied ≤ than a factor of 2 within each region. The two overall diversity measurements indicate similar regional trends and have a rank difference correlation coefficient (Tate and Clelland 1957), calculated across all regions, of 0.714 ($P < 0.05$).

Day-Night Differences in Abundance and Diversity

Day-night catch differences may bias abundance and diversity estimates. Bridger (1956) and Ahlstrom (1959) reported night:day ratios of ~ 3:1 for total (mixed taxa) larval fish abundances, and attributed these differences to daytime net avoidance. Consistent catch differences of this magnitude could introduce large errors in abundance estimates based on combined day and night data. Z tests were performed on mean day and mean night abundance values of each larval fish category by region and cruise and for the combined total of regions and cruises (Table 6). Only 33 of 183 day-night abundance comparisons were significantly different; in 6 cases day catches were larger, and in 27 cases night catches were larger. Twenty-three percent of the comparisons in the total larvae and OL categories yielded significant differences. Nine of the 13 significant night:day catch differences of total larvae were associated with significant catch differences of OL rather than PL categories. Significant day-night catch differences in the combined regional data occurred only within the total larvae and OL categories (Table 6). The ratio of night:day catches of zooplankton and ichthyoplankton varied widely within each region (Table 6). For most categories night catches were generally (but not significantly) larger than day catches. Night:day ratios were: total larvae, anchovy, and OL all 1.3:1; hake, 2.2:1; jack mackerel, 2.4:1. Zooplankton had a 1:1 night:day ratio. Night tows also generally yielded more larval fish taxa per tow (overall night:day ratio = 1.3:1); 11 of 61 comparisons were significant, and all 11 showed greater night than day catches.

Overview of Abundance and Diversity in the CalCOFI Area

Zooplankton abundance decreased from north to south and from inshore to offshore (Table 7; Figure 2). Mean zooplankton abundance off central California was significantly higher, and off central Baja California significantly lower, than in the other two areas ($P < 0.01$, Z test). Maximum mean and absolute

TABLE 5

Larval Fish Diversity Expressed as (A) Mean and Standard Deviations of Numbers of Larval Taxa per Tow by Region and Cruise and as (B) the Total Numbers of Larval Taxa Taken in 60 Samples Within Each Region

Cruise							Region					
A.		4	5	7	8	9	11	12	13	14	16	17
7412	χ	4.3	3.6	4.6	6.6	6.0	5.3	3.6	6.8	10.0	5.6	4.5
	σ	2.4	1.6	2.4	3.6	3.6	2.9	1.7	3.3	5.7	2.6	3.1
No. tows		27	10	80	10	18	26	28	13	4	38	13
7501	χ	7.3	6.0	6.7	7.9	10.9	7.6	6.3	7.3	14.9	5.6	6.9
	σ	2.8	4.1	2.2	4.0	4.0	2.3	2.1	3.4	3.0	2.9	1.9
No. tows		26	4	81	8	18	26	28	13	12	38	12
7503	χ	6.7	8.3	7.8	8.3	11.8	8.6	5.1	7.0	15.2	4.9	7.5
	σ	2.9	4.7	2.8	3.8	5.0	3.0	3.6	1.5	9.0	1.8	3.7
No. tows		23	18	81	9	16	19	17	10	4	18	4
7505	χ	5.1	7.0	4.1	4.9	10.3	4.5	5.4	7.0	12.8	5.5	9.0
	σ	2.3	4.8	2.5	3.5	5.3	2.2	2.6	2.8	3.4	3.5	—
No. tows		13	9	79	9	18	27	28	13	12	2	1
7507	χ	2.5	4.5	3.9	7.0	9.8	5.1	6.3	6.7	14.7	6.0	9.3
	σ	1.8	2.0	2.4	4.6	5.7	2.2	2.2	3.8	4.5	3.8	4.8
No. tows		24	12	77	9	18	26	28	13	15	37	13
7510	χ	—	—	6.9	5.2	7.0	6.9	7.6	8.7	12.2	10.6	6.8
	σ	—	—	3.1	1.5	3.0	3.7	4.2	4.9	4.6	5.3	4.8
No. tows		—	—	7	4	3	28	29	12	15	37	13
7511	χ	3.1	2.9	5.1	6.8	8.9	—	—	—	—	—	—
	σ	1.4	1.9	2.8	5.2	5.5	—	—	—	—	—	—
No. tows		25	11	74	4	14	—	—	—	—	—	—
Total	χ	4.8	5.6	5.4	6.7	9.5	6.2	5.8	7.2	13.5	6.6	7.0
	σ	2.9	4.0	2.9	3.9	5.1	3.1	3.0	3.4	4.6	4.1	4.0
No. tows		137	64	472	53	105	152	159	74	62	170	56
Region rank (total means)		11	9	10	5	2	7	8	3	1	6	4

					Region					
B.	4	5	7	8	9	11	12	13	14	16	17
No. taxa in 60 tows (* denotes < 60 tows)	49	62	51	62*	80	74	77	67	99	77	73*
Region rank	11	8.5	10	8.5	2	5	3.5	7	1	3.5	6

ichthyoplankton abundances occurred in the areas off southern California and northern Baja California; about 39% of the total estimated larval abundance was from each of these areas, whereas the central Baja California area yielded about 17% of the total, and only 5% of the total larvae occurred north of Point Conception. Mean larval fish abundances decreased from inshore to offshore and seaward areas (Table 7; Figure 3). Mean numbers of larval fish taxa/tow increased from north to south, reaching maximum levels off northern Baja California (Table 7; Figure 4). Unlike abundance, diversity increased with distance from shore, perhaps partly because of better identification ability for larvae of offshore fish species.

Regions differed in total larval fish abundance and in the relative abundances of the PL and OL fractions. Total larval abundances were highest in regions 7, 11, and 12 of southern California and northern Baja California and region 8 of southern California because of large numbers of PL (Figures 3 and 5). Here the PL (primarily anchovy) made up ≥ 80% of the regional totals (Table 3). Anchovy-dominated PL also constituted > 80% of the relatively moderate larval fish abundances of central Baja California region 16 and regions 9 and 13 of southern California and northern Baja California (Figures 3 and 5; Table 3). Total larval abundances were relatively low (Figure 3), and the proportions of PL and OL more similar, in regions 14 and 17 of northern and central Baja California. The PL of region 17 was primarily anchovy, whereas that of region 14 was mostly jack mackerel and hake (Table 3). Central California regions 4 and 5 had the lowest

TABLE 6
Results of Comparisons of Day and Night Catches of Zooplankton, Total Larvae, 5 Species of PL, and the Other Larvae (OL), and the Ratio of Night:Day Abundances of These Categories for (A) Individual Region and Cruise Data (239 Comparisons) and (B) Combined Region and Cruise Data (850 Day Samples, 636 Night Samples)

				Regional data				
	Zooplankton volume	Total larvae	Anchovy	Hake	Jack mackerel	Sardine	Pacific mackerel	Other larvae
No. signif. differences	9	13	2	2	1	2	0	13
No. comparisons	56	56	37	21	9	3	1	56
No. signif. larger day values	1	2	1	2	—	1	—	—
No. signif. larger night values	8	11	1	—	1	1	—	13
			Ratio of night:day abundance values					
Range	0.7-1.5	0.7-2.5	0.6-20	0.3-4.4	0.8-5.5	0.4-7.7	0.5	0.7-2.0
Mean	1.1:1	1.4:1	1.1:1	1.7:1	2.6:1	4.0:1	0.5:1	1.4:1
B.			Combined region and cruise data					
Probability level for signif. differences	$P=0.63$	$P=0.03$*	$P=0.16$	$P=0.19$	$P=0.15$	$P=0.55$	$P=0.39$	$P=0.003$*
Ratio night:day	1.0:1	1.3:1	1.3:1	2.2:1	2.4:1	0.8:1	0.4:1	1.3:1

Significance of abundance differences are based on the Z test ($P < 0.05$; 2 tailed); asterisk denotes significant comparisons.

TABLE 7
Areal Summary of Means and Standard Deviations of Zooplankton and Ichthyoplankton Abundances and of Ichthyoplankton Diversity Within the 1975 CalCOFI Survey Area

CalCOFI area	Zooplankton abundance (cc/1000m^3)	Ichthyoplankton abundance (no./10m^2)	Percentage of total CalCOFI area ichthyoplankton	Larval fish diversity (mean no. taxa/tow)
I: Central California (regions 4, 5; 46,599 nmi^2) 201 samples	227 ± 193	162 ± 214	4.98%	5.2
II: Southern California (regions 7, 8, 9; 60,906 nmi^2) 626 samples	173 ± 233	885 ± 1767	39.40%	7.2
III: Northern Baja California (regions 11, 12, 13, 14; 69,394 nmi^2) 447 samples	162 ± 258	917 ± 2293	38.16%	8.2
IV: Central Baja California (regions 16, 17; 36,653 nmi^2) 226 samples	93 ± 107	534 ± 994	17.46%	6.8
Inshore (regions 4, 7, 11, 12, 16; 72,024 nmi^2) 1,090 samples	181 ± 246	843 ± 1848	47.36%	5.8
Offshore (regions, 5, 8, 13, 17; 83,964 nmi^2) 246 samples	130 ± 168	538 ± 1415	33.62%	6.4
Seaward (regions 9, 14; 57,564 nmi^2) 164 samples	110 ± 103	405 ± 1530	19.02%	11.5

Areal estimates based on combined (6 cruises) regional sample data (regions are noted for each area considered). Zooplankton abundance as mean displacement volume (cc/1000m^3); ichthyoplankton abundance as mean numbers of larvae/10 m^2 sea-surface area and as the percentage of the total estimated numbers of larvae represented by each area; and larval fish diversity as mean numbers of larval taxa/tow. Regional areas given as numbers of square nautical miles.

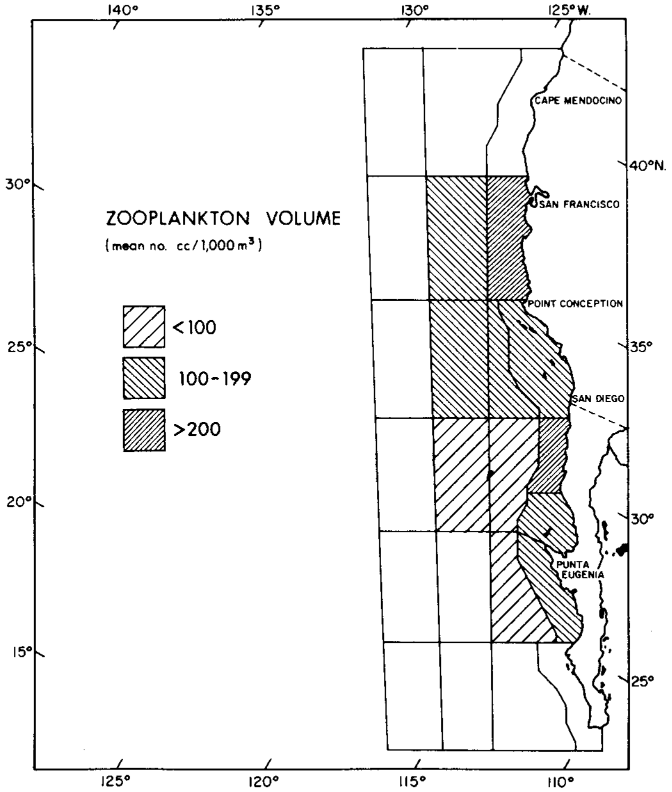

Figure 2. Mean zooplankton volume in 11 CalCOFI regions sampled during 1975.

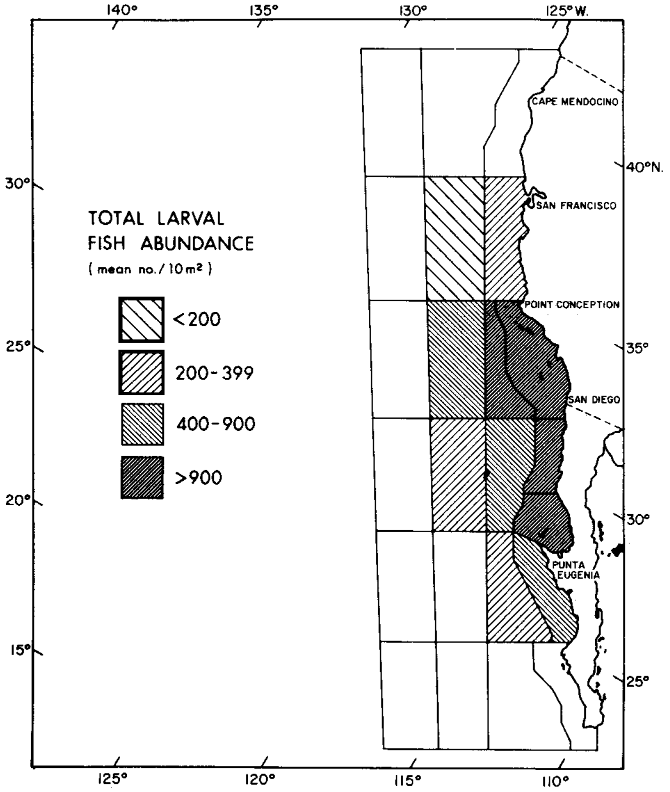

Figure 3. Mean larval fish abundance (total) in 11 CalCOFI regions sampled during 1975.

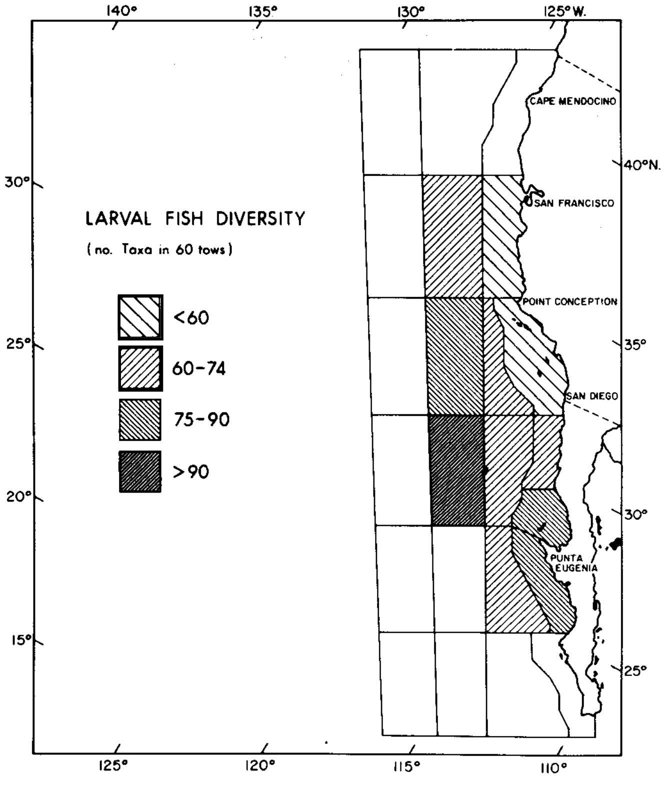

Figure 4. Larval fish diversity in 11 CalCOFI regions sampled during 1975. Diversity expressed as numbers of larval taxa taken in 60 samples within each region.

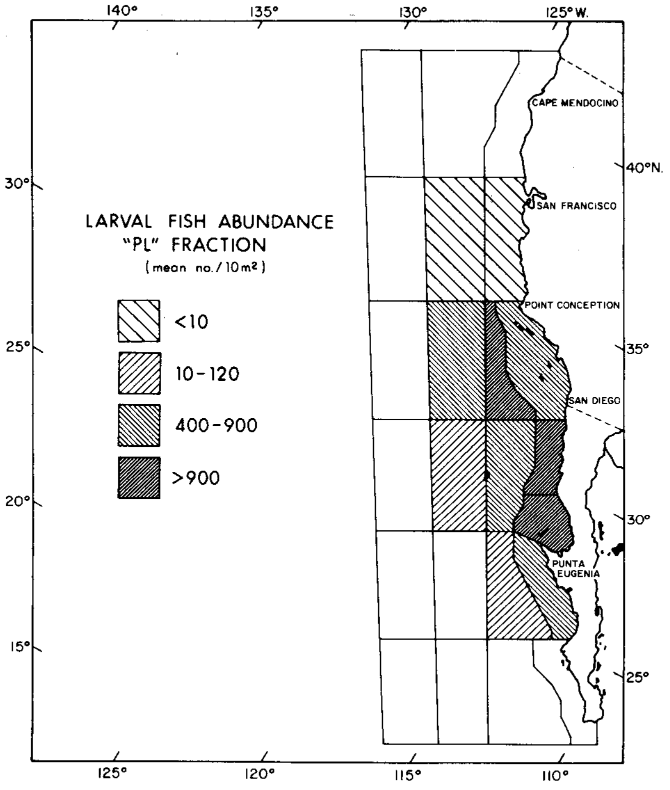

Figure 5. Mean larval fish abundance (PL fraction) in 11 CalCOFI regions sampled during 1975.

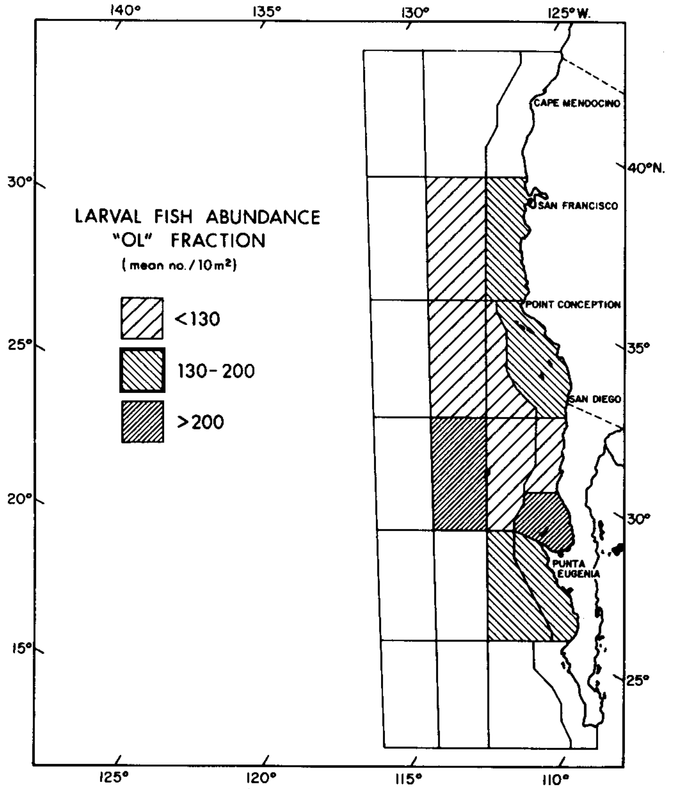

Figure 6. Mean larval fish abundance (OL fraction) in 11 CalCOFI regions sampled during 1975.

concentrations of larvae; absolute abundances here were an order of magnitude lower than in the south, and the PL made up only a small proportion (< 5%) of the total larvae.

Largest mean OL abundances occurred off northern Baja California in Viscaino Bay region 12 (because of flatfishes) and in seaward region 14 (because of mesopelagic fishes) (Figure 6). Absolute OL abundances were highest in northern and central Baja California regions 14 and 17 (19% and 15% of the total CalCOFI OL, respectively). Inshore southern California region 7, although dominated by PL, also contributed 12% of the total OL (Appendix). Although regions 4 and 5 were dominated by OL species, they contributed only 10% and 8% to the total OL.

Maximum larval fish diversity (both numbers of taxa per tow and numbers of taxa per 60 tows within a region) occurred off northern Baja California in seaward region 14 (Table 5, Figure 4) in association with maximum OL abundance. Southern California seaward region 9 ranked second in diversity, but had only moderate OL abundances. The mean numbers of larval fish taxa per tow in these two regions were significantly higher than in all other regions ($P << 0.01$). Minimal diversity values occurred off central and southern California in regions 4, 5, and 7.

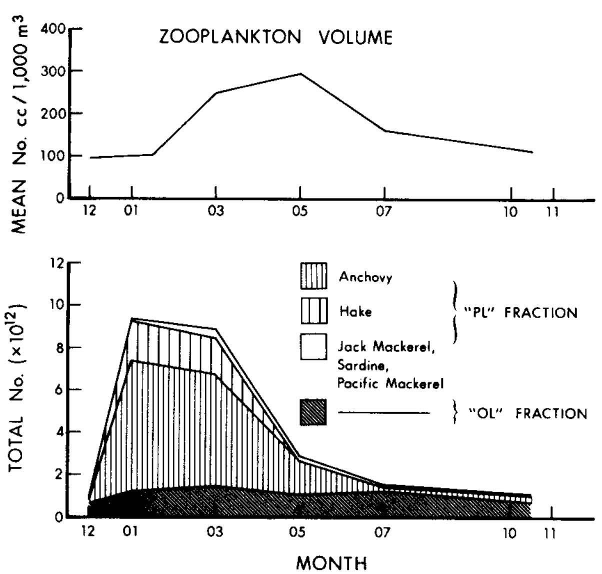

Figure 7. Seasonal variation in zooplankton volume and abundance of major ichthyoplankton components in CalCOFI area during 1975.

Seasonal Changes in Abundance: Areal Overview

Ichthyoplankton and zooplankton abundances underwent large seasonal fluctuations (Figure 7). Maximum larval fish abundances were found during January and March cruises, which captured > 60% of the total (summed six cruises) estimated numbers of larvae. This was due to peak abundances of two PL species—anchovy and hake (Figure 7). This larval abundance peak preceded maximum zooplankton abundance (March and May). The OL abundances from January through July were about twice the October-November and December values. Although the OL made up only a small proportion (≤ 16%) of the total absolute larval abundance during the January-March PL abundance peak, the proportion increased from May to November (May, 39%; July 75%; October-November, 68%) because of decreased PL abundances.

There were north-south differences in seasonal abundance peaks of zooplankton and larval fish (Figure 8). Northern zooplankton peaks occurred later, and northern ichthyoplankton peaks earlier, than their southern counterparts. Off central California, maximum zooplankton abundances were in May and July; off southern California, during May; off northern and central Baja California, during March. Central California peak larval abundances (almost entirely due to OL) occurred during January and March. Southern California peak OL and PL abundances were also in January and March, but the PL dominated. The northern Baja California area had a longer (January-May) period of elevated PL abundance, and a much later (July) OL abundance peak, than did the southern Cali-

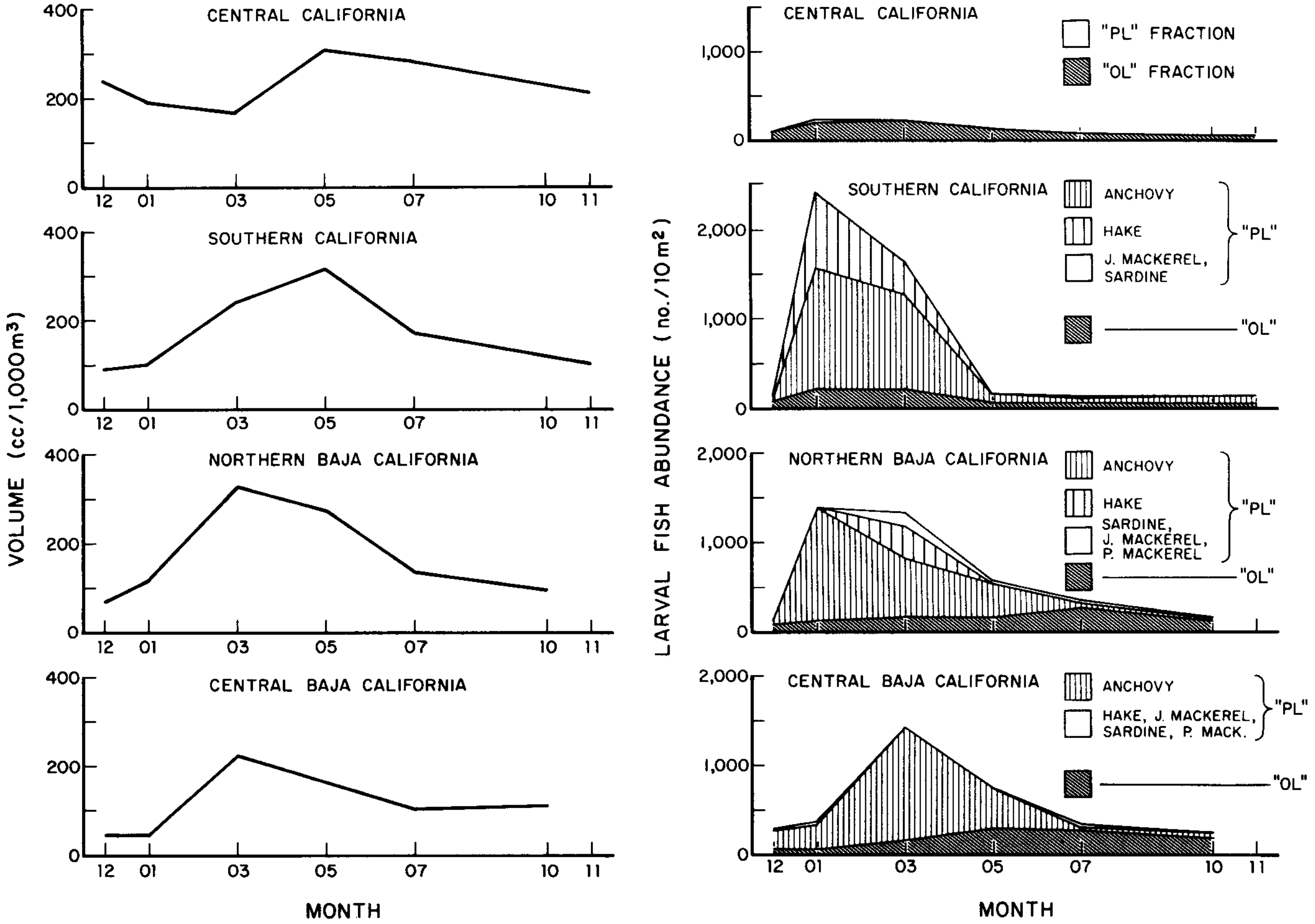

Figure 8. Seasonal variation in zooplankton volume and abundance of major ichthyoplankton components in four latitudinal portions of the CalCOFI area during 1975. Zooplankton abundance (mean displacement volume) based on combined regional sample data for each cruise; ichthyoplankton abundance as estimated total numbers of larvae of each component within each area (summed regional abundance estimates corrected for region surface area) by cruise.

fornia area. Off central Baja California, peak abundances of PL occurred during March, of OL during May and July. Seasonal ichthyoplankton and zooplankton abundance peaks within each area occurred during different months in all but the central Baja California area (Figure 8). Off southern California and northern Baja California, PL abundance peaks occurred before zooplankton abundance peaks. Peak OL abundances off central and southern California preceded, and off northern Baja California followed, peak zooplankton abundances. Off central Baja California, PL and zooplankton abundance peaks coincided; these preceded the OL abundance peak.

Seasonal Changes in Abundance and Diversity

Central California: regions 4 and 5. Central California regions 4 and 5 had similar abundance patterns (Figure 9), although zooplankton and ichthyoplankton abundance peaks in offshore region 5 occurred later than those of inshore region 4. The OL dominated the ichthyoplankton throughout the year in both regions. Significant peak larval abundances ($P < 0.01$; Z test) occurred in region 4 during January and March. Elevated, but significantly lower, abundance values occurred in region 5 at this time and extended through May. In both regions highest larval fish diversity values were associated with the months of maximum larval abundance. Zooplankton abundance within region 4 remained at fairly high levels throughout the year. Within region 5, May and July zooplankton abundances were significantly higher than during other months.

Southern California: regions 7, 8, and 9. The three southern California regions had peak PL and OL abundances during January and March (Figure 10). Inshore region 7 differed from the others by having a second (similar in value) OL peak in November and by having PL (primarily anchovy) dominate the ichthyoplankton throughout the year. Here the PL made up > 58%, and during most months >80%, of the total larvae. In contrast, the PL of offshore and

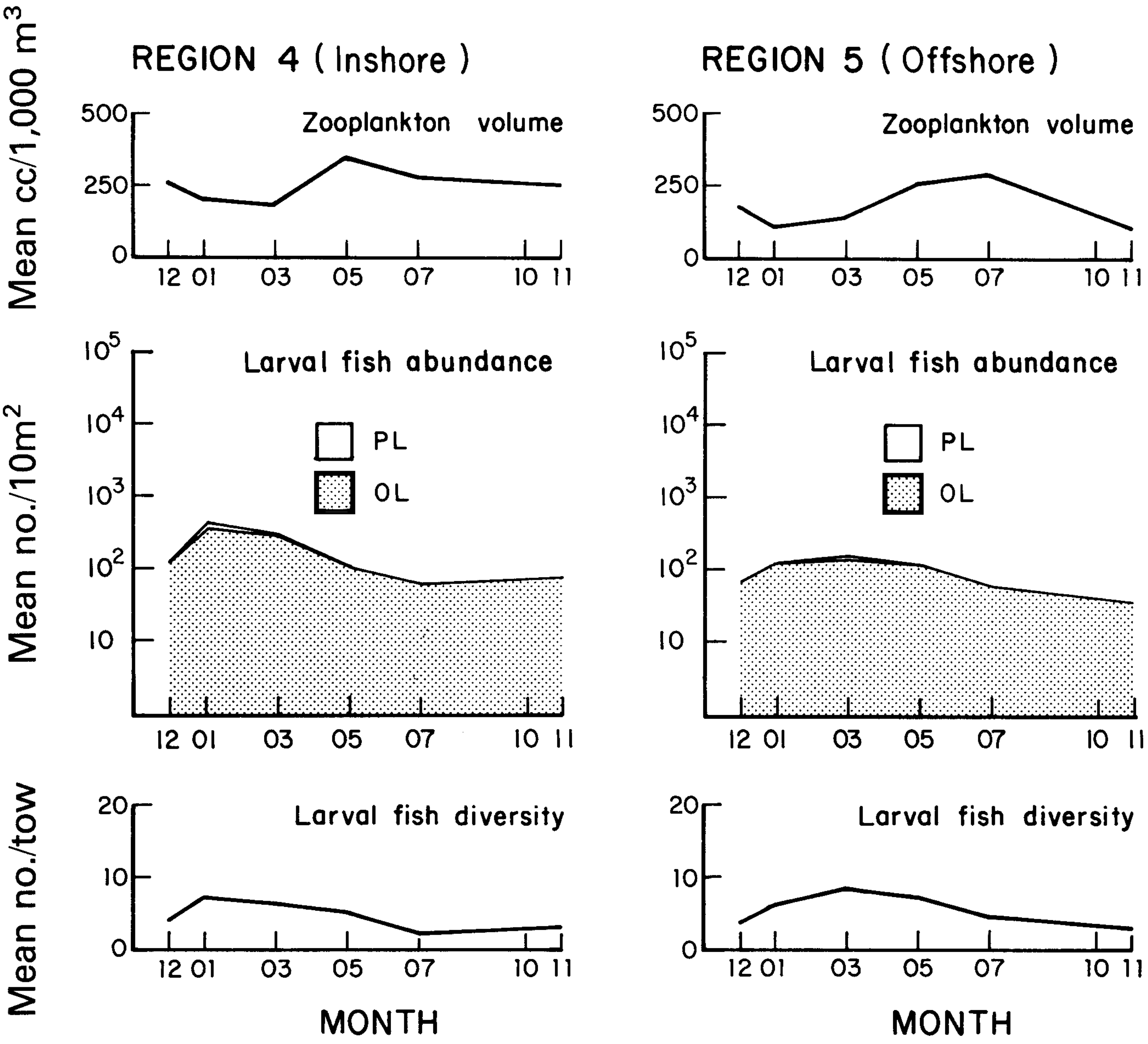

Figure 9. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI central California regions 4 and 5 during 1975. Zooplankton biomass expressed as mean displacement volume; abundance of total fish larvae, PL fraction, and OL fraction expressed as mean numbers/10 m^2 sea surface; and larval fish diversity expressed as mean numbers of taxa/cruise. Note use of log scale for larval fish abundance.

seaward regions 8 and 9 dominated from January to May, after which the OL made up > 50% of the total. The large January PL abundance of region 8 was due mostly to anchovy and was the highest for the entire CalCOFI area during 1975. Hake larvae made up most of the PL of region 9. In all three regions, larval diversity increased with OL abundance. Significant maximum zooplankton values occurred during March and May in region 7, and May in region 8.

Northern Baja California: regions 11, 12, 13, and 14. The inshore and Viscaino Bay regions 11 and 12 of northern Baja California demonstrated different patterns of seasonal abundance and diversity (Figure 11). Although both regions had January-May periods of maximum PL abundance (anchovy and hake in region 11; primarily anchovy in region 12), maximum OL abundance and diversity occurred during January and March in region 11 and during July in region 12. Overall, the OL in Viscaino Bay region 12 (dominated by flatfishes) made up a larger proportion of the ichthyoplankton (18.6% vs 9%) than in region 11 (primarily rockfishes and mesopelagic fishes). Maximum zoo-

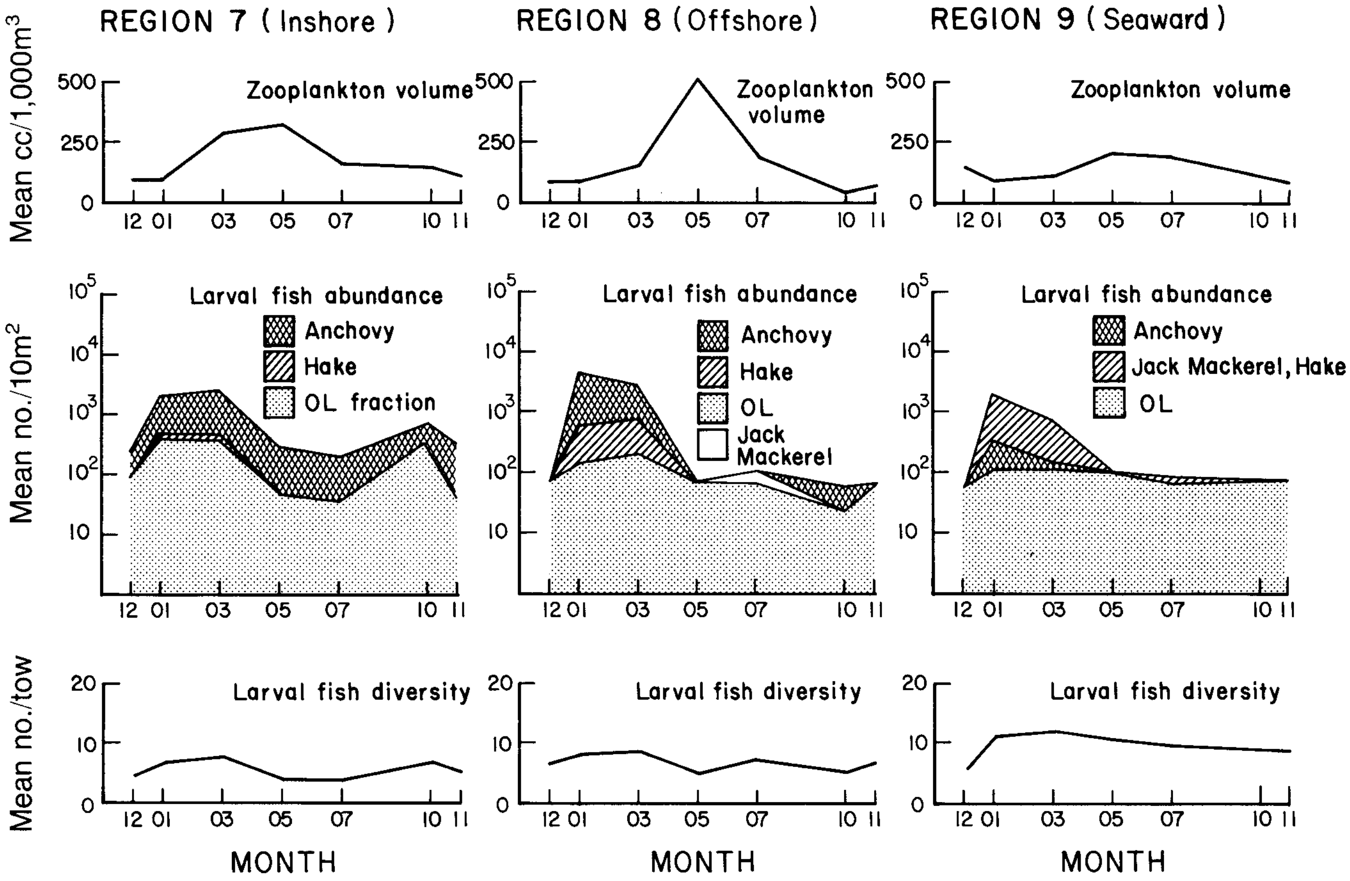

Figure 10. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI southern California regions 7, 8, and 9 during 1975. Values as in Figure 9.

plankton biomass values occurred earlier (March) in region 12 than in region 11 (May).

In regions 13 and 14, the PL abundance maximum was shorter (January-March in 13; only March in 14) and less marked than inshore. The January to May PL abundances in both regions were significantly lower than those of regions 11 and 12. Anchovy dominated the January abundance maximum in region 13 (96% of total larvae), but hake and jack mackerel contributed most of the larvae during March (58%); hake and jack mackerel dominated the March peak (67%) in region 14 (Figure 11). OL abundances in region 13 were relatively constant throughout the year. The OL dominated the ichthyoplankton of region 14 during all months but March; lowest abundances occurred in December. Diversity values within region 14 were the highest for the entire CalCOFI area and were relatively constant throughout the year. Zooplankton abundances in both regions were low; a small but significant maximum occurred in region 13 during May.

Central Baja California: regions 16 and 17. Inshore region 16 was unique in having significantly larger numbers of PL during December than any other region (Figure 12); this was primarily due to anchovy (88% of total). Anchovy and PL abundance remained high in January and increased significantly during March. OL abundance was low from December to March and increased significantly in July and October, while PL abundance decreased; the OL made up > 67% of the total ichthyoplankton during July and October. Larval diversity increased in October in conjunction with increased OL abundance. Zooplankton had a significant March abundance peak.

Little can be determined about March and May abundances in offshore region 17 because only five samples represented these months. Based on existing data, this region resembled adjacent region 14, which had peak PL and OL abundances in March and July, respectively (Figure 12). Zooplankton abundances were elevated during March and October.

Chelton (1981) reports that maximum zooplankton biomass values occur in the central Baja California area (regions 16 and 17) during late summer and fall (August-October); this peak is not evidenced here because we lack sample data covering this period.

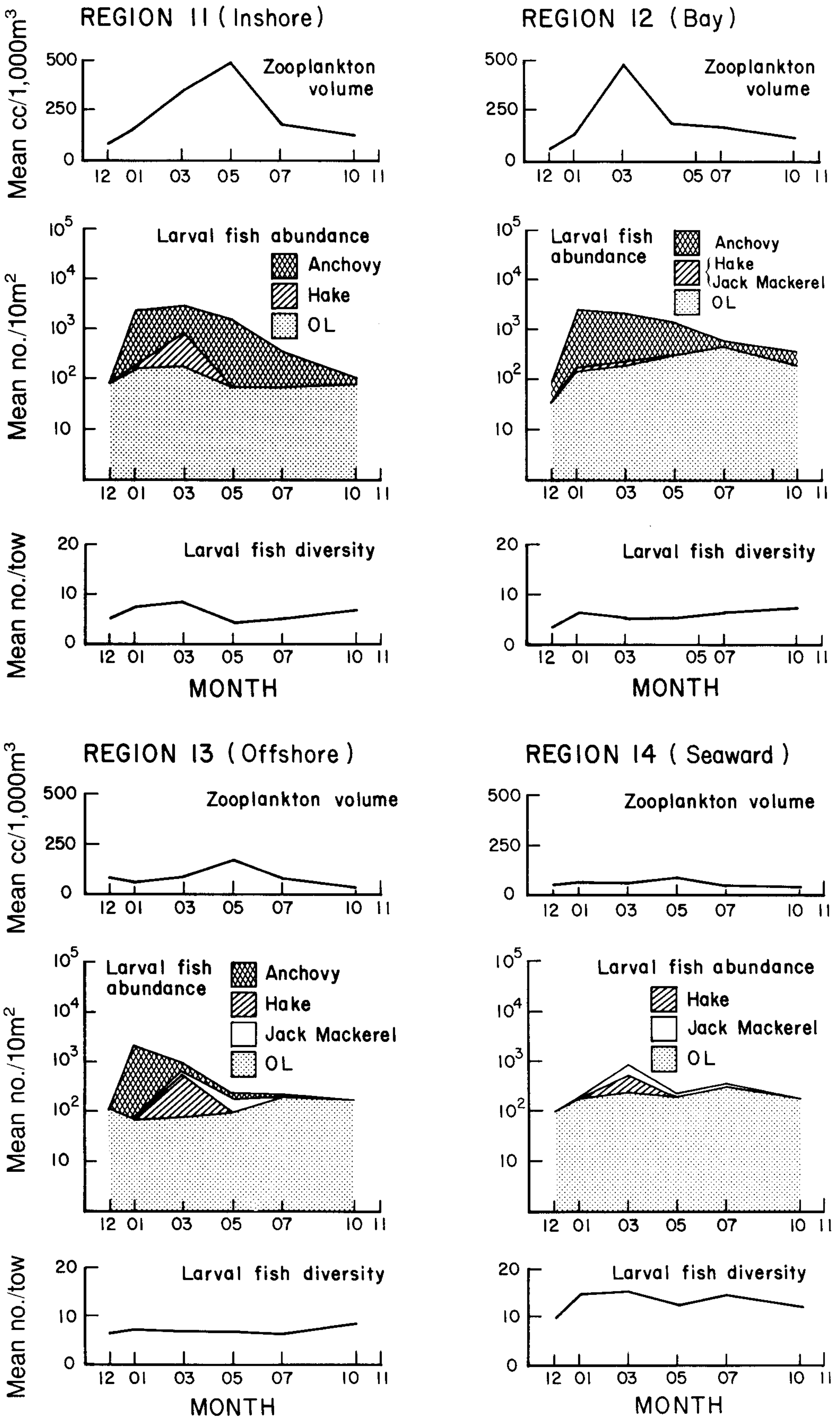

Figure 11. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI northern Baja California regions 11, 12, 13, and 14 during 1975. Values as in Figure 9.

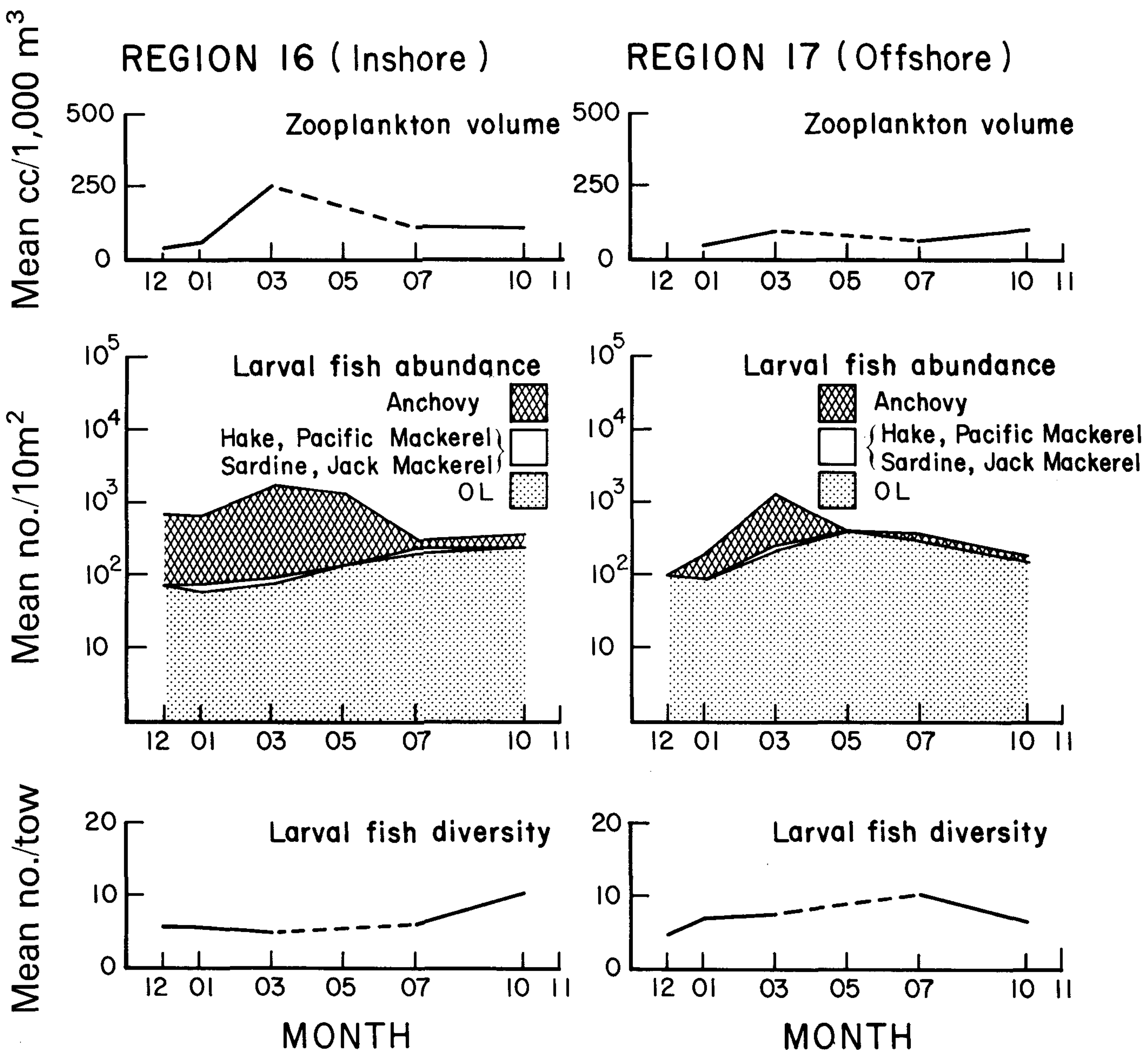

Figure 12. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI central Baja California regions 16 and 17 during 1975. Values as in Figure 9.

Sampling Variability, Patchiness, and Abundance Estimates

The large tow-to-tow variability of abundance and resulting large index-of-dispersion values (Table 4) indicate a high degree of zooplankton and ichthyoplankton patchiness throughout the area. Zooplankton biomass index-of-dispersion values during 1975 (range of monthly means 42.8-324.7) were typical for the CalCOFI area and resembled those from years of moderate intensity, coarse-scale (30 × 30 km) patchiness (Haury et al. 1978).

The intensity of zooplankton and ichthyoplankton patchiness varied geographically and seasonally. Within each cruise, zooplankton, total larval, and OL index-of-dispersion values were generally positively correlated with regional abundance values (rank difference correlation coefficients 0.49-0.98; $P \leqslant 0.05$ in 15/18 cases). However, during all but the December cruise maximum zooplankton index-of-dispersion values (1.2-2 times larger than next highest values) occurred in northern Baja California inshore region 11 and were never associated with maximum regional biomass values. Maximum indices of dispersion for total larvae and OL occurred in northern Baja California Viscaino Bay region 12 during all but the December and January cruises; these were associated with maximum regional abundances of total larvae during May, July, and October and of OL during May and July. These high index-of-dispersion values indicate generally greater intensities of both zooplankton and ichthyoplankton patchiness and suggest that throughout much of the year the coastal northern Baja California regions were subject to greater physically induced and/or inherent biological heterogeneity than were the other regions in the survey area.

Within each region, maximum zooplankton and OL patch intensities were generally associated with periods of maximum abundance. Greatest PL patch intensities, however, were associated with periods of maximum abundance only in offshore and seaward regions 9, 13, 14, and 17; most intense patchiness preceded maximum PL abundance in inshore regions 7, 11, and 16 by 2 months and followed maximum abundance in offshore region 8 and Viscaino Bay region 12 by 2 and 4 months, respectively. In all cases this was due to anchovy larvae, which exhibited most extreme patch intensity during the onset of spring spawning activity in the inshore regions and at the end of maximum spawning activity in regions 8 and 12. This suggests more localized or erratic anchovy spawning activity prior to or following peak spawning in inshore regions as compared to those offshore.

Despite sampling variability, both seasonal and geographical differences in abundance and diversity were apparent and statistically significant. In contrast, day-night differences in ichthyoplankton abundance estimates were generally nonsignificant statistically and were less than expected (Bridger 1956; Ahlstrom 1959). As a consequence, we combined day and night samples (day and night data are equally represented) for comparisons of relative abundances within and between regions. Absolute abundance estimates based on combined data will be $\sim$ 15% lower than if based on mean night values alone.

Geographical Abundance and Diversity Patterns

The pattern of decreasing zooplankton abundance from north to south and from inshore to offshore regions (Figure 2) has also been reported by Reid et al. (1958), Smith (1971), and Bernal (1980). The pattern of total larval abundance (Figure 3) is heavily influenced by the PL fraction (Figure 5), and resembles distributions of the more abundant pelagic schooling species: anchovy, hake, and jack mackerel (Kramer and Smith 1970a, b; 1971). The southern California and northern Baja California areas of maximum larval abundance coincide with areas of decreased zooplankton abundance and maximum zooplankton diversity (McGowan and Miller 1980). The OL abundance pattern (Figure 6) is complex and includes (1) decreasing abundance from inshore to offshore regions off California, (2) markedly increased abundances in northern Baja California Viscaino Bay and seaward regions, and (3) moderately high inshore and offshore abundances off central Baja California. This complexity is in part due to the large number of species represented in the OL (shelf, benthic, mesopelagic, and oceanic forms with differing hydrographic affiliations and fecundities). These are treated in Loeb et al. (1983a).

The overall zooplankton, PL, and OL abundance patterns differed markedly. There were no significant area-wide correlations between zooplankton biomass and ichthyoplankton abundances (Kendall's tau test; $P > 0.05$ in all comparisons of 6-month mean zooplankton biomass values and abundances of total larvae, PL, and OL). Additionally, no significant correlation was found between 6-month mean PL and OL abundances within regions. This suggests that overall regional patterns of zooplankton, PL, and OL abundances within the CalCOFI area are independent of one another (i.e., that zooplankton, PL, and OL are most abundant within different regions in the CalCOFI area).

The independence of zooplankton, PL, and OL abundances seen between regions on a 6-month basis is also seen within each region (between cruises) on a seasonal scale, and within each cruise on regional scales (30 × 30 km, samples only hours to days apart). Significant within-region differences occur in the timing of abundance fluctuations of the zooplankton, PL, and OL, as indicated by a lack of significant correlations between the ranked mean abundances of these three categories by cruise within each region (Kendall's tau, $P > 0.20$ in all cases). Additionally, there are few significant correlations between zooplankton biomass and ichthyoplankton abundance in samples by region and cruise (product-moment correlation coefficients; Table 8), and there is no overall trend in correlations between regions. This latter strongly suggests independently distributed patches of zooplankton and of larval fish taxa.

In seven regions, periods of peak OL abundances were associated with maximum larval diversity. However, OL abundance and diversity (by cruise) were significantly correlated ($P < 0.05$; Kendall's tau) throughout the year only within regions 4, 5, and 9. In no region was there a significant correlation between diversity and either PL or zooplankton abundance.

TABLE 8
Number of Significant Correlations ($P \leqslant 0.05$) Out of the Total Number of Within-Region Cruise Comparisons of Zooplankton Biomass (cc/1000m^3) and Abundances (no./10m^2 sea surface) of Four PL Species and the OL Category

Region	Zooplankton vs anchovy	Zooplankton vs hake	Zooplankton vs jack mackerel	Zooplankton vs sardine	Zooplankton vs OL	OL vs anchovy	OL vs hake	OL vs jack mackerel	OL vs sardine
4	0/6	0/4	—	—	2+/6	0/6	0/4	—	—
5	0/2	0/2	0/2	—	1+/6	0/2	0/2	0/2	—
7	0/6	1−/5	0/3	0/2	2+/6	0/6	1+/5	0/3	0/2
8	1+/6	1+/2	0/2	—	2+/6	1+/6 1−/6	0/3	0/2	—
9	3+/4	1+/3	1−/2	—	2+/6 1−/6	0/4	0/2	—	—
11	1+/3	1−/3	0/4	0/1	0/6	3+/4	1+/3	1+/4	0/1
12	1+/3	0/4	1−/3	1+/4 1−/4	1+/6	4+/6	1+/4	0/3	1+/3
13	1+/5	0/4	0/3	—	0/6	1+/5	1−/4	0/3	—
14	0/5	0/2	0/3	—	1+/6	0/5	0/2	1+/3	—
16	1+/5 2−/5	1−/4	0/2	2+/4	3+/5	1+/5	0/4	0/2	0/4
17	2+/4	0/2	0/2	—	1+/5 1−/5	0/4	1−/2	0/2	—
Sum: Positive correlations	10+/49 (20.0%)	2+/35 (5.7%)	—	3+/11 (27.3%)	15+/64 (23.4%)	10+/55 (18.2%)	3+/35 (8.6%)	2+/24 (8.3%)	1+/10 (10.0%)
Negative correlations	2−/49 (4.1%)	3−/35 (8.6%)	2−/26 (7.7%)	1−/11 (9.1%)	2−/64 (3.1%)	1−/55 (1.8%)	2−/35 (5.7%)	—	—

Significance is based on product-moment correlation coefficients derived from $\log_{10}$ abundances of each category within samples by region and cruise.

Seasonal Abundance and Diversity Patterns

Latitudinal differences in timing of peak zooplankton, PL, and OL abundances were tested using Kolmogorov-Smirnov (K-S) tests on cumulative percent curves constructed using summed mean cruise values of the three categories for each area (Figure 13). The cumulative percent curve for zooplankton biomass vs month for the central California area was significantly different ($P < 0.05$) from those of all other areas; that of southern California was significantly different from the northern Baja California (but not central Baja California) area curves; northern and central Baja California area curves did not differ significantly. Maximum differences among those curves occurred between March and May and indicate earlier seasonal zooplankton abundance peaks in the southern areas. Less than 50% of the total central California area zooplankton was captured between January and May, but over 60% of the southern California and central Baja California area zooplankton, and over 70% of the northern Baja California area zooplankton, was captured during this period. Adequate seasonal coverage of the reported (Chelton 1981) late-summer central Baja California zooplankton biomass peak, however, may distinguish this area from the others by establishing the existence of a significantly later zooplankton peak south of Punta Eugenia.

The cumulative percent curves of PL and OL abundance by cruise also showed significant latitudinal differences ($P < 0.05$) except between the OL of the central and southern California areas. For both PL and OL, maximum increases in cumulative percent abundance within southern areas occurred later in the year than in the northern areas (Figure 13). For the PL, the largest differences occurred between January and March; for the OL, the largest differences occurred between March and May. Additionally, within all four areas the cumulative percent curves for zooplankton, PL, and OL abundances were significantly different from one another ($P << 0.01$). This picture of significant differences in timing of zooplankton, PL, and OL abundance peaks is corroborated by lack of significant agreement of ranked abundance (by cruise) of these three categories (Table 9). Only in the northern Baja California area was there significant agreement (Kendall concordance test, $P < 0.05$) among the zooplankton, PL, and OL; abundances were highest in March-July and lowest in October-December.

Significant inshore-offshore differences also occur in the months of PL and OL peak abundances (Figure 14). K-S tests indicate that the timing of PL and OL abundance peaks was similar in the offshore and seaward regions within each area, but (except for the central California area) maximum PL abundances (pri-

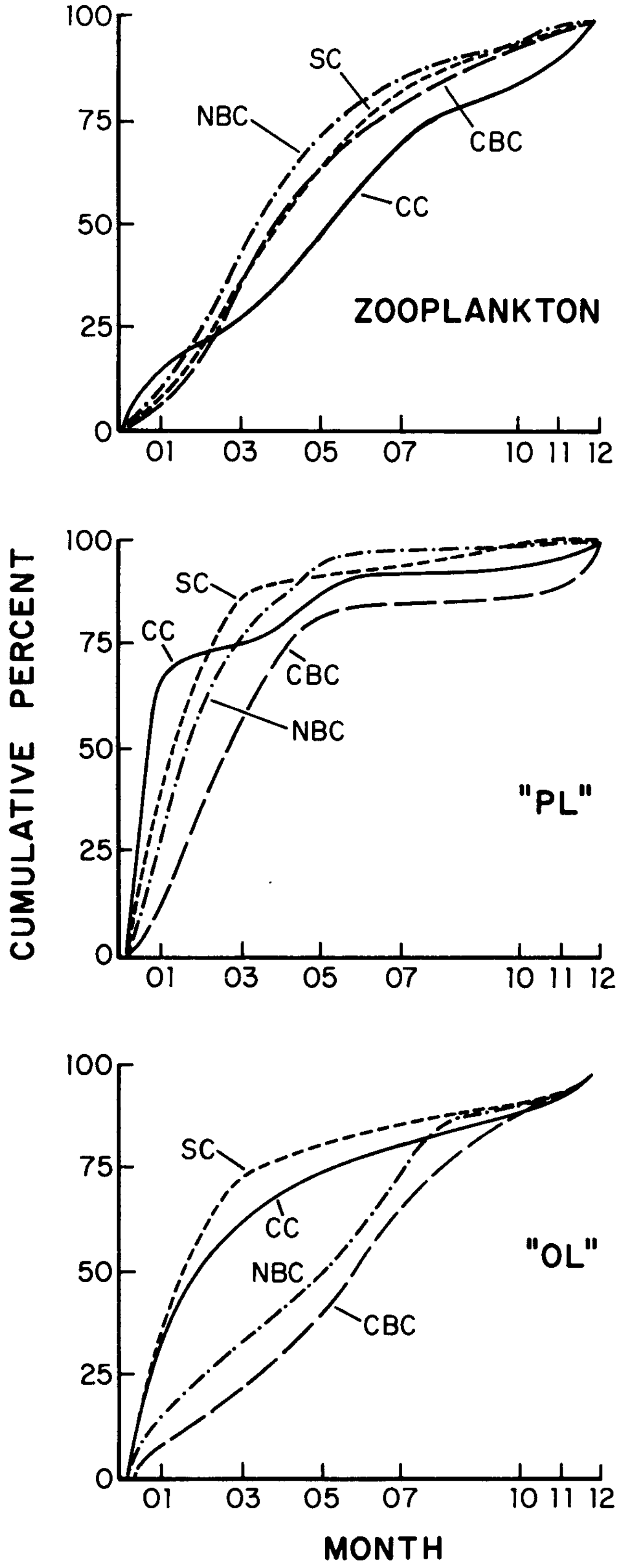

Figure 13. Cumulative percent curves of zooplankton biomass (cc/1000 m^3), PL, and OL abundance (mean no./10 m^2 sea surface) by cruise for four latitudinal CalCOFI areas. CC = Central California; SC = Southern California; NBC = Northern Baja California; CBC = Central Baja California.

TABLE 9

Kendall Concordance Test of Abundances of Zooplankton Biomass, PL, and Other Larvae (OL) Ranked by Cruise for Each of Four Latitudinal CalCOFI Areas

	Zooplankton	PL	OL			
Central California						
7412	3	3	3			
7501	5	1	1			
7503	6	4	2			
7505	1	2	4			
7507	2	5	6			
7510(11)	4	6	5	$W = 0.35$	$X_5^2 = 5.29$	$p > 0.05$
Southern California						
7412	6	6	3			
7501	5	2	1			
7503	2	1	2			
7505	1	4	4			
7507	3	5	6			
7510(11)	4	3	5	$W = 0.47$	$X_5^2 = 7.0$	$p > 0.05$
Northern Baja California						
7412	6	5	6			
7501	4	2	4			
7503	1	1	2			
7505	2	3	2			
7507	3	4	1			
7510(11)	5	6	5	$W = 0.77$*	$X_5^2 = 11.57$	$p = 0.05$
Central Baja California						
7412	6	4	5			
7501	5	3	6			
7503	1	1	4			
7505	2	2	3			
7507	4	6	1			
7510(11)	3	5	2	$W = 0.41$	$X_5^2 = 6.24$	$p > 0.05$

W is Kendall concordance coefficient value; probabilities are based on X_5^2 values at (n-1) degrees of freedom. Asterisk denotes significant correlation.

marily anchovy) in these regions occurred earlier ($P \leqslant 0.05$) than in the inshore regions. Zooplankton abundances in offshore and seaward regions lagged (nonsignificantly) behind those of inshore regions.

DISCUSSION

Ichthyoplankton is treated here as an element of the macrozooplankton. Larval fishes are a persistent, albeit relatively rare (McGowan and Miller 1980) zooplankton component, present in varying abundances throughout the year and area. Individuals are, however, only temporary members of the plankton; their residency lasts from hatching to metamorphosis, a period of weeks to months. The importance of larval fishes is not their abundance or competition/predation relations with the macrozooplankton, but how their distribution and abundance relate to adult fish populations, which do have a large collective impact on secondary and fish production in the water column. Fishes are most easily caught in their larval stages. Ichthyoplankton collections from the upper ~200m represent the offspring of a wide variety of fishes

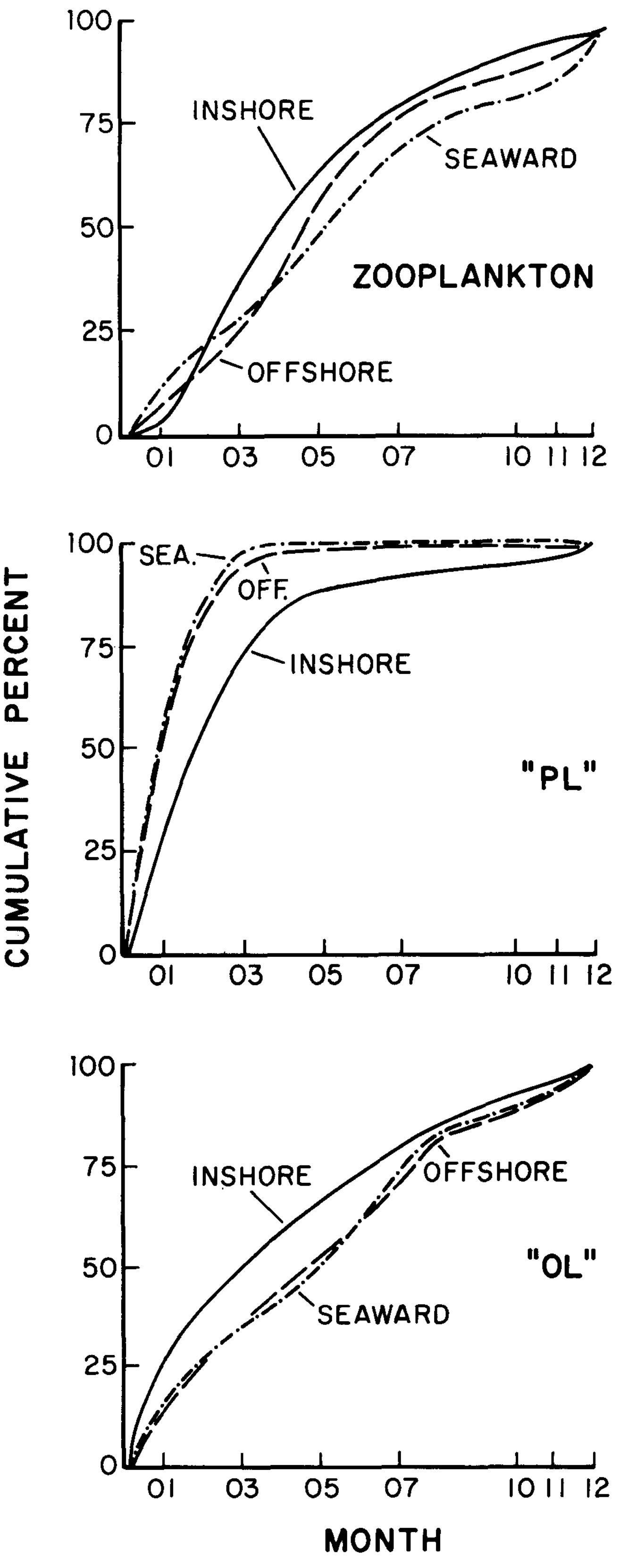

Figure 14. Cumulative percent curves of zooplankton biomass (cc/1000 m^3), PL, and OL abundance (mean no./10 m^2 sea surface) by cruise for inshore, offshore, and seaward CalCOFI zones during 1975.

occurring throughout the water column. Presumably, ichthyoplankton abundance is greatest when and where optimal physical and biological conditions occur for larval survival and ultimate recruitment. Conditions favorable for ichthyoplankton and holoplanktonic invertebrate zooplankton may differ radically, as may conditions favorable for different ichthyoplankton taxa within an area or ichthyoplankton taxa in different areas. These differences should be reflected by different patterns of distribution and abundance between the ichthyoplankton and zooplankton and within the ichthyoplankton.

The geographical and seasonal patterns of zooplankton and ichthyoplankton distribution and abundance described here appear to be related to the physical dynamics of the California Current system. These patterns reflect inshore-offshore and north-south differences in advection and mixing of water from the subarctic, central, and equatorial water masses, and also reflect surface-layer divergence (upwelling) and convergence (downwelling) systems (Reid et al. 1958; Parrish et al. 1981). The differences in distributional patterns and abundance fluctuations of the ichthyoplankton and zooplankton, as well as those of the PL and OL ichthyoplankton categories, suggest that physical processes are influencing these assemblages in different ways. Various patterns of zooplankton and PL distribution and abundance relative to physical processes are discussed below. Patterns within the complex multispecies OL fraction are treated in Loeb et al. (1983a).

The overall pattern of zooplankton abundance (Figure 2) is related to the distribution of surface nutrient levels; maximum abundances are in areas of increased nutrient levels because of advection of subarctic water and coastal upwelled water (Reid et al. 1958). High zooplankton volumes off California are associated with the influence of subarctic water and intense upwelling along the central coastal area extending to Point Conception; high volumes off Baja California are associated with coastal upwelling, especially in the vicinity of Punta Baja and Punta Eugenia (Parrish et al. 1981).

In coastal southern California waters (and presumably elsewhere) the seasonal zooplankton abundance cycle is closely associated with that of primary productivity (Smith and Eppley 1982); both primary productivity and zooplankton biomass increase with the seasonal onset of upwelling in early spring, and reach maximum values during peak upwelling (Smith and Lasker 1978; Smith and Eppley 1982). The zooplankton cycles along the coast (at least from Punta Eugenia northward) appear to follow the northward seasonal progression of coastal upwelling. Off Baja California, upwelling continues throughout the year, with maximum intensities during spring. Off southern and central California, upwelling begins in spring and reaches maximum intensities during summer; upwelling intensities off central California are stronger, and the peak occurs later than off southern California. Chelton (1981) found no significant correlations between zooplankton abundance and upwelling in the four latitudinal CalCOFI areas except off northern Baja California. However, this general lack of correlation may in part result from his use of 30-year averages of monthly biomass and upwelling values; these could obscure existing intra-annual correlations.

Maximum ichthyoplankton abundance (Figure 3) occurs in the coastal regions of southern California and northern Baja California (the Southern California Bight) and is due to large spawning stocks of migratory PL species. This area is characterized by minimal offshore surface water transport relative to the rest of the Pacific coast; Parrish et al. (1981) suggest that PL spawning here may be a reproductive strategy to minimize loss of egg and larval stages to less favorable seaward environments. Anchovy and hake abundances here peak in late winter (January-March), prior to the onset of spring upwelling. For anchovy (and possibly for hake), relatively stable water column conditions at this time may provide well-defined layers and aggregations of larval fish food, and this may favor successful feeding of the early stages (Lasker 1978). Later larval stages grow and develop during periods of upwelling and increasing zooplankton abundance, and actively feeding juvenile stages are contemporary with the May zooplankton abundance peak. The other PL species (jack mackerel, sardine, and Pacific mackerel) have peak spawning during periods of maximum upwelling and increasing zooplankton abundance (March-May); at this time the larval food stocks (copepod nauplii; Arthur 1977) are at their highest.

The persistent high intensity of zooplankton patchiness in northern Baja California region 11 is associated with a persistent zone of surface-layer convergence extending from offshore areas and impinging on the coast between Punta Baja and Punta Eugenia (Nelson 1977; Bakun and Nelson 1977; Parrish et al. 1981). This coastal area is characterized by strong upwelling, and Bakun and Nelson (1977) predicted that surface-layer convergence here may result in the formation of fronts and convergent patches of recently upwelled water. Convergence may also concentrate near-surface zooplankton in fronts or patches (Parrish et al. 1981). The extreme zooplankton patchiness, plus concentrations of characteristically offshore zooplankton species in the inshore northern Baja California region (Arthur 1977) appear to confirm the physical nature of these predictions.

The northern Baja California area of convergence and maximum upwelling separates the cyclonic eddy of the Southern California Bight and a seasonal eddy south of Punta Eugenia (Parrish et al. 1981). It also separates subpopulations of various pelagic fishes (anchovy, hake, sardine, jack mackerel, and Pacific mackerel; Nelson 1977; Hewitt 1981; Parrish et al. 1981) as well as coastal zones of high (northern Baja California) and low (central and southern Baja California) zooplankton diversity (McGowan and Miller 1980). Additionally, the reported late summer/fall zooplankton peak off of central Baja California (south of Punta Eugenia) distinguishes this area from the three northern areas. This late seasonal peak may result from surface expression of the nutrient-rich inshore countercurrent (Reid et al. 1958) and the onset of gyral circulation off the central and southern Baja California coast during the period of relaxed upwelling. These features suggest that the coastal region south of Punta Eugenia represents a separate biological regime (i.e., one with its own species composition and regulating influences).

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APPENDIX

Estimated absolute abundances (as numbers x 10^{11}) of total larvae, PL, and OL fractions of the total, and of the 5 species constituting the PL, by region and cruise. Abundances of total larvae, PL, and OL are ranked by cruise and by region (pooled cruises).

					Region								
Cruise	4	5	7	8	9	11	12	13	14	16	17	Total	Percentage of area total	Cruise rank
7412														
Total	8.08	7.48	14.75	3.44	5.26	5.62	3.40	9.12	10.51	33.21	5.40	106.27	3.70%	6
PL	0.19	0.84	8.62	0.39	—	2.80	2.26	0.32	—	29.62	—	45.04	2.46%	4
OL	7.89	6.64	6.13	3.05	5.26	2.82	1.14	8.80	10.51	3.59	5.40	61.23	9.56%	6
Anchovy	0.13	0.84	8.50	0.39	—	2.80	2.26	0.32	—	29.22	—	44.46		
Hake	0.05	—	0.12	—	—	—	—	—	—	0.03	—	0.20		
Sardine	—	—	—	—	—	—	—	—	—	0.37	—	0.37		
7501														
Total	25.92	12.60	134.09	190.69	186.43	69.21	92.42	151.88	19.13	30.58	15.50	928.45	32.37%	1
PL	2.48	—	107.13	184.42	176.14	64.13	86.75	147.03	2.39	27.81	8.46	806.75	43.89%	1
OL	23.44	12.60	26.96	6.27	10.28	5.08	5.67	4.85	16.74	2.77	7.04	121.70	19.08%	3
Anchovy	0.72	—	100.98	165.91	18.76	63.31	86.43	146.64	2.39	27.12	8.38	620.64		
Hake	1.76	—	6.14	18.51	157.39	0.82	0.05	0.39	—	0.27	0.08	185.41		
Jack mackerel	—	—	0.01	—	—	—	—	—	—	—	—	0.01		
Sardine	—	—	—	—	—	—	0.27	—	—	0.42	—	0.69		
7503														
Total	18.98	14.92	172.11	112.12	65.20	90.60	76.91	67.06	86.49	80.99	100.40	885.78	30.88%	2
PL	0.24	0.17	147.00	103.89	54.20	84.81	69.93	61.54	62.56	77.12	83.24	744.69	40.51%	2
OL	18.74	14.75	25.12	8.23	11.00	5.79	6.98	5.52	23.93	3.87	17.16	141.09	22.11%	1
Anchovy	0.12	0.04	141.27	81.30	1.51	65.11	68.56	22.30	0.25	76.73	82.06	539.25		
Hake	0.12	0.11	5.72	22.59	51.87	19.56	1.32	37.67	29.39	0.28	0.13	168.76		
Jack mackerel	—	0.02	—	—	0.82	0.14	0.05	1.57	32.92	0.12	1.04	36.68		
Sardine	—	—	0.05	—	—	—	—	—	—	—	—	0.05		

						Region								
Cruise	4	5	7	8	9	11	12	13	14	16	17	Total	Percentage of area total	Cruise rank
7505														
Total	6.30	11.77	20.27	3.15	9.62	44.26	54.99	17.66	21.84	64.52	30.72	285.10	9.94%	3
PL	0.34	1.11	16.77	0.11	0.16	42.16	44.31	9.76	1.11	58.00	—	173.83	9.46%	3
OL	5.96	10.66	3.50	3.04	9.46	2.10	10.68	7.90	20.73	6.52	30.72	111.27	17.44%	4
Anchovy	0.18	—	16.77	0.11	—	41.98	44.05	4.28	0.05	58.00	—	165.42		
Hake	0.16	1.11	0.003	—	0.16	0.01	—	0.07	—	—	—	1.51		
Jack mackerel	—	—	—	—	—	0.17	0.01	5.41	1.06	—	—	6.65		
Sardine	—	—	—	—	—	—	0.25	—	—	—	—	0.25		
7507														
Total	3.81	5.54	13.72	4.91	7.90	10.52	23.33	16.30	33.90	13.91	26.40	160.23	5.59%	4
PL	0.09	0.12	11.33	2.18	1.83	8.43	5.90	2.14	1.75	4.38	2.62	40.77	1.73%	6
OL	3.72	5.41	2.39	2.73	6.07	2.09	17.43	14.16	32.15	9.53	23.77	119.46	20.12%	2
Anchovy	0.09	—	11.29	0.15	0.02	8.34	5.83	1.24	0.01	3.32	2.61	32.90		
Hake	—	—	—	—	—	—	0.06	—	0.02	0.005	—	0.085		
Jack mackerel	—	0.12	0.05	2.03	1.81	0.09	—	0.90	1.72	0.05	0.01	6.78		
Sardine	—	—	—	—	—	—	0.01	—	—	0.99	—	1.00		
7510-11														
Total	4.81	3.17	23.29	2.20	6.72	3.22	13.00	5.69	18.00	16.37	14.03	110.50	3.85%	5
PL	0.005	—	20.31	1.31	0.15	0.76	5.65	0.02	0.08	5.45	2.13	35.87	1.95%	5
OL	4.81	3.17	2.97	0.89	6.57	2.46	7.35	5.67	17.92	10.92	11.90	74.63	11.70%	5
Anchovy	0.005	—	20.20	1.26	0.15	0.73	4.96	—	0.08	5.13	2.13	34.64		
Hake	—	—	0.11	—	—	—	0.006	0.02	—	—	—	0.14		
Jack mackerel	—	—	0.002	0.05	—	0.01	0.002	—	—	—	—	0.06		
Sardine	—	—	0.003	—	—	0.02	0.64	—	—	0.25	—	0.91		
Pac. mackerel	—	—	—	—	—	—	0.04	—	—	0.08	—	0.12		

						Region								
Cruise	4	5	7	8	9	11	12	13	14	16	17	Total		
Grand total for 6 1-month cruises	67.90	55.48	378.23	316.51	281.13	223.43	264.05	267.71	189.87	239.58	192.45	2,476.33 x 10^{11}	larvae	
Percentage (total)	2.74%	2.24%	15.27%	12.78%	11.35%	9.02%	10.66%	10.81%	7.67%	9.67%	7.77%			
Regional rank	10	11	1	2	3	7	5	4	9	6	8			
Total PL	3.34	2.24	311.16	292.30	232.49	203.09	214.80	220.80	67.88	202.38	96.46	1,846.94 x 10^{11}	PL	
Anchovy	1.24	0.88	299.01	249.12	20.44	182.27	212.09	174.77	2.77	199.52	95.18	1,437.31 x 10^{11}	anchovy	
Hake	2.10	1.22	12.13	41.10	209.42	20.39	1.44	38.15	29.41	0.59	0.21	356.16 x 10^{11}	hake	
Jack mackerel	—	0.14	0.01	2.08	2.63	0.41	0.06	7.87	35.70	0.17	1.05	50.13 x 10^{11}	jack mackerel	
Sardine	—	—	0.008	—	—	0.02	1.17	—	—	0.25	—	3.22 x 10^{11}	sardine	
Pac. mackerel	—	—	—	—	—	—	0.04	—	—	0.08	—	0.12 x 10^{11}	Pacific mackerel	
Total OL	64.56	53.24	67.07	24.21	48.64	20.34	49.25	46.91	121.97	37.20	95.99	629.39 x 10^{11}	OL	
Region:														
Percent PL	4.92%	4.03%	79.90%	92.35%	82.70%	91.01%	81.35%	82.48%	35.75%	84.47%	50.12%	Percent PL		74.23%
Percent OL	95.08%	95.97%	20.10%	7.65%	17.30%	8.99%	18.65%	17.52%	64.25%	15.53%	49.88%	Percent OL		25.77%
Regional contribution to														
Total PL	0.18%	0.12%	16.44%	15.90%	12.65%	11.06%	11.68%	12.01%	3.69%	11.01%	5.25%			
Total OL	10.12%	8.34%	11.91%	3.79%	7.62%	3.15%	7.72%	7.35%	19.12%	5.83%	15.04%			
Regional ranked abundance:														
PL	10	11	1	2	3	6	5	4	9	7	8			
OL	4	5	3	10	7	11	6	8	1	9	2			

GEOGRAPHICAL AND SEASONAL PATTERNS OF LARVAL FISH SPECIES STRUCTURE IN THE CALIFORNIA CURRENT AREA, 1975

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ABSTRACT

Analysis of 1,504 plankton tows from the 1975 CalCOFI cruise year yielded information on geographical and temporal patterns among 204 larval fish taxa. These taxa represented the spawn of fishes from a variety of habitats and water-mass affiliations. The larvae of certain commercially valuable pelagic spawning fishes (anchovy, hake, sardine, jack mackerel, and Pacific mackerel) dominated (75.5% of total larvae); these species are treated separately from the less abundant taxa (further separated into continental shelf, oceanic, and mesopelagic categories and taxa) to permit description of underlying hydrographically related distribution patterns within the California Current area.

The composition and species abundance relations of the ichthyoplankton were similar to those reported from 1955-58. Exceptions were decreased relative abundance of sardine and increased proportions of anchovy larvae in 1975 vs 1955-58.

Anchovy, hake, and jack mackerel larvae were most abundant south of Point Conception. Abundances of rockfishes and bathylagids decreased, while those of flatfishes, myctophids, and gonostomatids increased, from north to south and inshore to offshore. Absolute ichthyoplankton abundance varied by a factor of 10 between January-March (maximum) and September-December (minimum). Anchovy, hake, jack mackerel, rockfishes, sciaenids, myctophids, and bathylagids had January-March abundance peaks; myctophids and gonostomatids had July abundance peaks; flatfishes were most abundant from October-December. Regional ichthyoplankton abundance fluctuations and compositions were related to hydrographic regimes.

The area off northern Baja California marked a transition between predominantly cold-water or subarctic-transition zone species with January-March abundance peaks and predominantly eastern tropical Pacific or warm-water species with summer and fall abundance peaks. This transition zone coincides with a persistent lobe of negative wind stress curl (surface-layer convergence) extending to the coast from offshore waters; this zone may separate biological regimes of California and southern Baja California.

RESUMEN

Los análisis de 1504 colecciones de plancton correspondientes al crucero CalCOFI de 1975, proporcionan información sobre la distribución en espacio y tiempo de 204 taxones de larvas de peces. La puesta de peces procedentes de una variedad de habitats y masas de agua aparece representada en la diversidad taxonómica larval. Las larvas de peces de importancia comercial y de puesta pelágica, *Engraulis mordax* (anchoa), *Merluccius productus* (merluza), *Sardinops caerulea* (sardina), *Trachurus symmetricus* (jurel), eran dominantes, alcanzando el 75.5% del total. Estas especies se estudian en particular y se separan de las especies menos abundantes, clasificadas bajo características taxonómicas y del habitat (plataforma continental, oceánicas y mesopelágicas), para permitir así la descripción de los tipos de distribución en relación con las características hidrográficas dentro de la región de la Corriente de California.

La composición y abundancia de especies del ictioplancton aparecían similares a las presentadas durante el período 1955-58, excepto que en 1975 disminuye la abundancia de larvas de sardina y aumenta proporcionalmente la cantidad de larvas de anchoa.

Larvas de anchoa, merluza y jurel aparecían menos abundantes al sur de Punta Concepción. La abundancia de Scorpenidae y Bathylagidae disminuía, mientras que los peces planos, Myctophidae y Gonostomidae aumentaban de norte a sur y de la costa hacia mar abierto. La abundancia absoluta de ictioplancton fluctuaba en un factor de 10 entre los períodos de Enero-Marzo (máximo) y Septiembre-Diciembre (mínimo). Anchoa, merluza y jurel, Scorpenidae, Sciaenidae, Myctophidae y Gonostomidae aparecían con máximos de abundancia en Julio, y los peces planos eran más abundantes en el período de Octubre-Diciembre. Fluctuaciones en la abundancia regional y la composición del ictioplancton aparecían relacionadas con el régimen hidrográfico.

La zona frente al norte de Baja California marcaba una transición entre aguas predominantemente frias o de la zona subártica- transición, con máximos de abundancia en el período de Enero-Marzo, y especies

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de aguas cálidas, principalmente del Pacífico tropical oriental, mostraban máximos de abundancia en verano y otoño. Esta zona de transición coincide con un lóbulo de remolino persistente de presión eólica negativa (convergencia en el lecho superficial), extendiéndose desde mar afuera hacia la costa. Esta zona puede separar regímenes biológicos de California y la zona sur de Baja California.

INTRODUCTION

The California Current system is a typical eastern boundary current regime (Wooster and Reid 1963; Hickey 1979). The main current is slow, meandering, broad, and indistinct. Embedded in this current are dynamic mesoscale eddies of uncertain origin (Owen 1980), and the current includes water-mass mixtures of diverse origin. The mixed layer can include waters from the (1) North Pacific central water mass, (2) subarctic water mass, (3) Columbia River Plume, (4) subtropical water mass, (5) Davidson Current (a wintertime surface manifestation of the California Undercurrent), and (6) upwelling processes.

The biota of the area also is complex (McGowan and Miller 1980). Invertebrate "holoplankton" species can often be far from their water-mass centers of distribution because of long-range transport; older holoplankton individuals can be far from the reproductive locus of the population. The ichthyoplankton represents a brief phase in a generally longer life cycle, which is in most cases nektonic. Because larval fishes from pelagic spawn are localized at or near the spawning areas of the adults, the analysis of ichthyoplankton in the California Current area can achieve more advanced and precise localization of communities or biological regimes than can analysis of the holoplankton.

To date, most of the descriptive work from the vast set of stations included in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has concentrated on regional and seasonal characteristics of single oceanographic properties such as current flow, temperature, salinity, and zooplankton volume. The ichthyoplankton has been described only as single species (anchovy, sardine, jack mackerel, hake, individual mesopelagic fish, flatfish, and rockfish species) on distribution charts covering a variety of years. Aside from one paper on the co-occurrence of anchovy and sardine (Ahlstrom 1967) there have been no attempts to characterize the California Current system biota by means of larval fish assemblages.

In this paper we investigate seasonal and geographical distributions within the diverse larval fish assemblage sampled during 1975. We compare the overall composition of this assemblage with that reported from 1955-58. We then divide the ichthyoplankton into various categories based on adult habitats and analyze seasonal abundance relations of these categories (and of their dominant species) within and between pre-established and arbitrary regional divisions.

We emphasize various nonparametric analytical procedures (outlined in Fager 1963) to describe and compare regional ichthyoplankton assemblages. The procedures and results from this study will serve as a basis for subsequent analyses of and comparisons between data sets from other years in the 1951-81 CalCOFI survey. From such analyses we eventually hope to (1) compare variations in larval fish assemblages with variations of reproductive success of commercially valuable fish species; (2) establish the use of changing ichthyoplankton assemblages as indices of general, sustained, and widespread environmental change; and (3) establish the existence of functional relationships between abundances of major fish species and their invertebrate planktonic prey.

METHODS

The present data came from the same 1,504 samples used to describe geographical and seasonal patterns of ichthyoplankton and zooplankton distributions in Loeb et al. 1983a. These samples were from standard CalCOFI plankton tows taken with a 1-m diameter net (mesh size, 505 μm) fished from 0-210 m at basic CalCOFI stations and additional inshore stations. Larval fishes were sorted out, identified to the lowest taxon possible, and counted.

Data were formatted by cruise and standard CalCOFI regions. In 1975, 11 regions were "adequately" sampled; "adequate" means that a region was sampled during at least six one-month cruises and was generally represented by $>$ 10 samples per cruise. All regions were sampled in December, January, March, May, and July, and most were sampled in October. Central California regions 4 and 5 were sampled in November rather than October. November data for southern California regions 7, 8, and 9 were used rather than October data because larger numbers of samples were available (Loeb et al. 1983a). Regional data were combined into four latitudinal areas (central California, southern California, northern Baja California, and central Baja California) for broader overviews of patterns of species structure. For region and area locations see Loeb et al. (1983a).

We divide the total ichthyoplankton ("TL") into "PL" (the commercially important pelagic schooling species: anchovy, hake, sardine, jack mackerel, and Pacific mackerel) and "OL" (other larval fish) fractions. These two fractions are treated separately because abundances of the PL (especially anchovy and hake) mask abundance relations of the 200+ other larval fish taxa. The OL taxa are herein further divided into continental shelf ("shelf"), open-ocean epipelagic ("oceanic"), and "mesopelagic" categories for considerations of the major ichthyoplankton components. The shelf category is further divided into "rockfish" (*Sebastes* spp), "flatfish" (Pleuronectiformes), and "other" categories for consideration of regional and seasonal abundance variations.

Larval fish abundances are presented as mean numbers per 10 m^2 sea-surface area (Kramer et al. 1972) and as estimated absolute abundances for each region (mean numbers per 1 m^2 sea surface multiplied by sea-surface area). These latter estimates are summed to provide the total estimated abundances within the CalCOFI survey area by cruise and for all six cruises. As some categories were excluded (e.g., unidentified larvae) the total larval abundances presented here vary slightly from those in Loeb et al. 1983a. Species lists and abundance information for the total CalCOFI area and for each of the 11 regions during 1975 are on file at the Southwest Fisheries Center, La Jolla, California.

We describe species structure using several nonparametric tests. (A) Between-area and between-region comparisons of species percentage composition are made using the Percent Similarity Index (PSI; Whittaker 1975). PSI values compare two species lists based on the relative proportions of individual species within each list. PSI values may range from 0 (no species in common) to 100 (all species in common, and their proportions identical). PSIs are strongly influenced by abundant species. We define as "high" all PSI values > 60, and as "low" values < 40. (B) Comparisons of rank order of abundance of species between sets of data are made using Kendall's tau and concordance tests (Tate and Clelland 1957). Kendall's tau provides a correlation coefficient that is a measure of the similarity between the order of rankings within two data sets. The concordance test is a nonparametric analysis of variance performed on several sets of species' rankings; it is used to test for similarity (nonrandomness) of species' rankings across data sets.

These techniques are used to show similarities in species structure between geographical regions and between seasons. Similarities may occur in the proportions of individual taxa relative to the total ichthyoplankton and in ranks of abundance of individual taxa.

Taxonomic Problems

The 1975 data include 204 ichthyoplankton taxonomic categories: 104 species and 100 higher-level identifications. While many of the abundant larvae (especially the myctophids and bathylagids) have been identified to species, many of the coastal larvae have not. Problems are greatest with the scorpaenids (> 50 species are lumped into the *Sebastes* spp category), the *Citharichthys* category (5 species), the sciaenids (> 10 species), and some subtropical forms. Such multispecies groupings, especially within dominant taxa, impose limitations on analysis of species structure, and geographical or seasonal changes in the actual species constituting these groupings may be obscured. This is a relatively minor problem in offshore regions dominated by identifiable mesopelagic species; it is a much greater problem in inshore regions where groupings (primarily *Sebastes* spp, *Citharichthys* spp, and Sciaenidae) are among the dominant taxa. These groupings have increased apparent similarities between and within the inshore and southern regions.

RESULTS

Total CalCOFI Area Ichthyoplankton Composition

The PL contributed 75.5% of the total larval fish captured in 1975. The most abundant PL species were the northern anchovy (*Engraulis mordax;* 58.9%), Pacific hake (*Merluccius productus;* 14.5%), and jack mackerel (*Trachurus symmetricus;* 2.0%) (Table 1). The OL were dominated by mesopelagic fishes (89 taxonomic categories; 16.7% of the area total). Nine species made up over two-thirds of this fraction and 12.1% of the total larvae. These included one gonostomatid (*Vinciguerria lucetia*), three bathylagids (*Leuroglossus stilbius, Bathylagus wesethi,* and *B. ochotensis*), and five myctophids (*Triphoturus mexicanus, Stenobrachius leucopsarus, Protomyctophum crockeri, Diogenichthys laternatus* and *Tarletonbeania crenularis*). Continental shelf fishes (92 taxa) made up only 7% of the total; flatfishes (Pleuronectiformes; 3.4%), rockfishes (*Sebastes* spp; 3.1%), and croakers (Sciaenidae; 0.5%) predominated.

Geographical Differences in Species Composition

There were large geographical differences in ichthyoplankton composition. Latitudinal and inshore-offshore differences occurred in the relative abundances of the PL, mesopelagic, shelf, and oceanic fractions, and in the species making up these fractions. The greatest difference was the dominance of the PL south of Point Conception (36.1-92.0% regional totals) versus its relatively low abundance off central California (≤5%) (Table 2). This dominance was due primarily to anchovy and hake, and secondarily to jack mackerel, all of which were rare off central California and had greatest abundances off southern Cali-

TABLE 1
Comparison of Relative Abundances of Larval Fishes Taken during 1975 with Those Taken during Annual CalCOFI Surveys 1955-58

	1975		1955		1956		1957		1958	
	% of total	Rank*	% of total	Rank**	% of total	Rank**	% of total	Rank**	% of total	Rank**
Engraulis mordax	58.92	1	39.03	1	33.05	1	29.70	1	45.21	1
Merluccius productus	14.46	2	16.73	2	23.10	2	15.86	2	12.84	2
Sebastes spp	3.12	3	8.17	3	7.14	3	7.39	4	5.27	4
Citharichthys spp	2.79	5	5.68	4	5.79	4	3.20	9	1.46	11
Leuroglossus stilbius	1.46	8	4.21	5	4.56	5	5.98	5	1.07	12
Sardinops sagax	0.13	26	3.93	6	3.80	6	1.99	11	2.51	7
Trachurus symmetricus	2.03	7	3.69	7	1.97	10	4.05	6	1.41	10
Triphoturus mexicanus	2.84	4	3.67	8	2.65	8	3.28	8	3.63	5
Vinciguerria lucetia	2.17	6	3.52	9	2.41	9	11.17	3	12.27	3
Stenobrachius leucopsarus	1.40	9	2.08	10	3.71	7	3.70	7	2.62	6
Diogenichthys laternatus	0.77	13	1.33	11	0.77	13	2.35	10	1.55	8
Bathylagus wesethi	1.05	10	0.90	12	0.52	17	1.29	12	1.54	9
Lampanyctus ritteri	0.40	19	0.55	13	0.47	18	0.56	14	0.68	13
Scomber japonicus	0.005	—	0.54	14	0.37	20	0.38	18	0.28	20
Protomyctophum crockeri	0.78	12	0.51	15	0.45	19	0.29	22	0.39	15
Bathylagus ochotensis	0.98	11	0.36	18	0.55	15	0.22	25	0.34	16
Melamphaes spp	0.24	22	0.22	25	0.26	24	0.27	24	0.28	21
Cyclothone spp	0.63	14	0.43	16	0.20	—	0.58	13	0.62	14
Tarletonbeania crenularis	0.61	15	0.28	21	0.82	12	0.32	21	0.12	—
Argentina sialis	0.05	—	0.23	24	0.32	22	0.28	23	0.06	—
Prionotus spp	0.006	—	—	—	0.60	14	0.55	15	0.29	19
Synodus spp	0.03	—	0.18	—	0.23	25	0.47	17	0.27	23
Pleuronichthys spp	0.06	—	0.29	19	0.27	23	0.12	—	0.04	—
Diaphus theta	0.11	29	0.28	20	0.87	11	0.14	—	0.13	—
Sciaenidae	0.53	16	0.24	23	0.02	—	0.06	—	0.30	18
Symphurus spp	0.05	—	0.02	—	0.34	21	0.32	20	0.05	—
Ceratoscopelus townsendi	0.13	26	0.12	—	0.05	—	0.53	16	0.31	17
Symbolophorus californiense	0.29	20	0.18	—	0.11	—	0.33	19	0.27	22
Icichthys lockingtoni	0.09	30	0.39	17	0.22	—	0.16	—	0.10	—
Peprilus simillimus	0.05	—	0.26	22	0.15	—	0.16	—	0.02	—
Tetragonurus spp	0.03	—	0.14	—	0.53	16	0.14	—	0.01	—
Stomias spp	0.13	26	0.11	—	0.02	—	0.05	—	0.26	24
Hygophum spp	0.03	—	0.11	—	0.05	—	0.16	—	0.22	25
Diogenichthys atlanticus	0.49	17	0.20	—	0.19	—	0.16	—	0.14	—
Other larvae	3.14		1.42		3.41		4.10		3.44	

*Ranks provided for first 30
**Ranks provided for first 25
1955-58 data from Ahlstrom (1965); and Moser and Ahlstrom (1970) based on total numbers of larvae caught (pooled cruises) each year, 1975 data based on summed regional abundances (mean abundances corrected for region area) from six cruises; taxonomic categories adjusted (i.e., species lumped) to conform with earlier data sets.

fornia and northern Baja California (Tables 2, 3). The other PL species (sardine and Pacific mackerel) were caught in a few regions off Baja California and were comparatively rare (< 2% PL in each region).

As expected, both abundances and relative proportions of PL and shelf forms decreased, and those of mesopelagic and oceanic forms increased, with distance from shore. Within the PL, relative proportions of anchovy larvae generally decreased, while those of hake and jack mackerel increased, from inshore to offshore and seaward regions (Table 3).

Within the OL, major contributors to the shelf and mesopelagic categories had marked geographical differences (Table 2). Among the shelf forms, abundances of rockfishes decreased, and flatfishes increased, from north to south; both decreased offshore. Rockfishes dominated the OL of California inshore regions 4 and 7 (41.7-46.7% total OL) and were relatively abundant in northern Baja California region 11 (26.6%); they were relatively rare (≤ 3.9%) in other Baja California regions. Flatfish larvae were most abundant off Baja California in Viscaino Bay

TABLE 2
Percentage Contribution of Major Taxonomic Categories to the Total Ichthyoplankton Collected in Each of 11 CalCOFI Regions and to the Total (Pooled Regions) 1975 CalCOFI Survey Area

Taxonomic Category — Area: / Region:	Central California		Southern California			Northern Baja California				Central Baja California		Total
	4 (Inshore)	5 (Offshore)	7 (Inshore)	8 (Offshore)	9 (Seaward)	11 (Inshore)	12 (Bay)	13 (Offshore)	14 (Seaward)	16 (Inshore)	17 (Offshore)	
PL	5.01	4.09	82.72	91.94	83.15	91.06	81.49	82.84	36.11	85.47	59.12	75.56
Mesopelagic taxa	42.01	81.05	7.04	5.84	15.12	4.31	2.15	16.49	60.91	6.91	33.80	16.67
Myctophidae	22.42	46.40	2.10	2.55	8.42	2.46	1.57	9.37	25.91	4.85	20.18	8.66
Bathylagidae	18.44	23.60	4.62	2.45	3.45	0.96	0.18	2.30	9.70	0.50	0.89	3.65
Gonostomatidae	0.22	1.37	0.03	0.20	0.98	0.28	0.14	3.00	19.44	1.12	10.83	2.97
Others	0.93	9.68	0.29	0.64	2.27	0.61	0.26	1.82	5.86	0.44	1.90	1.49
Shelf taxa	52.85	14.45	10.23	2.20	1.50	4.60	16.35	0.53	2.77	7.55	7.03	7.58
Rockfishes	44.32	7.41	7.21	1.61	0.57	2.38	0.72	0.09	0.06	0.57	0.36	3.13
Flatfishes	3.71	6.37	0.80	0.34	0.51	0.92	14.39	0.37	2.47	3.95	5.51	3.14
Sciaenids	2.36	—	1.57	0.02	—	0.66	0.50	—	—	0.57	0.65	0.52
Others	2.46	0.67	0.65	0.23	0.42	0.64	0.74	0.07	0.24	2.46	0.51	0.79
Oceanic taxa	0.13	0.41	0.006	0.03	0.23	0.03	0.01	0.14	0.21	0.07	0.05	0.10
Total larval abundance (x 10^{13})	0.68	0.55	3.78	3.16	2.81	2.23	2.64	2.68	1.90	2.40	1.92	24.76

Estimated total abundances derived from summation of mean regional abundances adjusted for region area.

TABLE 3
The 18 Most Abundant Larval Fish Taxa (Including the 10 Most Abundant Species Identifications) in Order of Ranked Abundance, and Their Percentage Contribution to the Total Ichthyoplankton within Each of 11 CalCOFI Regions, 1975

Central California

Rank	Region 4 (inshore)	no/10m^2	%	Region 5 (offshore)	no/10m^2	%
1	*Sebastes* spp	441.6	40.2	*Stenobrachius leucopsarus*	97.5	17.5
2	*Stenobrachius leucopsarus*	142.2	12.9	*Bathylagus ochotensis*	87.2	15.6
3	*Leuroglossus stilbius*	93.6	8.5	*Tarletonbeania crenularis*	67.3	12.1
4	*Bathylagus ochotensis*	92.7	8.4	*Sebastes* spp	30.7	5.5
5	*Tarletonbeania crenularis*	74.4	6.8	*Protomyctophum crockeri*	30.5	5.5
6	*Merluccius productus*	34.7	3.2	*Leuroglossus stilbius*	28.1	5.0
7	*Sebastes jordani*	32.7	3.0	*Diaphus* spp	22.8	4.1
8	Sciaenidae	25.9	2.4	*Melamphaes* spp	19.2	3.4
9	*Engraulis mordax*	20.4	1.9	*Citharichthys stigmaeus*	16.5	3.0
10	*Citharichthys stigmaeus*	15.3	1.4	*Citharichthys sordidus*	13.5	2.4
11	*Protomyctophum crockeri*	13.3	1.2	*Merluccius productus*	12.3	2.2
12	*Sebastes paucispinis*	10.9	1.0	*Chauliodus macouni*	10.1	1.8
13	*Bathylagus pacificus*	10.1	0.9	*Sebastes paucispinis*	10.0	1.8
14	*Parophrys vetulus*	8.3	0.8	*Lampanyctus ritteri*	9.5	1.7
15	*Icichthys lockingtoni*	5.8	0.5	*Engraulis mordax*	9.0	1.6
16	*Citharichthys sordidus*	5.7	0.5	*Diogenichthys atlanticus*	7.5	1.3
17	*Citharichthys* spp	5.7	0.5	*Lampanyctus* spp	7.5	1.3
18	*Diaphus theta*	5.5	0.5	*Icichthys lockingtoni*	7.2	1.3
	94.6% of total larvae			87.1% of total larvae		

Ranks based on summed mean abundances (numbers per 10 m^2 sea-surface area) of each taxon from six cruises within each region.

Continued on next page

TABLE 3 (continued)

Southern California

Rank	Region 7 (inshore)	no/10m^2	%	Region 8 (offshore)	no/10m^2	%
1	*Engraulis mordax*	4333.1	79.5	*Engraulis mordax*	6016.0	78.3
2	*Sebastes* spp	349.7	6.4	*Merluccius productus*	997.7	13.0
3	*Leuroglossus stilbius*	226.3	4.1	*Sebastes* spp	119.9	1.6
4	*Merluccius productus*	177.0	3.2	*Leuroglossus stilbius*	117.3	1.5
5	*Stenobrachius leucopsarus*	87.8	1.6	*Stenobrachius leucopsarus*	59.0	0.8
6	Sciaenidae	81.0	1.5	*Bathylagus ochotensis*	58.8	0.8
7	*Bathylagus ochotensis*	24.7	0.4	*Trachurus symmetricus*	49.3	0.6
8	*Sebastes jordani*	20.5	0.4	*Protomyctophum crockeri*	37.0	0.5
9	*Sebastes paucispinis*	16.8	0.3	*Tarletonbeania crenularis*	28.2	0.4
10	*Citharichthys stigmaeus*	13.1	0.2	*Citharichthys stigmaeus*	17.7	0.2
11	Gobiidae	9.2	0.2	*Lampanyctus ritteri*	15.2	0.2
12	*Argyropelecus* spp	8.8	0.2	*Argyropelecus* spp	14.6	0.2
13	*Citharichthys stigmaeus*	8.0	0.1	*Lampanyctus* spp	14.0	0.2
14	*Tarletonbeania crenularis*	7.8	0.1	*Triphoturus mexicanus*	13.5	0.2
15	*Protomyctophum crockeri*	6.7	0.1	*Bathylagus wesethi*	12.5	0.2
16	*Sebastes levis*	6.0	0.1	*Chauliodus macouni*	12.2	0.2
17	*Parophrys vetulus*	5.6	0.1	*Cyclothone* spp	8.0	0.1
18	*Pleuronichthys verticalis*	5.5	0.1	*Diaphus theta*	6.3	0.1
	98.6% of total larvae			99.1% of total larvae		

Southern California

Rank	Region 9 (seaward)	no/10m^2	%
1	*Merluccius productus*	2119.6	74.9
2	*Engraulis mordax*	206.8	7.3
3	*Stenobrachius leucopsarus*	62.3	2.2
4	*Bathylagus ochotensis*	36.7	1.3
5	*Protomyctophum crockeri*	36.6	1.3
6	*Leuroglossus stilbius*	30.7	1.1
7	*Bathylagus wesethi*	27.0	1.0
8	*Trachurus symmetricus*	26.7	0.9
9	*Diogenichthys atlanticus*	23.3	0.8
10	*Tarletonbeania crenularis*	21.3	0.8
11	*Lampanyctus ritteri*	20.5	0.7
12	*Symbolophorus californiense*	17.8	0.6
13	*Sebastes* spp	14.8	0.5
14	*Diaphus* spp	13.2	0.5
15	*Argyropelecus* spp	11.3	0.4
16	*Melamphaes* spp	10.7	0.4
17	*Cyclothone* spp	10.6	0.4
18	*Chauliodus macouni*	10.1	0.4
	95.5% of total larvae		

Northern Baja California

Rank	Region 11 (inshore)	no/10m^2	%	Region 12 (inshore-Viscaino Bay)	no/10m^2	%
1	*Engraulis mordax*	5749.8	81.8	*Engraulis mordax*	5826.8	80.5
2	*Merluccius productus*	643.2	9.1	*Citharichthys* spp	709.6	9.8
3	*Sebastes* spp	163.8	2.3	*Citharichthys xanthostigma*	194.2	2.7
4	*Triphoturus mexicanus*	88.8	1.3	*Triphoturus mexicanus*	73.0	1.0
5	*Leuroglossus stilbius*	49.7	0.7	*Citharichthys stigmaeus*	55.2	0.8
6	Sciaenidae	44.1	0.6	*Sebastes* spp	45.7	0.6
7	*Citharichthys* spp	30.9	0.4	*Merluccius productus*	39.4	0.5
8	*Protomyctophum crockeri*	27.9	0.4	*Citharichthys sordidus*	35.9	0.5
9	*Lampanyctus ritteri*	20.6	0.3	Sciaenidae	34.7	0.5
10	*Argyropelecus* spp	20.0	0.3	*Sardinops sagax*	32.2	0.4
11	Clinidae	16.5	0.2	*Peprilus simillimus*	20.6	0.3
12	*Trachurus symmetricus*	13.1	0.2	*Paralichthys californicus*	18.6	0.3
13	Gobiidae	11.5	0.2	*Pleuronichthys verticalis*	9.6	0.1
14	*Lampanyctus* spp	10.7	0.2	*Protomyctophum crockeri*	9.3	0.1
15	*Vinciguerria lucetia*	10.1	0.1	*Lampanyctus ritteri*	9.0	0.1
16	*Bathylagus ochotensis*	9.9	0.1	*Leuroglossus stilbius*	8.7	0.1
17	*Citharichthys stigmaeus*	9.0	0.1	*Argentina sialis*	8.2	0.1
18	Cottidae	7.9	0.1	*Diogenichthys atlanticus*	7.7	0.1
	98.4% of total larvae			98.5% of total larvae		

Continued on next page

TABLE 3 (continued)

The 18 Most Abundant Larval Fish Taxa (Including the 10 Most Abundant Species Identifications) in Order of Ranked Abundance, and Their Percentage Contribution to the Total Ichthyoplankton within Each of 11 CalCOFI Regions, 1975

Northern Baja California

Rank	Region 13 (offshore)	no/10m²	%	Region 14 (seaward)	no/10m²	%
1	*Engraulis mordax*	2454.4	65.5	*Trachurus symmetricus*	361.7	19.0
2	*Merluccius productus*	535.8	14.3	*Merluccius productus*	297.9	15.6
3	*Triphoturus mexicanus*	199.6	5.3	*Vinciguerria lucetia*	269.1	14.1
4	*Trachurus symmetricus*	110.6	3.0	*Triphoturus mexicanus*	234.5	12.3
5	*Vinciguerria lucetia*	77.7	2.1	*Bathylagus wesethi*	171.6	9.0
6	*Bathylagus wesethi*	54.8	1.5	*Cyclothone* spp	68.2	3.6
7	*Protomyctophum crockeri*	46.9	1.2	*Diogenichthys atlanticus*	60.0	3.1
8	*Argyropelecus* spp	20.7	0.6	*Protomyctophum crockeri*	47.9	2.5
9	*Diogenichthys atlanticus*	20.6	0.6	*Citharichthys xanthostigma*	38.7	2.0
10	*Lampanyctus ritteri*	19.6	0.5	*Symbolophorus californiense*	34.6	1.8
11	*Cyclothone* spp	16.3	0.4	*Argyropelecus* spp	32.6	1.7
12	*Bathylagus ochotensis*	16.0	0.4	*Lampanyctus ritteri*	31.9	1.7
13	*Symbolophorus californiense*	14.6	0.4	*Engraulis mordax*	28.4	1.5
14	*Lampanyctus* spp	14.1	0.4	*Ceratoscopelus townsendi*	19.4	1.0
15	*Melamphaes* spp	12.7	0.3	*Stomias* spp	15.7	0.8
16	*Leuroglossus stilbius*	11.6	0.3	*Melamphaes* spp	14.8	0.8
17	*Citharichthys stigmaeus*	9.4	0.2	*Diogenichthys laternatus*	13.6	0.7
18	*Ceratoscopelus townsendi*	8.1	0.2	*Lampanyctus* spp	12.3	0.6
	97.2% of total larvae			91.8% of total larvae		

Central Baja California

Rank	Region 16 (inshore)	no/10m²	%	Region 17 (offshore)	no/10m²	%
1	*Engraulis mordax*	4079.9	83.9	*Engraulis mordax*	1439.5	58.3
2	*Triphoturus mexicanus*	166.0	3.4	*Vinciguerria lucetia*	239.0	9.7
3	*Citharichthys* spp	135.0	2.8	*Triphoturus mexicanus*	225.9	9.2
4	*Diogenichthys laternatus*	53.3	1.1	*Diogenichthys laternatus*	187.9	7.6
5	*Vinciguerria lucetia*	43.2	0.9	*Citharichthys* spp	118.0	4.8
6	*Sardinops sagax*	41.6	0.9	*Argyropelecus* spp	26.8	1.1
7	Sciaenidae	27.8	0.6	*Lampanyctus* spp	21.6	0.9
8	*Sebastes* spp	22.1	0.4	*Cyclothone* spp	19.1	0.8
9	*Leuroglossus stilbius*	18.7	0.4	*Ceratoscopelus* spp	16.0	0.6
10	*Sarda chiliensis*	17.5	0.4	Sciaenidae	16.0	0.6
11	*Hypsoblennius* spp	16.1	0.3	*Trachurus symmetricus*	13.4	0.5
12	*Chromis punctipinnis*	15.5	0.3	*Bathylagus wesethi*	12.4	0.5
13	Serranidae	14.9	0.3	*Diogenichthys atlanticus*	9.7	0.4
14	*Etropus* spp	12.8	0.3	*Gonichthys tenuiculus*	9.3	0.4
15	*Citharichthys xanthostigma*	12.5	0.3	*Stomias* spp	9.1	0.4
16	*Merluccius productus*	11.9	0.2	*Sebastes* spp	8.9	0.4
17	*Symphurus* spp	11.2	0.2	*Hippoglossina stomata*	8.9	0.4
18	*Argyropelecus* spp	10.2	0.2	*Bathylagus pacificus*	8.0	0.3
	96.9% of total larvae			96.9% of total larvae		

region 12 (77.8% OL), inshore region 16 (27.7%), and offshore region 17 (13.5%); they were relatively rare ($\leq$ 10% OL) in northern regions. Sciaenid larvae were most abundant (7.4-9.1% OL) in southern California and northern Baja California inshore regions 7 and 11. Among the mesopelagic forms, abundances of Bathylagidae decreased, while those of Myctophidae and Gonostomatidae increased, from north to south and inshore to offshore regions (Table 2). Bathylagid larvae were relatively abundant off central and southern California (19.4-30.4% OL) and rare off Baja California (1.0-15.2%); gonostomatids were rare (0.2-5.8% OL) in all California regions and inshore Baja California regions 11, 12, and 16 but were relatively abundant (17.4-49.4%) in Baja California offshore and seaward regions 13, 14, and 17.

Geographical differences in ichthyoplankton composition were tested using PSI comparisons of total species lists (six cruises combined) from each area and region. We found a high degree of similarity in species percentage composition of the total ichthyoplankton between areas and regions south of Point Conception (Table 4A). High PSI values (ranging from 60.0 to 90.0) resulted from overall comparisons of the southern California and northern and central Baja California areas and from comparisons of the regions

TABLE 4
Percent Similarity Index (PSI) Values for Between-Area and Between-Region Comparisons: (A) Total Ichthyoplankton and (B) Other Larvae (OL)

(A) Total ichthyoplankton PSI values

	Area		
	SC	NBC	CBC
CC	17.97	12.05	6.63
SC		74.29	62.15
NBC			77.08

		Region									
		CC	SC			NBC				CBC	
		5	7	8	9	11	12	13	14	16	17
CC	4	52.15	21.54	12.16	15.53	11.51	6.11	9.01	9.19	4.72	5.27
	5		16.88	11.71	18.50	9.33	4.97	10.68	16.10	3.79	6.29
SC	7			86.92	15.46	88.44	82.68	70.50	6.80	82.40	60.46
	8				27.16	92.13	80.84	82.42	18.72	80.60	61.20
	9					20.82	10.16	30.47	27.95	10.12	12.19
NBC	11						85.11	78.94	14.69	86.48	63.12
	12							68.71	6.53	87.96	66.33
	13								34.99	71.96	70.33
	14									8.84	27.56
CBC	16										69.31

(B) Other larvae PSI values

	Area		
	SC	NBC	CBC
CC	69.02	20.69	10.22
SC		34.88	19.45
NBC			62.28

		Region									
		CC	SC			NCB				CBC	
		5	7	8	9	11	12	13	14	16	17
CC	4	50.76	70.36	59.44	43.05	47.81	11.73	10.69	5.62	11.58	6.36
	5		29.26	57.44	62.54	29.17	13.46	23.98	16.25	9.94	8.02
SC	7			56.97	28.56	55.54	14.79	9.68	6.02	17.15	7.60
	8				62.78	53.30	14.80	31.57	23.14	15.78	14.86
	9					37.40	13.08	46.40	37.94	16.13	16.85
NBC	11						27.33	42.17	36.16	39.45	34.20
	12							14.10	14.71	42.19	25.12
	13								69.71	40.13	49.53
	14									36.34	55.67
CBC	16										58.66

Based on pooled (6 cruises) species lists for each area and region, 1975. CC = central California; SC = southern California; NBC = northern Baja California; CBC = central Baja California.

within each of these areas (Table 4A). Low PSI values (< 25) resulted from comparisons of the total species lists of regions and areas north and south of Point Conception and reflect the dominance of the PL species south of Point Conception. When PL species were excluded and comparisons were made between the relative proportions of the OL, high PSI values (62.3-69.0) were found for comparisons between the central and southern California areas and between the northern and central Baja California areas; low PSI values (10.2-34.9) were found for comparisons between the California and Baja California areas (Table 4B). Aside from dominance by the PL, the species proportions of the southern California ichthyoplankton were dissimilar to those of the northern and central Baja California areas, but were fairly similar to those of central California. Highest between-region OL PSI values occurred between inshore regions 4-7 (70.4) and offshore and seaward regions 5-9 (62.5) and 8-9 (62.8) of central and southern California and between offshore and seaward regions 13-14 (69.7) of northern Baja California (Table 4B). These high PSI values reflect similarities in proportions of the dominant shelf and mesopelagic taxa (Table 3) in these regions.

Geographical differences in taxonomic composition and relative abundance were tested using Kendall's tau test comparisons of the rank order of abundances of the 10 most abundant taxa (six cruises pooled) within each area and region (Table 3). All comparisons that included the PL in the rankings supported ($P > 0.10$) the null hypothesis of no agreement of species rank order of abundance. When the PL were excluded, significant agreement ($P < 0.05$) of rank order of abundance among the 10 most abundant OL taxa occurred between regions 4-7, 4-8, 5-8, and 5-9 off central and southern California and between regions 13-14 off northern Baja California.

Seasonal Differences in Ichthyoplankton Species Structure

The ichthyoplankton underwent large seasonal abundance fluctuations because of seasonal spawning of the main PL species (Figure 1). Maximum areawide abundances of anchovy, hake, and jack mackerel occurred in January and March, during which time the the PL made up 84% of the total larvae (TL). PL also dominated the ichthyoplankton during May (67% TL). Shelf forms were most abundant during January and March because of peak abundances of rockfish larvae, but because of PL dominance they made up only 4% (rockfishes 3%) of the total. Sciaenids had a January abundance peak (0.5% TL). Lower, relatively constant numbers of shelf forms occurred from May to October-November, and flatfishes predominated (8-

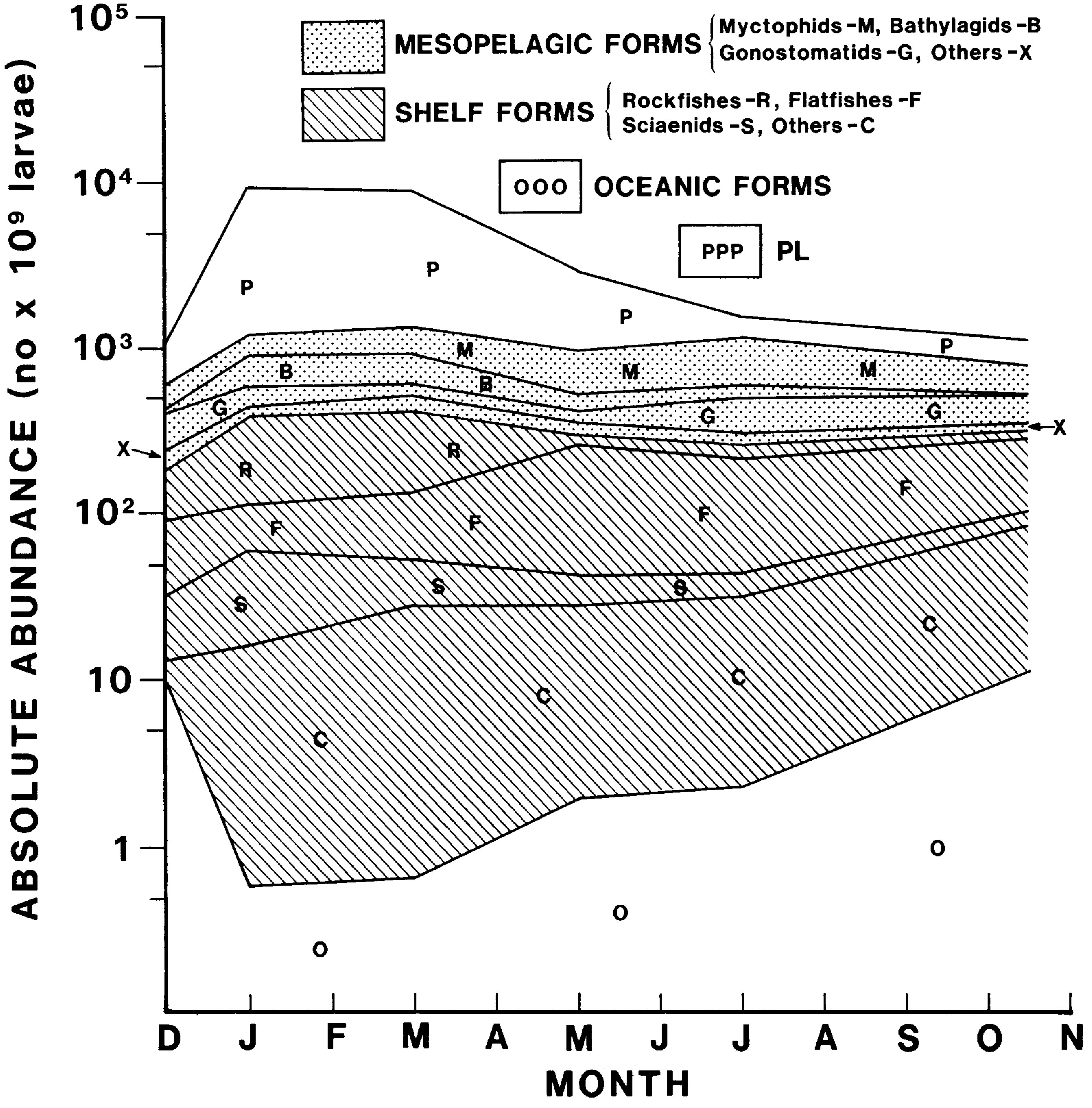

Figure 1. Seasonal abundance fluctuations of major ichthyoplankton categories in the CalCOFI area (all regions combined) during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others); shelf forms (rockfishes, flatfishes, sciaenids, others); and oceanic forms. Abundances expressed as estimated absolute numbers × 10^9 of larvae in the survey area during each cruise. Log scale is used to depict simultaneous abundance fluctuations of forms representing a wide range of relative abundances.

16% TL). Other shelf taxa were most abundant during October (7% TL). Mesopelagic forms had two abundance peaks caused by increased spawning of myctophids and bathylagids during January and March, and of myctophids and gonostomatids during July. Because of decreased PL abundances, mesopelagic species dominated the ichthyoplankton in July and October-November (57% and 40% TL), and were about equal to the PL in December (mesopelagics 39%; PL 43%). Oceanic species were most abundant (1% TL) during October-November and December.

Each region had seasonal changes in abundance and relative proportions of major taxa (Figures 2, 3) and species. Maximum PL abundances within all regions occurred between January and May because of peak spawning of anchovy, hake, and jack mackerel; these larvae dominated the ichthyoplankton of all regions south of Point Conception for part or all of this period. Dominance was greatest in inshore regions where the PL made up 80-96% of the total larvae caught from January to May (and July in southern California region 7). PL dominance in offshore regions was restricted to January and March in southern California regions 8 and 9 and northern Baja California region 13 (84-97% TL), and to March in northern and central Baja California regions 14 and 17 (72-84% TL). Seasonal abundance fluctuations of the PL are treated in greater detail in Loeb et al. (1983a).

Seasonal and regional patterns of OL composition and abundance relations were complex. However, four general patterns can be established based on regional similarities of overall dominant taxa. These occur between (1) inshore central and southern California and northern Baja California regions 4, 7, and 11; (2) offshore central and southern California regions 5, 8, and 9; (3) Viscaino Bay and central Baja California inshore regions 12 and 16; and (4) offshore Baja California regions 13, 14, and 17 (Figures 2, 3).

California and northern Baja California inshore regions 4, 7, and 11. OL abundances in the California and northern Baja California inshore regions were elevated from December to March and then (except in region 7 during October) decreased to low and relatively constant levels for the rest of the year. Maximum spring abundances occurred during January and March and were due to large numbers of rockfish, bathylagid, and myctophid larvae (64.6-94.7% OL within each region). Major contributing taxa were *Sebastes* spp, the bathylagids *Leuroglossus stilbius* and *Bathylagus ochotensis*, and myctophids *Stenobrachius leucopsarus* (regions 4 and 7) and *Protomyctophum crockeri* (regions 7 and 11). Abundances of all major categories (except myctophids in region 11) decreased in May and, except for flatfishes, remained low for the rest of the year. In region 11 myctophids had a July abundance maximum dominated by *Triphoturus mexicanus*. Large regional differences occurred in the composition and proportions of major taxa from May to November. Flatfish abundance peaks occurred during October-November in all three regions and were primarily due to large numbers of *Citharichthys* spp, *C. stigmaeus*, *C. sordidus*, and (in region 4) *Parophrys vetulus*. Flatfish abundance was most extreme in region 7 during October, when maximum OL abundance (81% because of flatfishes) occurred. Flatfishes made up 25.5% of the October OL in region 11 and 19.6% and 34.6% of the November OL in regions 4 and 7, respectively.

Central and southern California offshore and seaward regions 5, 8, and 9. OL abundances in California offshore and seaward regions were elevated during January and March (and May in regions 5 and 9) primarily because of peak spawning of myctophids and bathylagids. Five species—*Leuroglossus stilbius* and *Bathylagus ochotensis* (Bathylagidae) and *Stenobrachius leucopsarus*, *Protomyctophum crockeri*, and *Tarletonbeania crenularis* (Myctophidae)—were consistently abundant and made up 37.8%-70.5% of the OL in each region during this period. Rockfish larvae were also abundant during January and March in regions 5 and 8 (9.0-26.8% OL) and during May in region 9 (6.3%). OL abundances in all three regions decreased from May to October-November, and species composition and relative proportions varied with region and cruise. Flatfishes (*Citharichthys* spp, *C. stigmaeus*, and *C. sordidus*) were most abundant during November (region 8, 24.0%) and December (regions 5 and 9, 25.6% and 12.2% OL, respectively). Oceanic forms were most abundant in region 8 during December (2.3% OL) and in region 9 during November and December (3.6-4.0%).

Viscaino Bay and central Baja California inshore regions 12 and 16. Flatfishes dominated region 12 OL throughout the year (51.6-83.9% within each cruise). Flatfishes dominated region 16 OL during December (48.5%) and were major contributors (31.9-43.0%) during May and October; myctophids dominated during January, May, and July (40.3-52.7%); other shelf forms dominated in October (39.8%). In contrast to the northern inshore regions, January and March OL abundances were relatively low; maximum numbers of rockfishes, bathylagids (primarily *Leuroglossus stilbius*), and sciaenids (in region 12) occurred during this time. Greatest OL abundances occurred during May and July in region 12, and July and October in region 16 because of maximum numbers of flatfishes (primarily *Citharichthys* spp, *C. xanthostigma*, *C. sordidus*, *C. stigmaeus*, *Paralichthys californicus*, and *Symphurus* sp); myctophids (primarily *Triphoturus mexicanus* in region 12, *T. mexicanus* and *Diogenichthys laternatus* in region 16); gonostomatids (in region 16, *Vinciguerria lucetia*); sciaenids (region 16); and other shelf taxa (*Peprilus simillimus* in region 12, *Chromis punctipinnis*, Serranidae, *Etropus* sp, and *Chloroscombrus* sp in region 16). The peak July OL abundances in Viscaino Bay were the highest for the entire CalCOFI area during 1975; the July and October abundances of other shelf taxa in region 16 were greater than in any other region during the year.

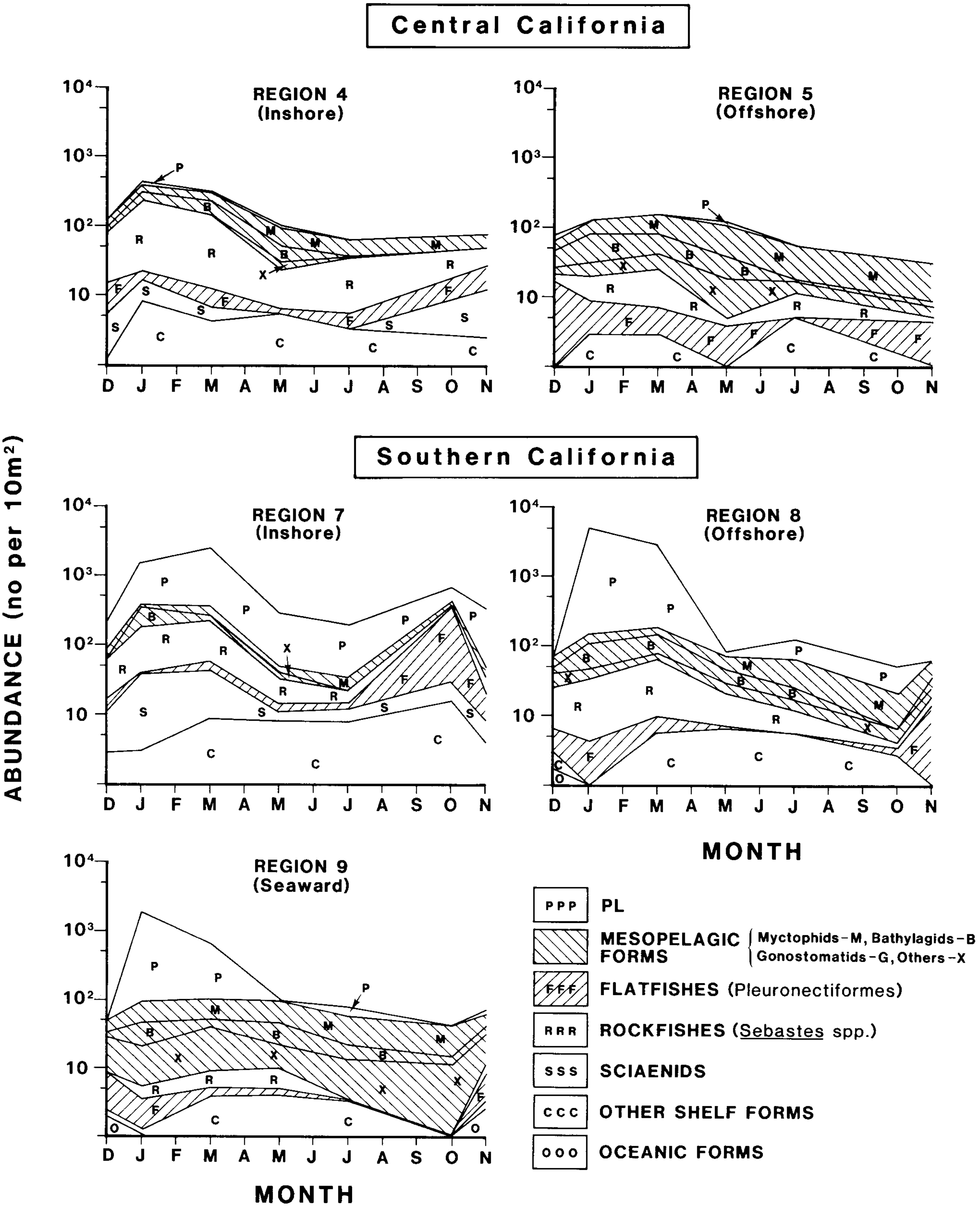

Figure 2. Seasonal abundance fluctuations of major ichthyoplankton categories within CalCOFI regions 4, 5, 7, 8, and 9 during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others); shelf forms (rockfishes, flatfishes, sciaenids, others); and oceanic forms. Abundances are expressed as mean numbers of larvae per 10 m^2 sea-surface area during each cruise. Log scale is used to depict simultaneous fluctuations of forms representing a wide range of relative abundances.

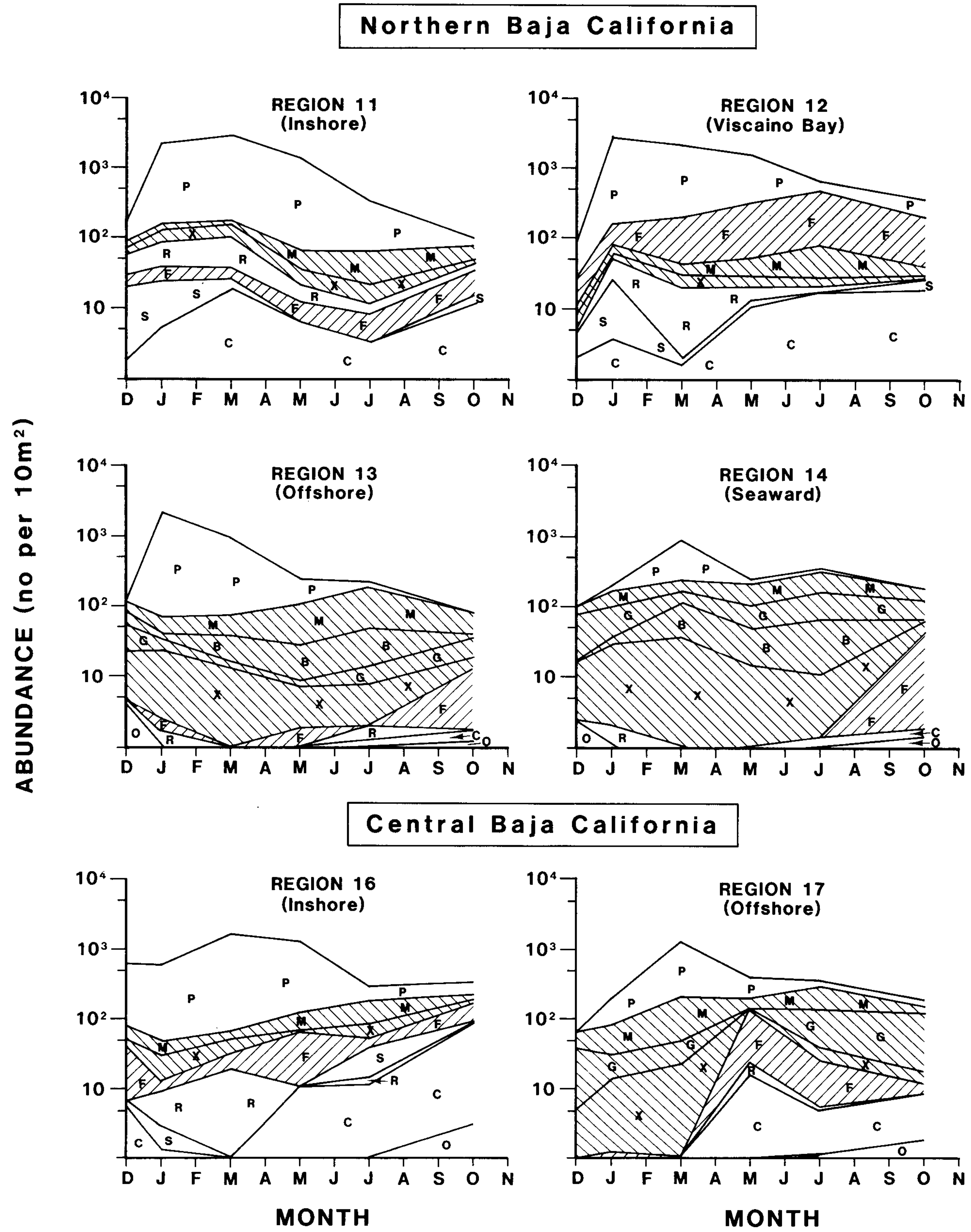

Figure 3. Seasonal abundance fluctuations of major ichthyoplankton categories within CalCOFI regions 11-14, 16, and 17 during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others); shelf forms (rockfishes, flatfishes, sciaenids, others); and oceanic forms. Abundances are expressed as mean numbers of larvae per 10 m^2 sea-surface area during each cruise. Log scale is used to depict simultaneous fluctuations of forms representing a wide range of relative abundances.

Northern central Baja California offshore and seaward regions 13, 14, and 17. OL abundances in the Baja California offshore and seaward regions increased from relatively low December-January values to July maxima because of peak abundances of myctophids (mostly *Triphoturus mexicanus*: 38.0-62.9% OL) and, in regions 14 and 17, high gonostomatid abundances (21.4-27.0%; primarily *Vinciguerria lucetia*). Bathylagids (primarily *Bathylagus wesethi*) were most abundant in regions 13 and 14 from March to July (13.0-32.4%); flatfishes were rare or absent in these two regions except during October (13.9% region 13 OL, primarily *Citharichthys stigmaeus* and *C. sordidus;* 26.0% region 14 OL, primarily *C. xanthostigma* and *Symphurus* sp). Because region 17 was undersampled during March and May (5 samples total) little can be determined about the OL during that time. Flatfishes, rockfishes, and sciaenids were abundant in the one May sample; relatively large numbers of flatfishes (6.7% OL, primarily *Citharichthys* spp) were also collected during July. Oceanic forms were most abundant in regions 13 and 14 during December (2.1-3.3%) and in region 17 during October (1.2%).

Within- and Between-Region Comparisons of Ichthyoplankton Species Structure

Seasonal changes in ichthyoplankton composition and abundance relations are reflected by PSI values resulting from between-cruise comparisons of species lists. PSI values from comparisons of the total ichthyoplankton and of the OL fraction (all regions combined) were highest (91 and 73, respectively) for January and March cruise comparisons, and lowest (30-41) for January and March vs July and October-November comparisons. These indicate a marked shift in relative proportions of both PL and OL species between spring and summer/fall. These changes were primarily due to decreased abundances of the main PL species (anchovy, hake, and jack mackerel), rockfishes (*Sebastes* spp), *Leuroglossus stilbius* and *Bathylagus ochotensis* (Bathylagidae), and *Stenobrachius leucopsarus* (Myctophidae), and increased abundances of *Triphoturus mexicanus* (Myctophidae), *Vinciguerria lucetia* (Gonostomatidae), and flatfishes (primarily *Citharichthys* spp) during July and October-November. Kendall's concordance test of the rank order of abundance of the 10 most abundant species taken during each cruise showed significant agreement ($P < 0.01$) of rank order of abundance throughout the year. This indicates that despite marked seasonal changes in relative proportions, the same abundant taxa tended to dominate the ichthyoplankton throughout the year.

TABLE 5

Range and Mean of Percent Similarity Index (PSI) Values from Between-Cruise Comparisons of the Total Ichthyoplankton and of the Other Larval Fraction (OL) in 11 CalCOFI Regions, 1975

		Total ichthyoplankton		Other larvae	
	Region	Range	Mean	Range	Mean
Central California					
	4	31.81-70.50	51.62	33.50-74.46	52.06
	5	26.25-59.40	40.61	27.54-64.00	46.68
Southern California					
	7	69.17-93.84	83.12	41.23-72.46	56.57
	8	1.80-85.16	23.51	20.75-75.89	43.69
	9	4.07-87.06	25.88	29.47-67.98	42.64
Northern Baja California					
	11	28.32-93.52	58.97	27.14-68.90	43.91
	12	29.54-93.38	59.81	26.47-82.66	51.88
	13	2.36-50.68	23.87	21.22-73.16	37.44
	14	15.52-86.73	39.76	26.70-86.20	48.06
Central Baja California					
	16	31.26-93.57	54.40	23.90-60.33	37.33
	17	13.93-70.94	40.89	30.57-61.89	48.47

Comparisons based on species lists from each of 6 cruises.

Within each region, marked seasonal shifts in relative proportions of larval fish species are reflected by low between-cruise PSI values (Table 5). The ranges of between-cruise PSI values were smallest in central California regions 4 and 5 (which had little seasonal input of PL) and southern California inshore region 7 (which was dominated by anchovy larvae during all cruises). The other eight regions had large proportions of their total ichthyoplankton contributed by one or more of the PL species during at least two cruises during the year. Because of more equitable abundances among the OL, OL PSI values (except in regions 4, 5, and 14) were lower, and varied less than those for the total ichthyoplankton (Table 5). High ($\geq$ 60) total ichthyoplankton PSI values were associated with periods of maximum PL abundance in all regions except 4 and 5 (central California) and 13 and 14 (northern Baja California); in these four regions, highest values were associated with periods of peak OL abundances. Maximum OL PSI values were also generally associated with periods of peak OL abundances; exceptions were in central Baja California regions 16 and 17, where maximum January-March PSI values preceded July peak OL abundance, and in northern Baja California region 11, where maximum May-July PSI values followed January-March peak abundances.

As with area-wide comparisons, low total and OL regional PSI values generally resulted from comparisons of October-November species lists with those of other months. This indicates that, within all regions, the species composition and abundance relations dur-

TABLE 6

Percent Similarity Index (PSI) Values from Between-Region Comparisons of the Other Larvae (OL) Category of Ichthyoplankton Taken in CalCOFI Cruises, 1975

Areas	Regions	Cruise					
		7412	7501	7503	7505	7507	7510(11)
CC-CC	4-5	36.77	40.92	56.73	53.11	56.19	46.21
CC-SC	4-7	67.20*	62.63*	70.45*	47.53	41.76	57.92
CC-SC	4-8	48.54	53.64	66.51*	63.88*	44.47	29.26
CC-SC	4-9	22.27	40.83	51.76	49.00	31.26	20.44
CC-SC	5-7	25.04	26.56	34.18	25.46	31.68	25.23
CC-SC	5-8	40.56	42.61	50.66	58.13	51.40	45.31
CC-SC	5-9	28.72	57.47	71.12*	61.16*	47.31	26.80
SC-SC	7-8	53.04	66.14*	56.73	42.71	34.04	38.01
SC-SC	7-9	17.83	29.54	34.84	33.39	25.15	24.43
SC-SC	8-9	49.25	54.34	50.04	55.32	66.19*	50.36
SC-NBC	7-11	50.91	57.59	67.71*	41.79	28.37	49.92
SC-NBC	7-12	26.28	26.80	17.29	13.83	11.26	42.98
SC-NBC	7-13	7.24	9.87	8.96	15.18	18.08	50.36
SC-NBC	7-14	6.84	4.72	10.24	9.47	13.13	41.52
SC-NBC	8-11	47.85	46.86	53.73	28.21	31.63	41.52
SC-NBC	8-12	16.46	20.25	14.63	4.82	10.77	29.76
SC-NBC	8-13	27.15	24.29	20.83	18.01	33.96	41.18
SC-NBC	8-14	29.47	15.59	20.17	10.67	26.56	24.86
SC-NBC	9-11	28.11	42.58	34.42	23.74	30.71	33.57
SC-NBC	9-12	14.12	45.71	11.78	6.98	11.49	15.04
SC-NBC	9-13	37.64	13.76	33.67	33.90	34.43	51.51
SC-NBC	9-14	41.24	33.94	33.87	27.85	30.27	33.22
NBC-NBC	11-12	32.43	41.26	22.21	17.74	18.89	35.25
NBC-NBC	11-13	26.15	34.54	27.58	57.80	65.81*	43.32
NBC-NBC	11-14	21.07	30.47	23.68	45.26	48.46	29.06
NBC-NBC	12-13	9.93	17.09	11.48	10.22	12.23	21.38
NBC-NBC	12-14	9.39	14.67	7.50	9.54	12.42	28.08
NBC-NBC	13-14	68.31*	46.26	53.85	63.89*	63.60*	57.78
NBC-CBC	11-16	27.14	44.36	44.21	40.99	51.33	35.23
NBC-CBC	11-17	21.02	17.69	13.23	24.93	48.23	17.84
NBC-CBC	12-16	60.97*	38.59	35.82	47.57	20.95	36.99
NBC-CBC	12-17	14.74	10.20	6.45	60.97*	17.41	9.03
NBC-CBC	13-16	13.15	28.80	18.77	38.47	51.85	27.39
NBC-CBC	13-17	59.32	24.72	24.70	16.42	50.58	32.71
NBC-CBC	14-16	11.27	26.37	12.42	40.79	55.55	33.78
NBC-CBC	14-17	53.55	45.69	24.64	16.20	67.45*	48.03
CBC-CBC	16-17	35.18	49.72	26.09	65.70*	67.68*	27.20

Comparisons are between regions of the same area and between regions of adjacent areas.
Asterisk denotes high values (i.e., ≥60).
CC = central California; SC = southern California; NBC = northern Baja California; CBC = central Baja California.

ing fall were markedly different from those during the rest of the year.

Geographical and seasonal differences in taxonomic composition are shown by within-cruise PSI comparisons between the OL of adjacent regions (Table 6). Most of the PSIs were low (< 40), indicating a great degree of geographical heterogeneity throughout the year. High PSI values were generally associated with comparisons between north-south adjacent regions for the central and southern California areas and with comparisons between inshore-offshore adjacent regions within the northern and central Baja California areas. High between-region similarities were seasonally restricted. Highest PSI values in the California and northern Baja California inshore regions (62.6-70.4) occurred between regions 4-7 during December, January, and March and between regions 7-11 during March. Highest inshore-offshore and offshore-seaward values off California occurred between regions 4-8 and 5-9 during March and May, regions 7-8 in January, and regions 8-9 in July. Except for the last, these high PSI values reflect similar proportions of dominant rockfish, bathylagid, and myctophid species (*Sebastes* spp, *Leuroglossus stilbius, Bathylagus ochotensis, Stenobrachius leucopsarus, Tarletonbeania crenularis, and Protomyctophum crockeri*) during periods of elevated and peak OL abundances. High July values between regions 8-9 reflect similar proportions of a variety of myctophid and bathylagid species during a time of relatively low OL abundance. High PSI values in the Baja California areas (63.9-68.3) occurred between offshore and seaward regions 13-14 during December, May, and July because of similar proportions of dominant myctophid, gonostomatid, and bathylagid species (primarily *Triphoturus mexicanus*, *Vinciguerria lucetia*, and *Bathylagus wesethi*); high values also occurred between regions 11-13, 14-17, and 16-17 during July, and reflect shared dominance by *T. mexicanus* and (in all but region 11) *V. lucetia* during peak OL abundance.

DISCUSSION

Total Ichthyoplankton, 1975

Despite the large interannual variability in flow and biology of the California Current system (Reid et al. 1958; Sette and Isaacs 1960; Colebrook 1977; Bernal 1980), the 1975 ichthyoplankton resembled that taken on CalCOFI cruises between 1955 and 1958 (Table 1). Ahlstrom (1965) found that 12 kinds of larvae consistently contributed between 90% and 93% of the total CalCOFI ichthyoplankton. Eleven of the 12 are among the 13 most abundant taxa taken during 1975 (species were lumped into higher taxonomic categories in 1975 data to conform to the 1955-58 data; Table 1). The one major exception was the sardine (adjusted rank 26 during 1975 vs rank 6-11 in 1955-58).

The 12 most abundant taxa taken during 1975 included 91% of the total ichthyoplankton. The rank order of abundance within these 12 taxa was quite similar to that of 1955-58 (Kendall's tau tests, $P < 0.01$). However, while the proportion of hake larvae (14.5% of the total ichthyoplankton) in 1975 was similar to 1955-58 values, the proportion of anchovy larvae (58.9%) was 1.3 to 2 times higher, and the proportions of the other 10 taxa were reduced (and more similar to each other) in 1975 as compared to 1955-58 (Table 1). Caution must be used in making such direct rank and proportion comparisons between the two sets of data (especially between the less abundant taxa) because the 1955-58 values are based on actual total numbers of larvae caught and not on abundances adjusted for the area sampled (used here). Also, because the 1955-58 data were not standardized, direct comparisons of numerical abundances between 1975 and the earlier years cannot yet be made.

The large-scale CalCOFI sampling plan covers the spawning areas of the major pelagic fishes (sardine, anchovy, hake, jack mackerel) off California and Baja California (Ahlstrom 1965), and the sampled ichthyoplankton is dominated by these abundant and fecund species and by other offshore (mesopelagic) species. Shelf species other than *Sebastes* spp and *Citharichthys* spp (which have long larval periods) make limited contributions.

Geographical differences in larval fish species distributions within the CalCOFI area are to some extent obscured by the widespread distributions of anchovy, hake, and jack mackerel. However, there are distinct underlying patterns of distribution among the other larvae. Some of these species are associated with major Pacific Ocean water masses, or with cold-water (northern) or warm-water (southern) conditions, and year-to-year variations in these species' distributions and abundances have been related to changes in flow within the California Current system (Ahlstrom 1965, 1969; Paxton 1967; Moser and Ahlstrom 1970; Moser et al. 1977). Regional mean abundances of the dominant OL species during 1975 reflected their documented water-mass affiliations (Table 7). Two of three subarctic-transition zone myctophids (*Stenobrachius leucopsarus* and *Tarletonbeania crenularis;* Paxton 1967) and the two "northern" *Sebastes* species (*S. paucipinis* and *S. jordani;* Moser et al. 1977) occurred in greatest abundance off central and southern California. The warm-water cosmopolite *Diogenichthys atlanticus* (Ahlstrom 1965) was most abundant off northern Baja California, and the restricted California Current species (*Protomyctophum crockeri;* Ahlstrom 1965) and eastern tropical Pacific species (*Triphoturus mexicanus, Vinciguerria lucetia,* and *Diogenichthys laternatus;* Ahlstrom 1965; Paxton 1967) were most numerous off of northern and central Baja California.

Within the central and southern California areas, maximum abundances of mesopelagic species occurred in inshore region 4, while offshore and seaward regions 8 and 9 were locations of maximum anchovy (region 8) and hake (region 9) abundances (Table 7). In contrast, within the northern and central Baja California areas, mesopelagic species were most abundant in seaward region 14, while inshore regions 11 and 12 had maximum anchovy (region 12) and hake (region 11) abundances (Table 7). These shifts suggest inshore-offshore differences in adult distributions and spawning activities and possible differences in net larval transport between the areas off California and Baja California.

The northern Baja California area was one of faunal transition with marked north-south shifts in regional dominance by rockfishes and bathylagids to dominance by gonostomatids, flatfishes, and other shelf taxa. It also marked shifts in dominance by subarctic, cold-water, and northern species to eastern tropical

TABLE 7
Regional Ranks of Abundance of the 22 Most Abundant Larval Fish Species in the CalCOFI Area, 1975

	Affil-iation	Central California		Southern California			Northern Baja California				Central Baja California	
		Region										
		4	5	7	8	9	11	12	13	14	16	17
Stenobrachius leucopsarus	S-T	1	2	3	5	4	7	—	—	6	8	—
Bathylagus ochotensis	N	1	2	5	3	4	7	9	6	8	—	—
Tarletonbeania crenularis	S-T	1	2	5	3	4	7	—	—	6	—	—
Sebastes jordani	N	1	5	2	3	6	4	—	—	—	—	—
Sebastes paucispinis	N	2	3	1	6	5	4	—	—	—	—	—
Leuroglossus stilbius	M	3	6	1	2	5	4	9	8	10	7	11
Engraulis mordax	M	10	11	4	1	8	3	2	6	9	5	7
Merluccius productus	M	8	9	6	2	1	3	7	4	5	10	11
Citharichthys sordidus	N	4	2	10	6	7	5	1	8	—	3	9
Citharichthys stigmaeus	N	4	3	7	2	8	6	1	5	10	9	11
Symbolophorus californiense	T	—	6	10	5	2	4	7	3	1	9	8
Diogenichthys atlanticus	C	11	5	10	8	2	7	6	3	1	9	4
Lampanyctus ritteri	S-T	9	6	10	5	3	2	7	4	1	11	8
Protomyctophum crockeri	CA	7	5	9	3	4	6	8	2	1	11	10
Trachurus symmetricus	M	—	9	10	3	4	6	8	2	1	7	5
Ceratoscopelus townsendi	CA	—	8	9	4	3	7	10	2	1	5	6
Bathylagus wesethi	S	—	9	10	4	3	7	8	2	1	6	5
Citharichthys xanthostigma	S	—	—	—	—	—	—	1	5	2	3	4
Sardinops sagax	M	—	—	4	—	—	3	1	—	2	—	—
Triphoturus mexicanus	ETP	—	—	9	7	8	5	6	3	1	4	2
Vinciguerria lucetia	ETP	—	9	—	8	7	5	6	3	1	4	2
Diogenichthys laternatus	ETP	—	—	7	—	—	6	4	5	3	2	1

Ranks based on total mean numbers of larvae (6 cruises, summed) in each region. Water mass or habitat affiliations assigned to each species: S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern/cold water; S, southern/warm water; CA, restricted to California Current; M, multiple affiliations. Affiliations from Ahlstrom (1965), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

Pacific, warm-water, and southern species. Offshore and seaward regions 13 and 14 contained mixtures of species from all three water-mass source areas plus restricted California Current species; dominant OL of inshore regions 11 and 12 included subarctic and eastern tropical Pacific species. The transitional nature of the northern Baja California area is reflected by the relatively low OL PSI values resulting from comparisons of its regions with north-south adjacent regions (Table 4B). Despite its transitional nature, the northern Baja California area had relatively large numbers of larval fishes (Loeb et al. 1983a): PL abundance was extremely high in inshore regions 11 and 12, and maximum areawide OL abundances occurred in regions 12 (primarily flatfishes) and 14 (mesopelagic taxa).

Seasonal changes were evident in both larval fish abundance (Loeb et al. 1983a) and relative abundance of species. However, within each region there was a general dominance by a limited suite of taxa throughout the year. Seasonal differences were probably due to differences in the timing of peak spawning activity among these few abundant taxa. Highest area-wide abundances occurred during the peak January-May PL spawning period. Highest OL abundances occurred during January and March in the central and southern California areas and in inshore region 11 of northern Baja California; this was primarily due to peak spawning of *Sebastes* spp and four mesopelagic species with subarctic-transition zone, northern/cold-water, or restricted affiliations (*Stenobrachius leucopsarus, Protomyctophum crockeri, Leuroglossus stilbius,* and *Bathylagus ochotensis;* Table 8). Low OL abundances prevailed within all of these regions (except region 7) from May to December because of minor sumer/fall spawning input; within region 7, the October OL abundance peak was attributed to *Citharichthys* spp. Within the central Baja California regions and regions 12, 13, and 14 of northern Baja California, maximum OL abundances occurred between May and October primarily because of peak summer or fall spawning of flatfish and southern shelf species and three eastern tropical Pacific or warm-water mesopelagic species (*Triphoturus mexicanus, Vinciguerria lucetia,* and *Bathylagus wesethi;* Table 8).

Ichthyoplankton Distribution and Seasonal Abundance Patterns in Relation to California Current Flow

The dominant OL taxa of the central and southern California areas are subarctic-transition zone, northern, and cold-water forms, and reflect the northern sources of the California Current. These species,

TABLE 8
Cruise Ranks of Abundance of the 22 Most Abundant Larval Fish Species in the CalCOFI Area, 1975

	Affil-iation	Cruise					
		7412	7501	7503	7505	7507	7510(11)
Stenobrachius leucopsarus	S-T	4	2	1	3	5	6
Bathylagus ochotensis	N	4	1	2	3	5	6
Tarletonbeania crenularis	S-T	6	5	4	2	3	1
Sebastes jordani	N	—	—	1	—	—	—
Sebastes paucispinis	N	3	1	2	4	—	5
Leuroglossus stilbius	M	3	1	2	4	5	6
Engraulis mordax	M	4	1	2	3	6	5
Merluccius productus	M	4	1	2	3	5	6
Citharichthys sordidus	N	2	3	5	6	4	1
Citharichthys stigmaeus	N	2	4	3	6	5	1
Symbolophorus californiense	T	6	3	1	4	2	5
Diogenichthys atlanticus	C	3	2	1	5	6	4
Lampanyctus ritteri	S-T	5	1	2	4	3	6
Protomyctophum crockeri	CA	3	1	2	4	5	6
Trachurus symmetricus	M	—	5	1	3	2	4
Ceratoscopelus townsendi	CA	5	4	3	6	2	1
Bathylagus wesethi	S	6	5	1	3	2	4
Citharichthys xanthostigma	S	—	—	—	3	2	1
Sardinops sagax	M	4	3	6	5	1	2
Triphoturus mexicanus	ETP	6	5	4	2	1	3
Vinciguerria lucetia	ETP	3	4	6	5	1	2
Diogenichthys laternatus	ETP	4	3	1	6	2	5

Ranks based on summed adjusted abundances of larvae from 11 CalCOFI regions for each cruise. Water mass or habitat affiliations assigned to each species: S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern/cold water; S, southern/warm water; CA, restricted to California Current; M, multiple affiliations. Affiliations from Ahlstrom (1965), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

although present and generally dominant throughout the year, were most abundant in January-March, during reduced surface countercurrent flow and the onset of upwelling. During 1975 the upwelling period in the central and southern California areas extended from March to late September; maximum intensities occurred from May to July (Parrish et al. 1981). Decreased and relatively constant OL abundances prevailed here during most of this upwelling period and throughout most of the surface countercurrent period. The OL species proportions of the inshore regions of the central and southern California areas and inshore region 11 of northern Baja California were most similar from December or January to March (Table 6), possibly because these regions experienced similar environmental conditions at the onset of increased spawning activity by shared dominant taxa. Except for regions 7 and 8, greatest similarity of species proportions between inshore-offshore regions occurred later (March to May or July) than for the inshore regions; this corresponds to the period of maximum offshore advection of surface water associated with upwelling (Bakun and Nelson 1977) and may implicate larval drift. Regions 7 and 8 were most similar during December, January, and March (Table 6), perhaps because of similar wintertime conditions prevailing within the Los Angeles bight area (Lasker 1978). Between-region PSI values were relatively low during summer and fall, suggesting greater environmental heterogeneity (on regional scales) during the period of surface countercurrent flow and reduced upwelling.

The dominant OL taxa of the central Baja California area, and to a lesser degree of the northern Baja California area, are eastern tropical Pacific, southern, and warm-water forms. In these southern regions (except region 11) highest OL abundances occurred during summer and fall. This is a period of decreased upwelling, weakened southward flow, increased surface temperatures, and surface countercurrent flow off Baja California. Throughout the year 67% of all between-region PSI values in these areas were < 40.0 as compared to the regions of central and southern California, where only 33% of all comparisons were < 40.0 (Table 6). This suggests a greater degree of between-region heterogeneity in species composition in the south, because of the transitional nature of the northern Baja California area. Greatest similarity of species proportions between inshore-offshore regions generally occurred during the May-July period of maximum OL abundance (Table 6) and reflect dominance by a few summer-spawning species.

Among the 11 regions, only offshore and seaward regions 13 and 14 of northern Baja California did not have significant seasonal OL abundance peaks (Loeb et al. 1983a). These were the only regions that, despite marked seasonal changes in species proportions (i.e., low within-region PSI values; Table 5), had generally high between-region similarities of species proportions throughout the year. They also had similar ranked abundances of their dominant species. These facts imply that more homogeneous environmental conditions existed offshore of northern Baja California than elsewhere in the CalCOFI area during 1975, and probably reflect decreased influence by coastal processes in this locale.

Among the PL species, anchovy and hake most resembled the northern OL species, whereas jack mackerel and sardine were more like the southern OL species, in their distributions and seasonal abundance peaks (Tables 7 and 8). These associations are corroborated by the results of recurrent group analysis on the 1975 ichthyoplankton data (Loeb et al. 1983b). During January-March peak spawning, anchovy and hake in the southern California area had maximum abundances in offshore and seaward regions, while off northern Baja California they were most abundant in inshore regions. These differences were apparently not directly related to coastal upwelling timing or intensity, because the February onset and subsequent spring upwelling intensities were similar in both areas (Bakun and Nelson 1977; Lasker 1978). They may, however, reflect differences in spawning stocks. Apparently, central and southern spawning stocks of the northern anchovy and hake (as well as subpopulations of sardine and jack mackerel) are separated near the northern Baja California coast (Nelson 1977; Vrooman and Paloma 1977; Bakun and Parrish 1980; Hewitt 1981; Parrish et al. 1981).

The northern Baja California area is a transition zone for subarctic/cold-water and eastern tropical Pacific/warm-water fishes, as well as for copepods and euphausiids, and marks a separation of spawning stocks of the major pelagic fish species (Hewitt 1981). It separates areas that have significantly different periods of both zooplankton and OL seasonal abundance peaks (Loeb et al. 1983a). Its inshore regions have concentrations of characteristically offshore zooplankton species plus extreme zooplankton patchiness throughout the year (Arthur 1977; Loeb et al. 1983a). These features may be related to the unique hydrography of the area.

In general, wind-driven surface-layer (Ekman) transport along the coast is directed offshore (positive wind stress curl), creating a coastal divergence or upwelling zone, the extent of which varies seasonally and annually with changes in wind field and intensity. Offshore, surface convergence or downwelling (negative wind stress curl) predominates throughout the year. The boundary between convergence and divergence zones parallels the coast 100-300 km offshore except off northern Baja California (Figure 4; Bakun and Nelson 1977; Parrish et al. 1981). Here a lobe of surface convergence (negative wind stress curl) extends shoreward and impinges on the coast in the Baja California maximum upwelling area between Punta Baja and Punta Eugenia (regions 11 and 12). This feature persists throughout the year and separates the cyclonic eddy of the Southern California Bight and a seasonal coastal eddy south of Punta Eugenia. As indicated by the results presented in this study and in Loeb et al. (1983a), this feature also appears to separate both coastal and offshore biological regimes within the California Current area.

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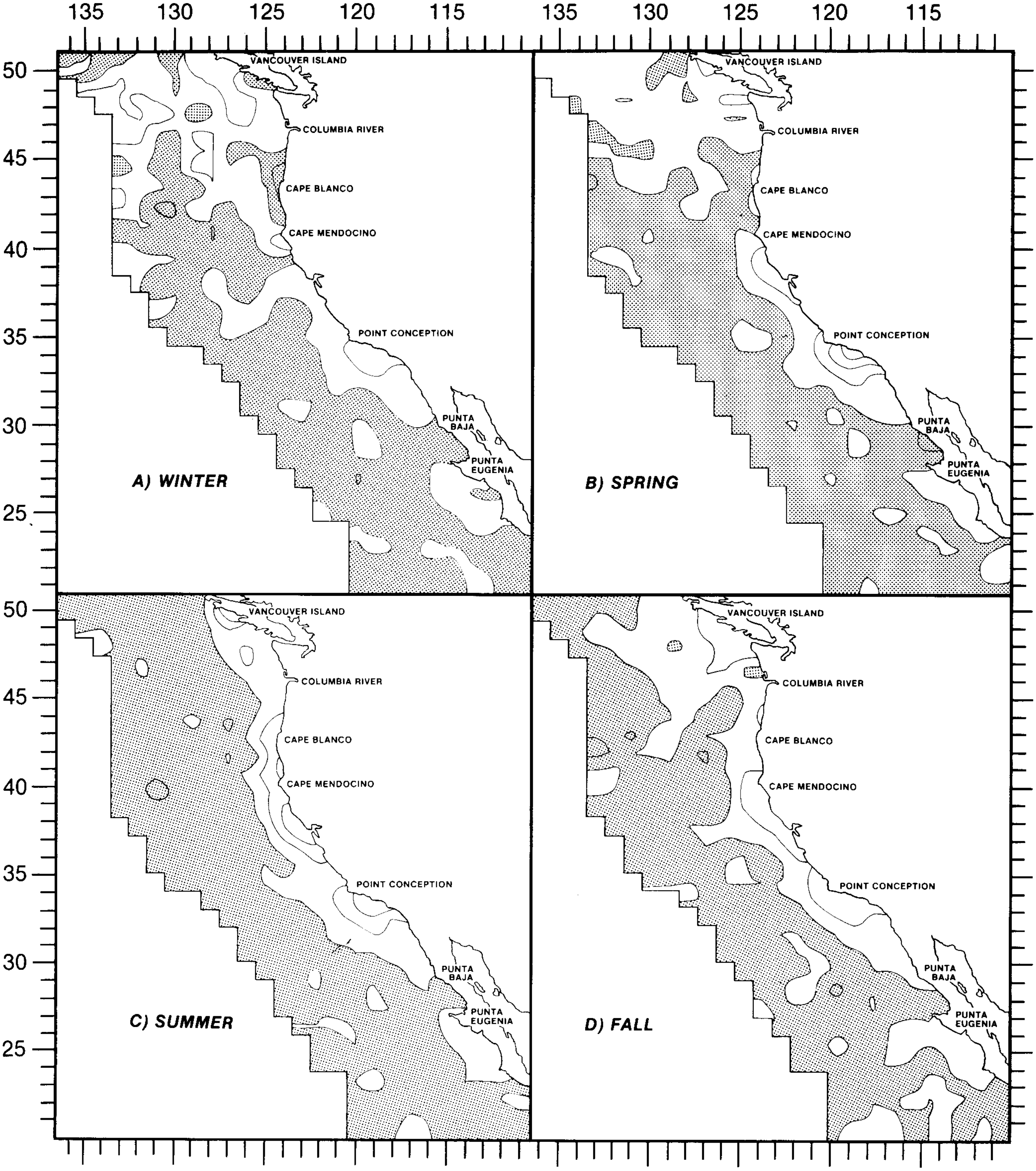

Figure 4. Patterns of wind stress curl, and divergence and convergence zones off California and Baja California, reproduced from Parrish, Nelson, and Bakun (1981). Monthly composite fields of wind stress curl were computed from surface wind stress fields for (*A*) winter (December-February), (*B*) spring (March-May), (*C*) summer (June-August), and (*D*) fall (September-November). The contour interval is 0.25 dyne/cm^2/100 km. Negative values are shaded and indicate surface Ekman convergence. Unshaded areas indicate surface Ekman divergence.

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RECURRENT GROUPS OF LARVAL FISH SPECIES IN THE CALIFORNIA CURRENT AREA

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ABSTRACT

Recurrent group analysis was performed on larval fish species collected during the 1975 CalCOFI survey. We arranged 27 species in 11 groups based on frequencies of co-occurrence in samples; 5 other species had "high" affinities with some members of the groups. The 2 largest groups (5 and 4 species, respectively) and their 5 associated species pair groups represented 2 major ichthyoplankton assemblages in the CalCOFI area.

Species of each group were frequently taken together in CalCOFI samples, shared generally similar geographical and seasonal distributions, and appeared to be relatively constant parts of one another's environments. However, based on existing vertical distribution information, most group members and associated group species appear to inhabit different depths within the upper water column. This probably indicates limited interspecific contacts (e.g., competition for food). Within-group differences in timing of peak abundances and, in one case, regions of maximum abundance, also reduce the probability of such interactions. As a result, direct interactions at the larval stage may be negligible in controlling the larval abundances and distributions of these species. More detailed vertical distribution information is needed to verify this observation.

RESUMEN

Se efectuaron análisis de grupos recurrentes con varias especies de larvas de peces recolectadas en 1975 durante las exploraciones del programa CalCOFI. 27 especies se distribuyeron en 11 grupos, tomando como base la frecuencia en que aparecían juntas en las muestras, y otras 5 especies presentaban afinidad elevada con alguno de los integrantes del grupo. Los dos grupos mayores, con 5 y 4 especies respectivamente, así como el grupo incluyendo 5 pares de especies asociadas, representaban dos amplias agregaciones de ictioplancton en la zona explorada.

Especies de cada grupo aparecían juntas frecuentemente en las muestras de CalCOFI, presentando distribuciones similares, tanto en espacio como en época del año, apareciendo como partes constantes de ambos ambientes marinos. Sin embargo, tomando como base la información que existe sobre la distribución batimétrica de las especies, la mayor parte de los integrantes del grupo y las especies asociadas, habitaban al parecer diferentes profundidades en la columna de agua atravesada durante el arrastre de la red. Esto indica que, probablemente existen contactos limitados interespecíficos, por ejemplo, competición por alimento. Diferencias dentro del grupo en cuanto a la època de máxima abundancia y regiones de abundancia máxima, reducen también la probabilidad de tales interrelaciones. Las interacciones a nivel de fase larval pudieran resultar de valor directo insignificante, en cuanto al control de la abundancia de larvas y la distribución de estas especies. No obstante, se precisa obtener más información detallada sobre la distribución batimétrica de las especies para poder comprobar estas observaciones.

INTRODUCTION

The ichthyoplankton of the California Current system contains many disparate members, including the larvae of (1) demersal fishes that spawn on the continental shelf and slope, (2) mesopelagic species whose spawning distributions extend across the Pacific, (3) migratory species that feed in rich boreal and northern temperate waters but enter the area to spawn, (4) subarctic and temperate/tropical species whose spawning ranges extend into the northern and southern regions of the area, and (5) species whose distributions are limited to offshore California Current waters.

In addition to the broad geographic sources of the ichthyoplankton, there is a finer-scale structure to larval fish distribution, on the order of meters to tens of kilometers. Although population breadth prevents delimitation of many species, fine-scale structure may also obscure descriptions of coincidence and possible interaction among species. The fundamental CalCOFI sample is of an oblique column of water 800 m long and only a few meters wide from a depth of 210 m. Consequently, species occurring horizontally within several tens of meters of each other and which could be interacting may not be found in the same samples. Conversely, species coming from widely different depths and which may have minimal interaction may be found in the same integrated sample.

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There are sufficient differences in the biota at different water-column depths to minimize the problem of oblique integrated samples (Gruber et al. 1982). To overcome the problem of using small samples to represent wider, possibly more relevant community units, it is necessary to consider "recurrent groups" of species in many samples. Aggregation (patchiness) of larval fishes appears to be the rule rather than the exception (Loeb et al. 1983a). Thus it is necessary when forming useful recurrent groups to initially disregard the numbers of fishes and consider instead only species presence/absence in each sample. To do otherwise would grant the occasional coincidence of large numbers of two or more species greater importance than its frequency would warrant. Thus interrelationships among group species are not dominated by localized situations favoring the abundance of some or all members. Once groups are established based on significant frequency of co-occurence of all member species in samples, one may consider abundances of individual species. In doing this, one may categorize abundance relationships indicating predator-prey or no apparent interactions, and may explore aspects of concordance among member species as to optimal environmental conditions.

The study of definitive interactions between any two fish species or among any number of species can only be guided by the results of analysis we report here. The sampling grid is too large; the water volume filtered by each sample is too small; and the number of individuals of the proposed interacting species are too few to offer conclusive findings at this stage of analysis. It is the purpose of this paper, therefore, to explore an existing set of CalCOFI data sufficiently that future specific sampling and surveys may be conducted to delineate species interactions in recurrent groups and make substantive inferences about the nature of their interactions.

METHODS

The recurrent group analysis was based on larval fish species presence/absence data from 1,531 standard CalCOFI samples taken on seven cruises between December 1974 and November 1975 (Loeb et al. 1983a). Subsequent analyses of species abundance relations are based on pooled data representing 11 basic CalCOFI regions. Regional and seasonal sampling information is presented in Table 1. Samples were collected using a net of 1 m mouth diameter, fitted with 505-μm mesh, and fished obliquely to ~ 210 m (Kramer et al. 1972).

Recurrent groups analysis was per Fager (1957, 1963). In this analysis an index of affinity (*A*) is calculated between all possible species pairs. This index may range from 0.0 (species pair never caught together) to 1.0 (species pair co-occurred in every sample). It is difficult to assign probability levels to affinity values because the distribution of the affinity values is a function of both the number of occurrences of individual species and the frequency of co-occurrences of paired species. The investigator specifies a significant affinity level (*a*) to be used in developing groups: an *a* level near 1.0 represents a more stringent grouping criterion than does a lower value. A recurrent group is defined as a set of species each of which has a significant affinity level value (i.e., $A \geqslant a$) with every other member of the set. Each group species has affinity values with every nongroup species; some of those values may also be significant. Additionally, a member of one group can have significant affinity values with members of other groups. Selection of a "significant" affinity level is subjective; the subsequent grouping procedure is en-

TABLE 1
Regional Sampling Effort, 1975 CalCOFI Survey

		Cruise/month							
Area	Region	7412 Dec.	7501 Jan.	7503 Mar.	7505 May	7507 July	7510 Oct.	7511 Nov.	Total no. samples
Central	4	26	26	23	13	24	—	25	137
California	5	10	4	18	9	12	—	11	64
Southern	7	80	81	81	79	77	7	74	479
California	8	10	8	9	9	9	4	4	53
	9	18	18	16	18	18	—	14	102
	10	2	2	—	—	—	—	—	4
Northern	11	26	26	19	27	26	28	—	152
Baja	12	28	28	18	28	28	29	—	159
California	13	13	13	10	13	13	12	—	74
	14	4	12	4	12	15	15	—	62
Central	16	38	38	18	2	37	37	—	170
Baja	17	13	12	4	1	13	13	—	56
California	18	—	2	1	2	2	2	—	9

tirely objective. The criterion for selection of a significant affinity value is interpretability of results. In the present study an affinity value $a \geqslant 0.30$ was used; this is lower than used in many other studies (e.g., Fager and McGowan 1963, $a \geqslant 0.50$; McGowan and Walker 1979, $a \geqslant 0.50$; Venrick 1982, $a \geqslant 0.50$, $\geqslant 0.65$, and $\geqslant 0.80$) primarily because of the low numbers of larval fish taxa taken per sample (Loeb et al. 1983a) and the resulting low numbers of co-occurrences. Intergroup connections are reported as the fraction of possible significant affinities between group member species which actually occurred (i.e., the number of affinities $\geqslant a/MN$) where M is the number of species in one group and N is the number of species in a second group.

Seventy-eight species were included in the present analysis; higher taxonomic categories and rare species (captured in $\leqslant 5$ samples total) were excluded. We emphasize the largest groups determined and their associated groups; independently distributed species groups and individual group associate species receive only cursory attention. Groups are numbered according to intergroup affinities rather than according to the conventional size-dependent grouping order. Water-mass or hydrographic affiliations are assigned to many of the grouped species. These affiliations are based on the works of Ahlstrom (1965, 1969), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

Three nonparametric statistical tests—Kendall's concordance and tau tests, and rank difference correlation coefficients (Tate and Clelland 1957)—are used to examine regional and seasonal abundance relationships of the grouped species. Kendall's concordance test is a nonparametric analysis of variance used here to examine regional and seasonal abundance ranking across several data sets. The tau and rank difference tests each provide a correlation coefficient that measures the similarity between the order of species abundance rankings within two data sets.

Depth-vs-abundance information for many of the grouped species has been provided by Ahlstrom (1959). Differences between these reported species depth-vs-abundance distributions are tested here using Kolmogorov-Smirnov (K-S) tests (Conover 1971). These tests are based on the maximum differences between cumulative percent curves (here cumulative percent of each species total abundance vs depth curves) for two sets of data.

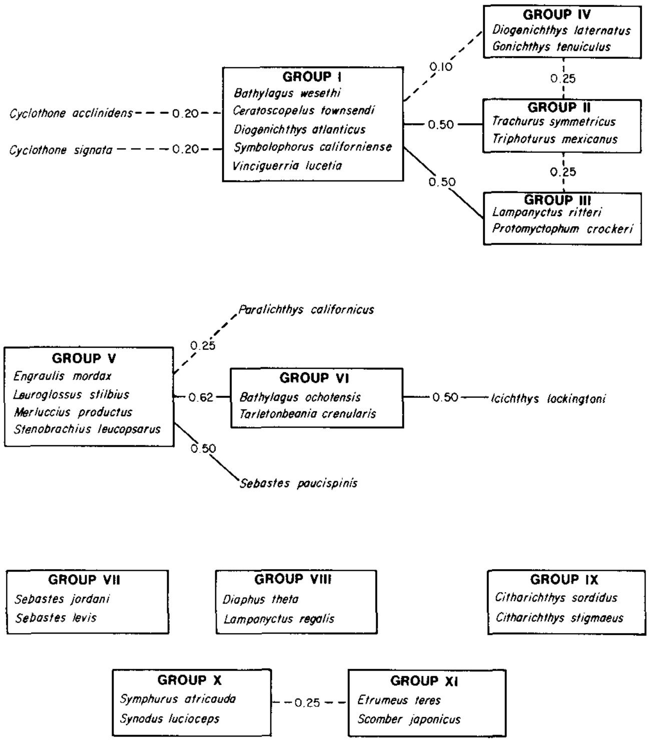

Figure 1. Composition and intergroup affinities of 11 recurrent groups of larval fish species, 1975 CalCOFI survey. Dashed lines denote nonsignificant (< 0.30) intergroup affinity values.

RESULTS

Species Groupings

Twenty-seven species formed 11 groups (Figure 1); these included one group of five species (Group I) with three associated species pairs (Groups II, III, and IV); one group of four species (Group V) with one associated species pair (Group VI); and five other species pairs (Groups VII, VIII, IX, X, and XI). Five individual species had affinities $\geqslant 0.30$ with group members. No other species had any affinities $\geqslant 0.30$. The grouped species and group associate species are presented along with their water-mass affiliations in Table 2; within- and between-group affinities are illustrated in Figures 2 and 3.

Group I consisted of five mesopelagic species of mixed hydrographic affiliations: one southern bathylagid; one eastern tropical Pacific gonostomatid; and one each warm-water cosmopolite, restricted California Current, and transition-zone myctophid (Table 2). The four species of Group V included one subarctic-transition zone myctophid, one California Current bathylagid, and the two dominant pelagic species—anchovy (*Engraulis mordax*) and hake (*Merluccius productus*). The nine other groups included three pairs of mesopelagic species (5 myctophids, 1 bathylagid) with northern, subarctic-transition zone, and restricted California Current affiliations (Groups III, VI, and VIII); a California Current myctophid and a pelagic species, jack mackerel (*Trachurus symmetricus*) (Group II); a pair of eastern tropical Pacific myctophids (Group IV); a pair of northern rockfishes (VII); a pair of

TABLE 2
Species Composition of Recurrent Groups and the Water Mass or Habitat Affiliations of Member Species

Group no.	Species name	Affiliation	Group associate species	Affiliation
I	*Diogenichthys atlanticus*	C		
	Bathylagus wesethi	S		
	Symbolophorus californiense	T		
	Vinciguerria lucetia	ETP	*Cyclothone acclinidens*	S
	Ceratoscopelus townsendi	CA	*Cyclothone signata*	S
II	*Triphoturus mexicanus*	CA		
	Trachurus symmetricus	PL		
III	*Protomyctophum crockeri*	CA		
	Lampanyctus ritteri	S-T		
IV	*Diogenichthys laternatus*	ETP		
	Gonichthys tenuiculus	ETP		
V	*Leuroglossus stilbius*	N	*Sebastes paucispinis*	N
	Stenobrachius leucopsarus	S-T		
	Engraulis mordax	PL	*Paralichthys californicus*	M
	Merluccius productus	PL		
VI	*Tarletonbeania crenularis*	S-T	*Icichthys lockingtoni*	M
	Bathylagus ochotensis	N		
VII	*Sebastes jordani*	N		
	S. levis	N		
VIII	*Lampanyctus regalis*	S-T		
	Diaphus theta	S-T		
IX	*Citharichthys sordidus*	N		
	C. stigmaeus	N		
X	*Symphurus atricauda*	M		
	Synodus lucioceps	M		
XI	*Etrumeus teres*	M		
	Scomber japonicus	M		

S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern or cold water; S, southern or warm water; CA, restricted California Current; PL, pelagic; M, multiple affiliations. Affiliations based on Ahlstrom (1965), Moser and Ahlstrom (1970), Moser et al. (1977), and Paxton (1967).

northern flatfishes (IX); and two pairs of the comparatively rare larvae of southern coastal and pelagic species (X and XI) (Table 2).

The two largest groups (I and V) had connections with several of the smaller groups (Figure 1). Some of the Group I species had high affinities with members of Groups II and III. Three other mesopelagic species (two individual group associate species and one species from Group IV) each had affinities > 0.30 with one of the Group I species (Figure 1). Group II was also weakly associated (one of four possible significant affinities) with both Groups III and IV. Some of the four Group V member species had high affinities with both Group VI species. One and two of the Group V species were also associated with one flatfish and one rockfish species, respectively. Group VI also had a single-species associate. Only two of the five other species pairs had intergroup affiliations; these were weakly associated (intergroup connection = 0.25) Groups X and XI.

Within Group I, affinity levels ranged from 0.323 to 0.478; highest values (0.439-0.478) occurred between *Diogenichthys atlanticus, Symbolophorus califor-*

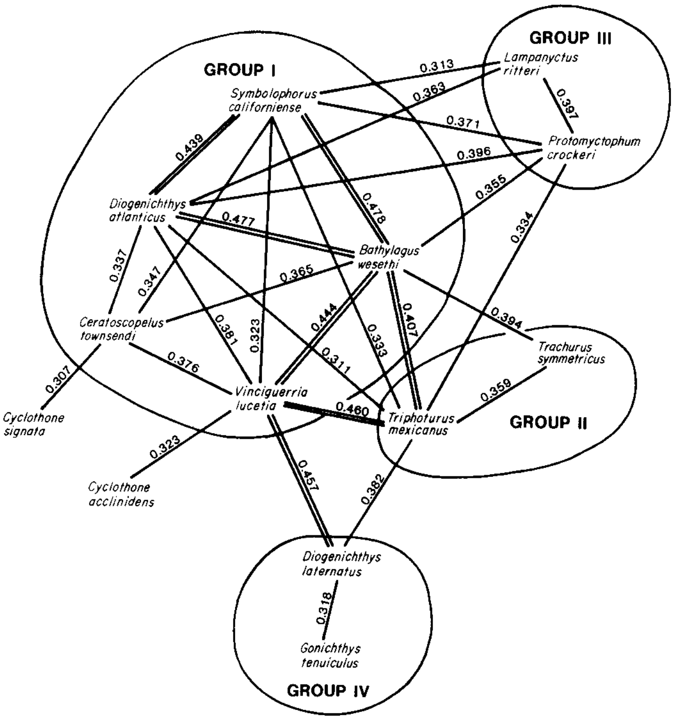

Figure 2. Within- and between-group species affinity values for recurrent Group I and associated Groups II, III, and IV, CalCOFI survey, 1975. Double lines denote species affinity values 0.40-0.49; single lines, affinity values 0.30-0.39.

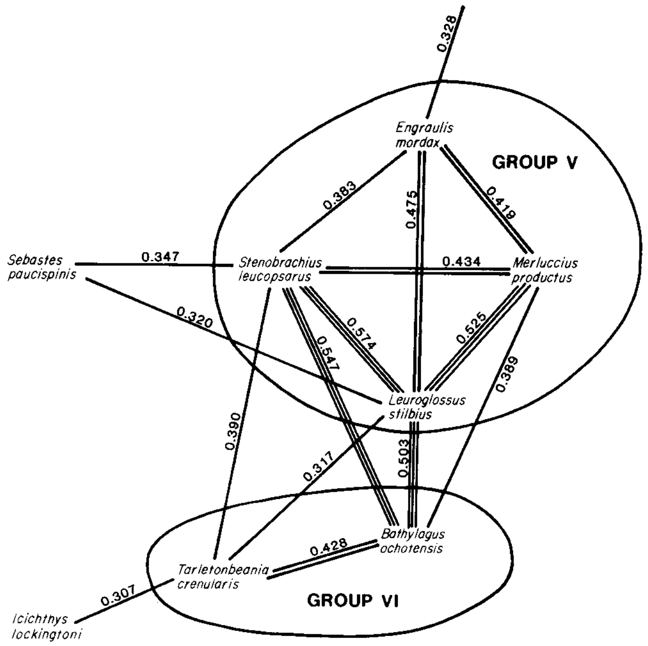

Figure 3. Within- and between-group species affinity values for recurrent Group V and associated Group VI, CalCOFI survey, 1975. Triple lines denote species affinity values ≥ 0.50; double lines, affinity values 0.40-0.49; single lines, affinity values 0.30-0.39.

niense, and *Bathylagus wesethi* and between *Bathylagus wesethi* and *Vinciguerria lucetia* (Figure 2). These four species all had affinities > 0.30 with *Triphoturus mexicanus* of Group II; three of the four (*D. atlanticus, S. californiense*, and *B. wesethi*) also had significant affinities (0.313-0.396) with *Lampanyctus ritteri* and/or *Protomyctophum crockeri* of Group III. Additionally, *V. lucetia* had a high affinity (0.457) with Group IV species *Diogenichthys laternatus*. The fifth Group I species, *Ceratoscopelus townsendi*, had relatively low affinities (0.337-0.376) with the other member species, and affinities < 0.30 with members of the three associated groups. Group II species *T. mexicanus*, in addition to its associations with Group I members, also had significant affinities with *D. laternatus* (Group IV) and *P. crockeri* (Group III).

The affinity values between the four Group V species (0.383-0.574) were generally higher than between the Group I species (Figure 3). Highest values occurred between *Leuroglossus stilbius* and hake (*Merluccius productus*) (0.525) and between *L. stilbius* and *Stenobrachius leucopsarus* (0.574). *Leuroglossus stilbius* and *S. leucopsarus* also had high affinity values with Group VI species *Bathylagus ochotensis* (0.503-0.547) and *Tarletonbeania crenularis* (0.317-0.390); hake had an affinity > 0.30 only with *B. ochotensis*, and anchovy (*Engraulis mordax*) had affinities < 0.30 with both species. Both *S. leucopsarus* and *L. stilbius* were also associated with *Sebastes paucispinis*.

Group Distribution and Abundance Relationships

The five Group I species were widely distributed within the CalCOFI area; each was captured in all regions except 4 and 7 (inshore central and southern California) and during all cruises. Co-occurrence in samples by all five species was restricted, however, to offshore and seaward regions 9, 13, and 14 of southern California and northern Baja California; four of the five species also co-occurred in samples within offshore central California and central Baja California regions 5 and 17 (Figure 4). Highest frequencies of co-occurrence were in northern Baja California seaward region 14, where the five species were caught together in 17.7% of all samples; four of five species were caught together in an additional 30.6% of the samples within this region (Table 3). Members of Group I had abundance peaks in the same regions (Kendall's concordance, $P < 0.01$). The regions of maximum abundance (9, 13, and 14) were those of maximum frequency of occurrence of the individual species (rank difference correlation coefficient = 0.85-0.95; $P < 0.01$ in all cases) and of maximum frequency of co-occurrence of the five species (Tables 3, 4). Within regions 9, 13, and 14 there was significant agreement of species rank order of abundance throughout the year (i.e., similar species rankings across all cruises within each region; Kendall's concordance, $P < 0.05$). However, species rankings differed between regions (Table 5), and there was no overall agreement of regional rank order of abundance (Ken-

TABLE 3
Regional Distribution of Six Main Recurrent Groups of Larval Fish Species Based on Frequency of Co-occurrence in Samples by Group Member Species

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
5 spp	—	—	—	—	2.0%	—	—	4.0%	17.7%	—	—
					(3)			(2)	(1)		
4/5 spp	—	1.6%	—	—	7.8%	—	—	6.8%	30.6%	—	1.8%
	—	(5)	—	—	(2)	—	—	(3)	(1)	—	(4)
Group II											
2 spp	—	—	0.2%	3.8%	5.9%	11.2%	0.6%	25.7%	40.3%	2.4%	5.4%
	—	—	(9)	(6)	(4)	(3)	(8)	(2)	(1)	(7)	(5)
Group III											
2 spp	1.5%	10.9%	0.8%	11.3%	25.5%	7.9%	3.8%	17.6%	32.2%	0.6%	—
	(8)	(5)	(9)	(4)	(2)	(6)	(7)	(3)	(1)	(10)	—
Group IV											
2 spp	—	—	—	—	—	0.6%	—	—	—	2.4%	23.2%
	—	—	—	—	—	(3)	—	—	—	(2)	(1)
Group V											
4 spp	2.9%	0.2%	13.4%	13.2%	9.8%	2.6%	—	—	1.6%	—	—
	(4)	(7)	(1)	(2)	(3)	(5)	—	—	(6)	—	—
Group VI											
2 spp	24.8%	35.9%	2.5%	17.0%	28.4%	—	—	—	—	—	—
	(3)	(1)	(5)	(4)	(2)	—	—	—	—	—	—

Frequency of co-occurrence presented as the percentage of all samples taken within each CalCOFI region containing all member species. For Group I frequency of co-occurrence is also provided for 4 of the 5 member species. Regional values are ranked for each group (in parentheses).

TABLE 4
CalCOFI Regions Ranked by Abundance for Member Species of Six Main Recurrent Groups of Larval Fish Species

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
Bathylagus wesethi	—	9	10	4	3	7	8	2	1	6	5
Ceratoscopelus townsendi	—	8	9	4	3	7	10	2	1	5	6
Diogenichthys atlanticus	11	5	10	8	2	7	6	3	1	9	4
Symbolophorus californiense	—	6	10	5	2	4	7	3	1	9	8
Vinciguerria lucetia	—	9	—	8	7	5	6	3	1	4	2
Group II											
Trachurus symmetricus	—	9	10	3	4	6	8	2	1	7	5
Triphoturus mexicanus	—	—	9	7	8	5	6	3	1	4	2
Group III											
Lampanyctus ritteri	9	6	10	5	3	2	7	4	1	11	8
Protomyctophum crockeri	7	5	9	3	4	6	8	2	1	11	10
Group IV											
Diogenichthys laternatus	—	—	7	—	—	6	4	5	3	2	1
Gonichthys tenuiculus	—	—	—	—	—	—	4	3	—	2	1
Group V											
Engraulis mordax	10	11	4	1	8	3	2	6	9	5	7
Leuroglossus stilbius	3	6	1	2	5	4	9	8	10	7	11
Merluccius productus	8	9	6	2	1	3	7	4	5	10	11
Stenobrachius leucopsarus	1	2	3	5	4	7	—	—	6	8	—
Group VI											
Bathylagus ochotensis	1	2	5	3	4	7	9	6	8	—	—
Tarletonbeania crenularis	1	2	5	3	4	7	—	—	6	—	—

Regional abundance estimates (mean abundances, pooled cruises) from Loeb et al. (1983b).

TABLE 5
Relative Abundances of Group Member Species Within Regions of Species Co-occurrence in Samples, for Six Main Recurrent Groups of Larval Fish

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
Bathylagus wesethi	—	3	—	—	1	—	—	2	2	—	2
Ceratoscopelus townsendi	—	4	—	—	4	—	—	5	5	—	4
Diogenichthys atlanticus	—	1	—	—	2	—	—	3	3	—	3
Symbolophorus californiense	—	2	—	—	3	—	—	4	4	—	5
Vinciguerria lucetia	—	5	—	—	5	—	—	1	1	—	1
Group II											
Trachurus symmetricus	—	—	2	1	1	2	2	2	1	2	2
Triphoturus mexicanus	—	—	1	2	2	1	1	1	2	1	1
Group III											
Lampanyctus ritteri	2	2	2	2	2	2	2	2	2	2	—
Protomyctophum crockeri	1	1	1	1	1	1	1	1	1	1	—
Group IV											
Diogenichthys laternatus	—	—	—	—	—	—	1	—	—	1	1
Gonichthys tenuiculus	—	—	—	—	—	—	2	—	—	2	2
Group V											
Engraulis mordax	4	4	1	1	2	1	—	—	2	—	—
Leuroglossus stilbius	2	2	2	3	4	3	—	—	4	—	—
Merluccius productus	3	3	3	2	1	2	—	—	1	—	—
Stenobrachius leucopsarus	1	1	4	4	3	4	—	—	3	—	—
Group VI											
Bathylagus ochotensis	1	1	1	1	1	—	—	—	—	—	—
Tarletonbeania crenularis	2	2	2	2	2	—	—	—	—	—	—

Ranked abundances based on pooled samples (all cruises) within each region (from Loeb et al. 1983b).

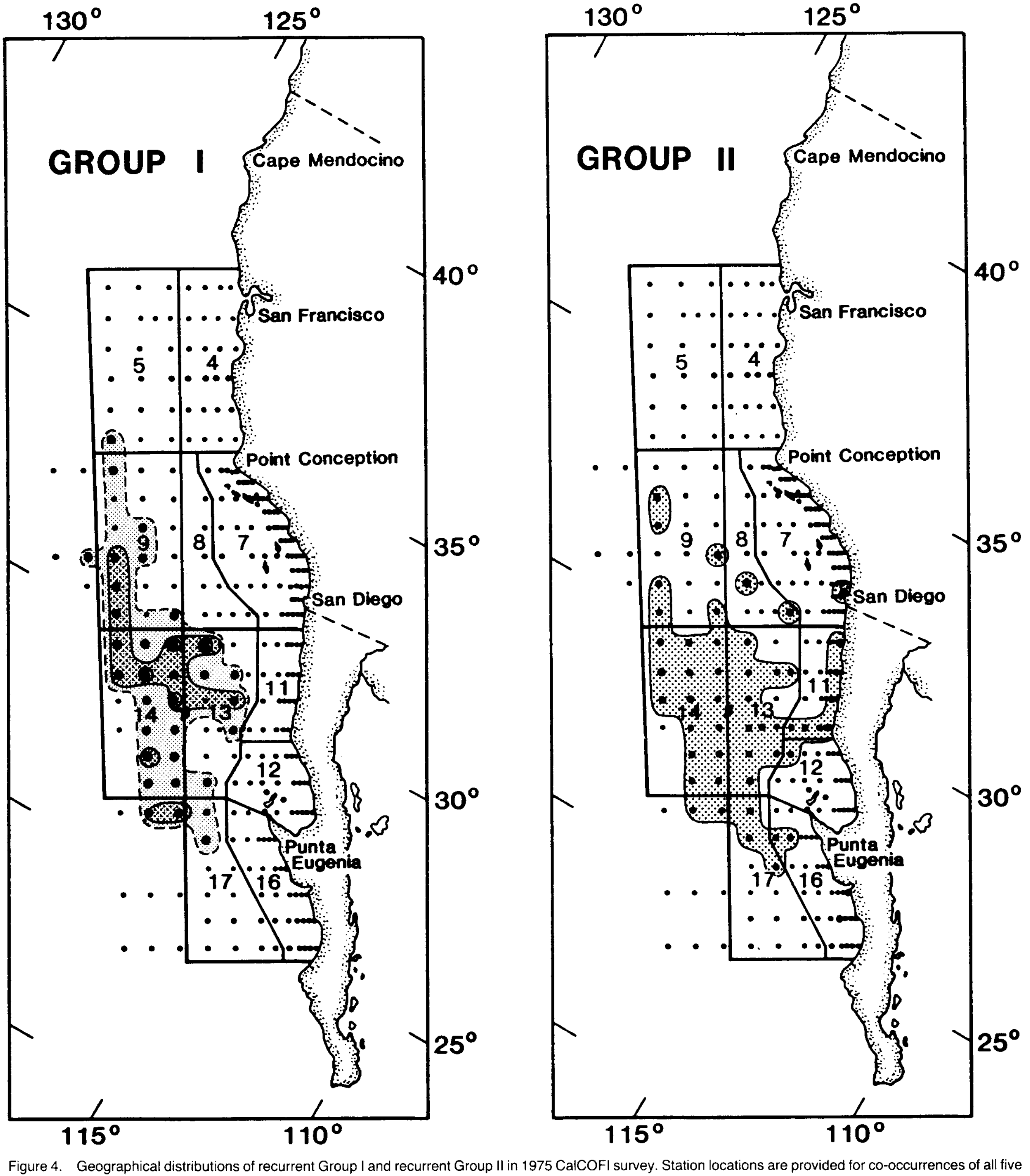

Figure 4. Geographical distributions of recurrent Group I and recurrent Group II in 1975 CalCOFI survey. Station locations are provided for co-occurrences of all five (dark stippling) and four of five (light stippling) Group I species and for both Group II species.

dall's concordance, $P < 0.05$). This is directly due to *Vinciguerria lucetia*'s dominance in southern regions 13, 14, and 17 and its rarity in northern regions 5 and 9; significant agreement of rank order of abundance ($P < 0.01$) exists among the four other species. There was no agreement on season of maximum abundance among the member species (Kendall's concordance, $P > 0.05$). *Diogenichthys atlanticus, Bathylagus*

TABLE 6
Cruises Ranked According to Abundances of Member Species of Six Main Recurrent Groups of Larval Fish Species

	Cruise					
	7412	7501	7503	7505	7507	7510
Group I						
Bathylagus wesethi	6	5	1	3	2	4
Ceratoscopelus townsendi	5	4	3	6	2	1
Diogenichthys atlanticus	3	2	1	5	6	4
Symbolophorus californiense	6	3	1	4	2	5
Vinciguerria lucetia	3	4	6	5	1	2
Group II						
Trachurus symmetricus	6	5	1	3	2	4
Triphoturus mexicanus	6	5	4	2	1	3
Group III						
Lampanyctus ritteri	5	1	2	4	3	6
Protomyctophum crockeri	3	1	2	4	5	6
Group IV						
Diogenichthys laternatus	4	3	1	6	2	5
Gonichthys tenuiculus	1	3	5.5	5.5	2	4
Group V						
Engraulis mordax	4	1	2	3	6	5
Leuroglossus stilbius	3	1	2	4	5	6
Merluccius productus	4	1	2	3	5	6
Stenobrachius leucopsarus	4	2	1	3	5	6
Group VI						
Bathylagus ochotensis	4	1	2	3	5	6
Tarletonbeania crenularis	6	5	4	2	3	1

Ranks based on cruise abundance estimates (pooled regions) presented in Loeb et al. (1983b).

wesethi, and *Symbolophorus californiense* had March abundance peaks; *Vinciguerria lucetia* and *Ceratoscopelus townsendi* were most abundant in July and October (Table 6).

The Group III member species (*Protomyctophum crockeri* and *Lampanyctus ritteri*) co-occurred throughout the CalCOFI area (Figure 5; Table 3), but their association throughout the year (all 6 cruises) was limited to offshore and seaward southern California and northern Baja California regions 9, 13, and 14. Maximum frequencies of co-occurrence were in northern Baja California region 14 (32% of all samples) and southern California region 9 (25% of all samples) (Table 3). The two species had significant concordance of abundance across regions (Kendall's tau test, $P < 0.01$), and both were most abundant in region 14 (Table 4). Both species had January-March abundance peaks (Table 6). In most regions and cruises *P. crockeri* was more abundant than *L. ritteri* (Table 5).

Group II species (*Trachurus symmetricus* and *Triphoturus mexicanus*) had a more restricted geographical and seasonal distribution than did Group III. There were few co-occurrences of the two species north of Baja California (Figure 4; Table 3); *T. symmetricus* was absent from December samples and was very rare in January samples (Table 6). The two species co-occurred most frequently from March to July in northern Baja California regions 11, 13, and 14 (Table 3), with maximum co-occurrences in seaward region 14 during April (83% of all samples) and July (93% of samples). They showed significant agreement as to regions of maximum abundance (13 and 14; Kendall's tau, $P < 0.01$). Peak abundances of *T. symmetricus* were in March, of *T. mexicanus*, in July (Table 6). Their relative abundances varied with region (Table 5) and cruise.

Group IV (*Diogenichthys laternatus* and *Gonichthys tenuiculus*) was the most geographically restricted group (Figure 5; Table 3). Co-occurrence was limited to southern regions, primarily central Baja California regions 16 and 17. Maximum frequency of co-occurrence and maximum abundances of both species were in region 17 during December and July; these maxima may be artifacts caused by undersampling of regions 16 and 17 during March and May (Table 1). *Diogenichthys laternatus* was consistently more abundant than *G. tenuiculus* (Table 5).

Co-occurrence of all four Group V species was primarily within the regions of central and southern California (Figure 6) and was limited to winter and spring. Highest frequencies of co-occurrence were within southern California regions 7, 8, and 9 during January and March, when all four species were captured together in from 25%-56% of the samples. The four species had different regions of maximum abundance and of frequency of occurrence (Kendall's concordance, $P > 0.05$ in both cases). *Engraulis mordax* (anchovy) was most abundant and frequent in offshore southern California region 8 and inshore northern Baja California regions 11 and 12; *Merluccius productus* (hake) in southern California offshore and seaward regions 8 and 9; *Stenobrachius leucopsarus* in southern California inshore and offshore regions 7 and 8; and *Leuroglossus stilbius* in central California inshore and offshore regions 4 and 5 (Table 4). Although species rank order of abundances within each region were somewhat consistent between cruises, there was no overall between-region agreement (Kendall's concordance, $P > 0.05$; Table 5). All four species had abundance peaks during January-March, and minimum abundances in July and October/November (Kendall's concordance, $P < 0.01$; Table 6).

Group VI was distributed within the five regions of central and southern California (Figure 6). In contrast to associated Group V, the member species of Group VI co-occurred throughout the year in their regions of maximum abundance (4, 5, and 8) (Table 4). *Bathylagus ochotensis* was overall the more abundant species (Table 5), but because of differing periods of peak abundance (Table 5; January-March for *B. ochotensis*, July-November for *Tarletonbeania crenularis*), species abundance relations within regions changed seasonally.

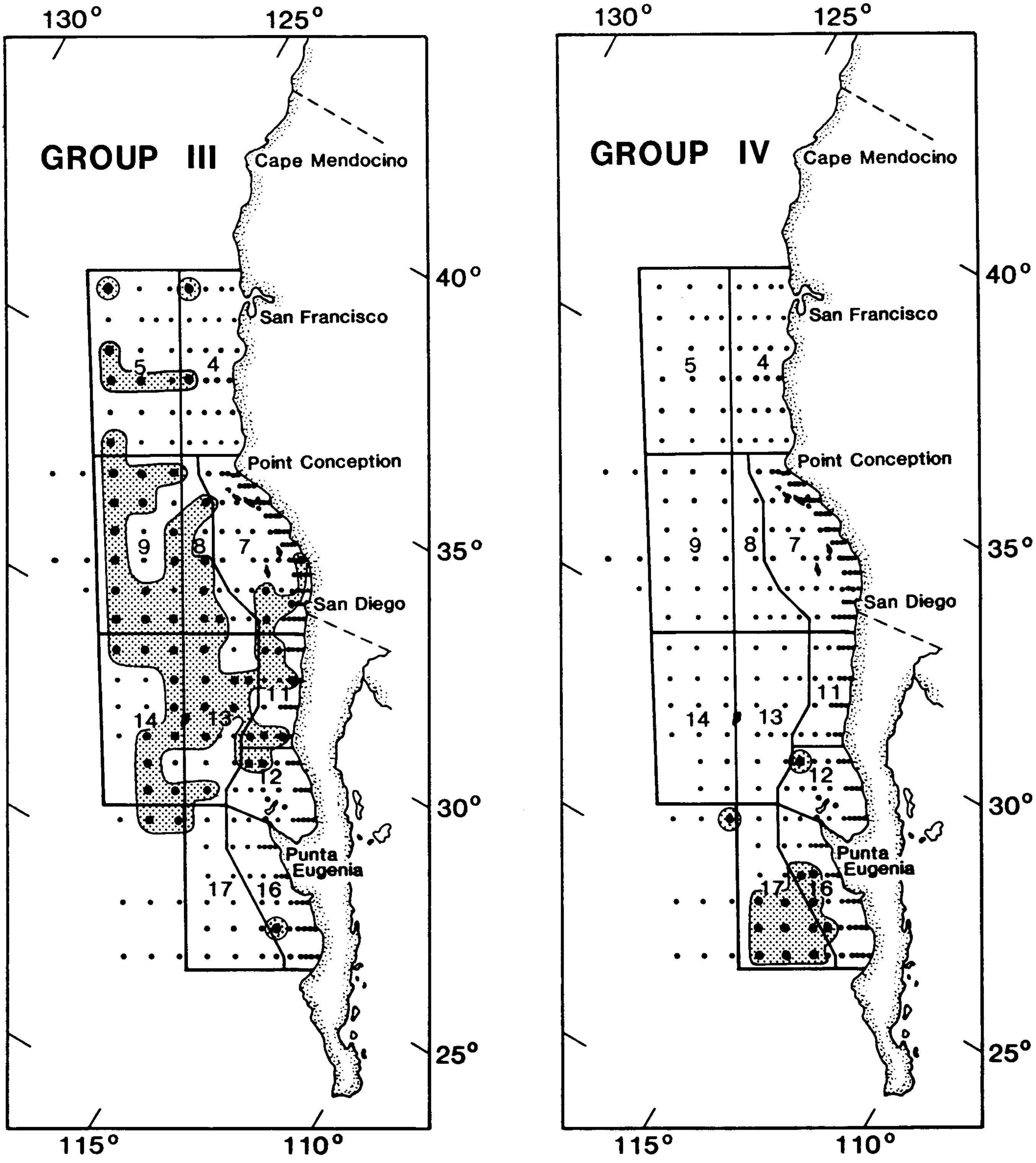

Figure 5. Geographical distributions of recurrent Group III and recurrent Group IV in 1975 CalCOFI survey. Station locations are provided for co-occurrences of both Group III species and both Group IV species.

DISCUSSION

The species forming the major groups (I and V) and their associated groups (II, III, IV, and VI) were the more abundant and widespread species in the CalCOFI area (Loeb et al. 1983b). The species composition of Groups I and V and their associated groups is in general agreement with the two subjectively determined species assemblages described in Loeb et al. 1983b

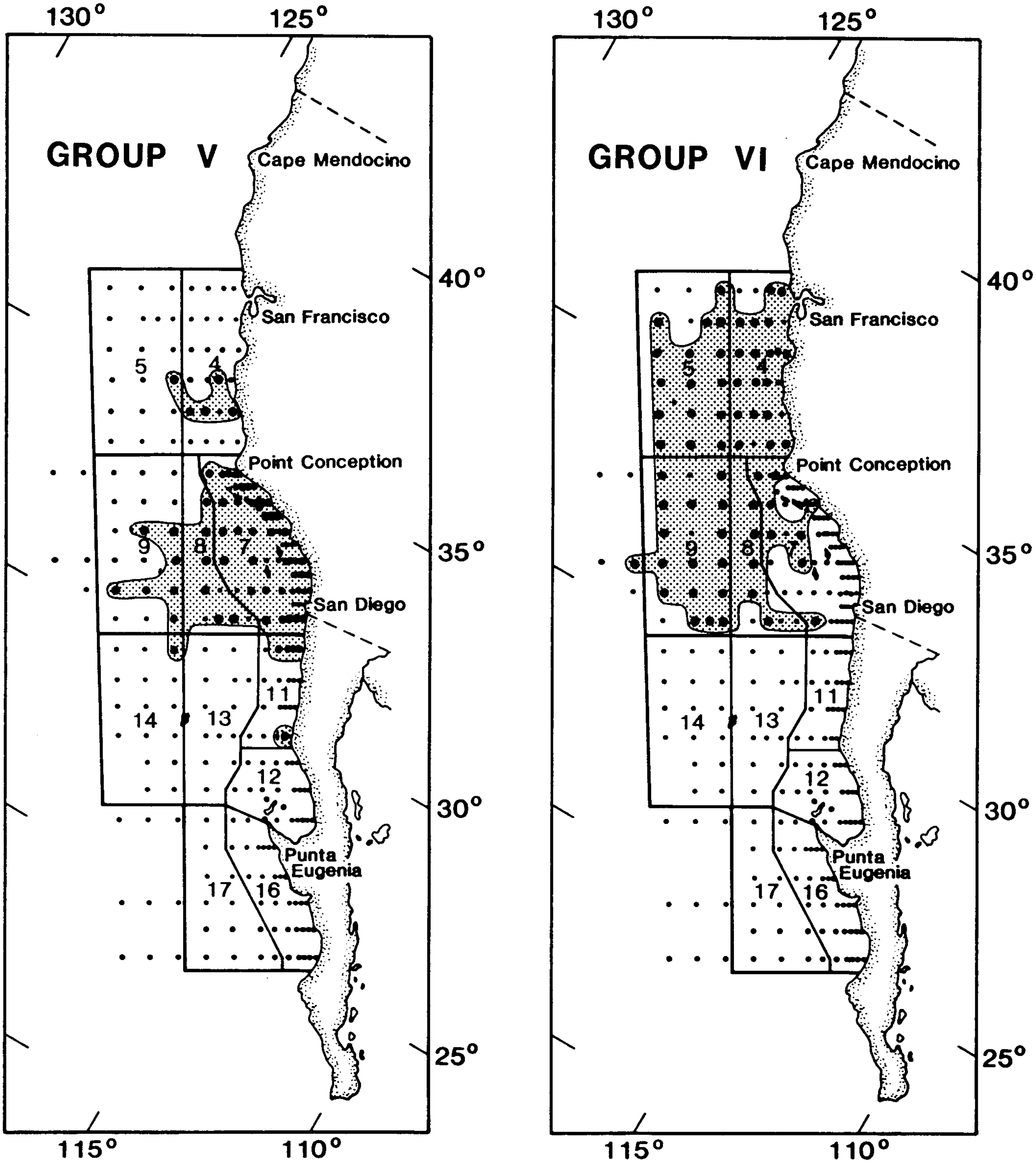

Figure 6. Geographical distributions of recurrent Group V and recurrent Group VI in 1975 CalCOFI survey. Station locations are provided for co-occurrences of all four Group V species and both Group VI species.

(i.e., species with mixed but predominantly warm-water affiliations and highest abundances in northern and central Baja California areas, and species with subarctic-transition zone or northern cold-water affiliations and highest abundances in central and southern California areas). This is probably due to the fact that in all cases the frequency of occurrence of group member species was significantly correlated with their abundance (rank difference correlation coefficients = 0.72-0.96; $P \leq 0.05$ in all cases). However, the objectively formed species groups (based on frequency of co-occurrence rather than on agreement of mean regional abundances) had more restricted geographical distributions (Figures 4-6) than did the subjectively determined assemblages. Group I and associated Group II and III members (predominantly warm-water mesopelagic species) were most frequent in the offshore and seaward regions of southern California and northern Baja California; associated Group IV species (eastern tropical Pacific forms) were restricted to central Baja California regions. Group V (anchovy, hake, and cold-water mesopelagic species) co-occurred most frequently in the southern California regions, and is quite similar to Southern California Bight Group I reported by Gruber et al. (1982); associated Group VI (cold-water mesopelagic species) was most frequent in the regions of central California and the offshore region of southern California.

The groups differed in constancy of species rank order of abundance. Although the members of Group III had widespread distributions, they had similar species rank order of abundance within their regions of maximum frequency of occurrence and between all regions within their distributional range. Group VI was less widely distributed, but also demonstrated between-region constancy. In contrast, Groups I and V had within-region similarity of species rank order of abundance across cruises but had significant between-region differences; Group II had significant differences in species abundance relations both within and between regions. The variability of rank order of abundance within Groups II and V may be related to seasonal and geographical differences in abundances of pelagic schooling species (anchovy and hake in Group V; jack mackerel in Group II). Marked between- and within-region differences in the relative abundances of the two Group V mesopelagic species, however, indicates that variability within this group was not restricted to the pelagic species. Group V variability may be partially due to greater heterogeneity and range of environmental conditions (i.e., coastal vs offshore differences) within the group's range. The geographical variability of rank order of abundance of Group I is primarily due to the northern distributional limit of one member species (*Vinciguerria lucetia*); the other four species have relatively constant abundance relations.

Environments of the Recurrent Groups

Recurrent group analysis identifies groups of species, based on co-occurrence in samples, which are likely to be frequent parts of one another's environment. Groups might then be investigated with respect to interspecific relationships of possible importance in controlling the distribution and abundances of the component species. Interspecific relations such as competition for limited food resources may be extremely important in the survival of larval fishes and their ultimate recruitment to adult populations. The groups identified here were based on geographical and seasonal co-occurrence. Because the data were derived from open oblique plankton tows in the upper ~ 200 m, we do not know if the group member larvae were in fact frequent parts of one another's immediate environments or were separated either vertically or horizontally. Larval depth vs abundance distributions of some of the species of the six major groups are available (Ahlstrom 1959), and are presented here as cumulative percent vs depth curves.

The curves for 8 of the 11 species of Group I and associated Groups II, III, and IV (Figure 7A) and for 5 of the 6 species of Group V and associated Group VI (Figure 7B) show a wide variety of depth-abundance distributions. Within Group I, two species (*D. atlanticus* and *S. californiense*) had similar distributions (K-S test, $P > 0.05$); most of these larvae occurred below those of *V. lucetia* and above those of *B. wesethi* ($P < 0.01$ in all four curve comparisons). The depth vs abundance distributions of the two Group II species also differed significantly ($P < 0.01$); most of the *T. symmetricus* larvae occurred above the *T. mexicanus* larvae. Additionally, only four of the total 21 intergroup comparisons showed similar species distributions. *Trachurus symmetricus* (Group II) had the shallowest distribution of the eight species considered (Figure 7A); this distribution resembled only that of *V. lucetia* (Group I) ($P > 0.05$). The distributions of *T. mexicanus* (Group II) and *L. ritteri* (Group III) were also relatively shallow and similar to each other and to *V. lucetia* (Group I) ($P > 0.05$ in all cases), but significantly different from those of the other four species. The species with deepest distributions—*D. laternatus* (Group IV) and *B. wesethi* (Group I)—were significantly different from each other and from all other species in the Group I and associated group assemblage ($P < 0.01$ in all cases).

The vertical distributions of the four Group V species (Figure 7B) differed significantly ($P < 0.05$). Associated Group VI species *T. crenularis* had a relatively shallow distribution similar to that of Group V species *S. leucopsarus* ($P > 0.05$); most *T. crenularis* larvae were significantly deeper than those of *E. mordax* (anchovy; $P < 0.01$) and shallower than those of *M. productus* (hake) and *L. stilbius* ($P < 0.01$).

It appears likely that although group members were frequently collected within the same locales and seasons they were probably not constant members of each

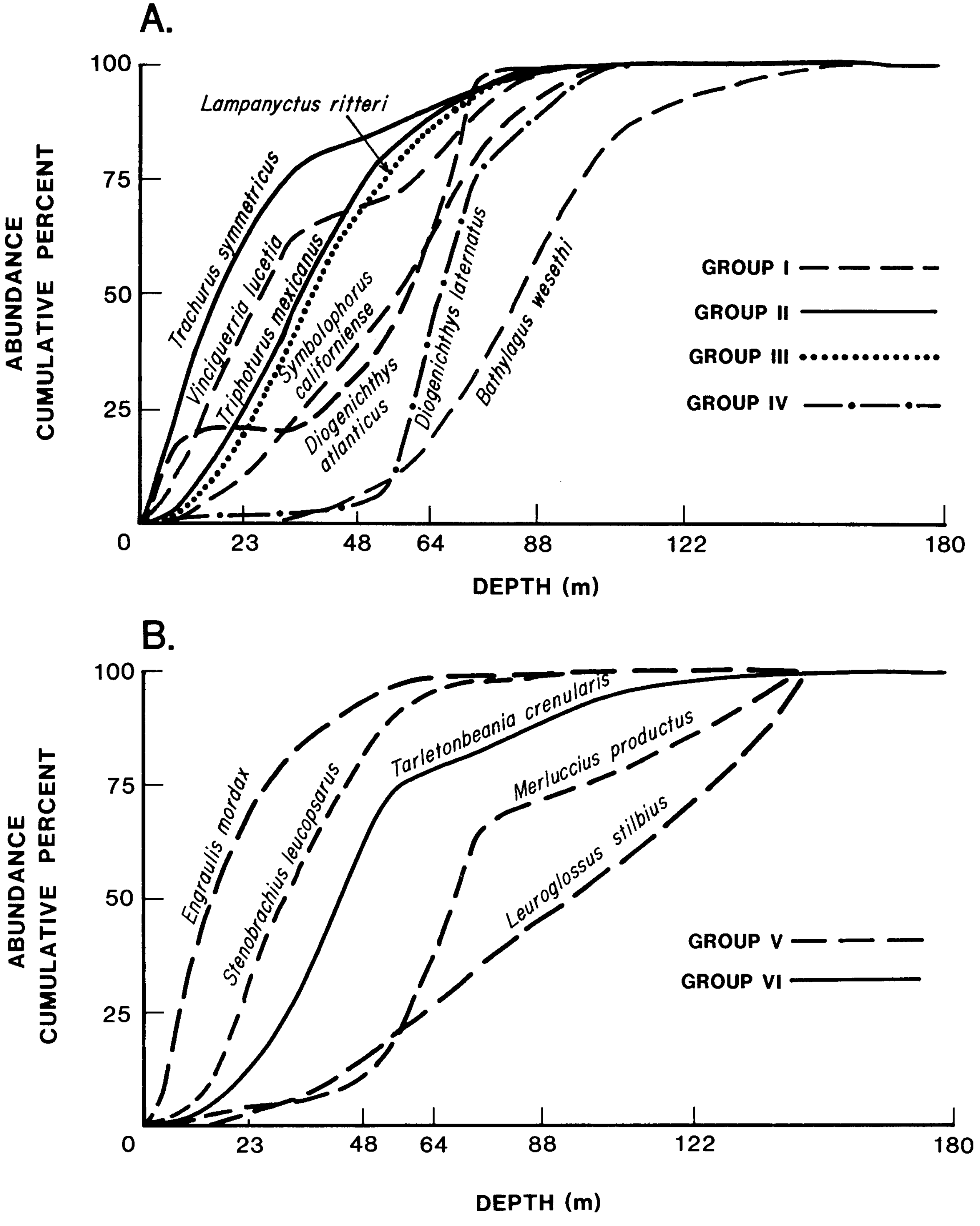

Figure 7. Cumulative percent curves of larval fish species abundance vs depth for (*A*) four Group I species and four species from associated Groups II, III, and IV; and (*B*) four Group V species and one associated Group VI species. Vertical abundance distributions from Ahlstrom (1959).

other's immediate environment (except for *D. atlanticus* and *S. californiense* of Group I) because of significantly different depth distributions. Also the group member species generally were not frequent parts of the immediate environments of species from associated groups.

In addition to vertical separation, there were seasonal abundance differences to further reduce the potential impact of interspecific relations within a group. The periods of peak abundances of two of the five Group I species differed from the others; peak abundance periods of both species within the Group II, IV, and VI species pairs differed significantly from each other; and timing of peak abundance of one of the four Group V species differed from the rest. Within Group V, the regions of maximum abundance of the member species differed, thereby further reducing the potential for interspecies impacts.

Because of within-group differences of seasonal, vertical, and (for Group V) geographical distributions, it is probable that, within each group, ecologically important interactions such as direct competition for limited food resources are minimal. This indicates that (based on the present data) within the CalCOFI area such interspecific processes during the larval stages are likely to be negligible in controlling fish species abundances and distributions. However, more detailed vertical distribution information is definitely needed to verify this observation.

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YEAR-TO-YEAR FLUCTUATIONS OF THE CALIFORNIA COUNTERCURRENT AND EFFECTS ON MARINE ORGANISMS

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ABSTRACT

Interannual fluctuations of alongshore currents off California can be inferred from fluctuations of dynamic height at a nearshore, deepwater station in Monterey Bay (station H-3) and from sea level at coastal tide gages. Hydrographic data for the period 1969 to 1978 at station H-3 show anomalous depressions of the 8° to 12°C isotherms by as much as 100 m during some years. The depressions are associated with anomalous elevations of dynamic height and sea level, and appear to occur in a double wave, one in summer and a second the following fall or winter. The anomalous depressions are apparently caused by two processes: (1) a remote forcing caused by propagation of coastal trapped waves poleward from El Niño conditions in the tropics and (2) a local forcing caused by anomalously strong onshore Ekman transport.

By geostrophy, anomalous elevations of the sea surface along the coast are associated with anomalous increases in northward alongshore currents. These increases in northward flow have a variety of effects on marine organisms, including range extensions of plankton and anomalous shifts of salmon's migration routes.

RESUMEN

Las fluctuaciones anuales en las corrientes costeras de California pueden determinarse mediante los datos obtenidos de varias fuentes; la elevación dinámica cerca de la costa, información obtenida en la estación localizada en aguas profundas de la Bahía de Monterey (Estación H-3), y los mareógrafos costeros. Los datos hidrográficos correspondientes al período de 1969 a 1978 en la Estación H-3 indican que durante algunos años se produce un descenso de las isotermas de 8° y de 12°C hasta los 100 m. de profundidad. Estos descensos están asociados con elevaciones dinámicas anómalas y del nivel del mar, presentándose una ondulación doble, una onda para el verano y otra a continuación en otoño o invierno. Estos descensos anómalos son aparentemente el resultado de dos procesos, uno local, ocasionado por el transporte Ekman, fuerte y anómalo hacia la costa, y otro con la acción alejada de esta región y en relación con el fenómeno del Niño en el trópico, produciendo la propagación hacia el polo de las olas atrapadas en la zona costera.

Elevaciones geostróficas anómalas de la superficie del mar a lo largo de la costa, están asociadas con incrementos también anómalos en la progresión de las corrientes costeras hacia el norte. Estos aumentos en el flujo hacia el norte ocasionan diversos efectos en los organismos marinos, incluyendo la amplitud de distribución del plancton y cambios en las rutas migratorias del salmón.

INTRODUCTION

The major alongshore currents of the California coast are normally described as an offshore, southward flow—the California Current—and a nearshore, northward flow—the California Countercurrent. Similar coastal currents and countercurrents are found in other eastern boundary current regions such as off the west coasts of South America, northwest Africa, and southwest Africa. The nearshore current flows northward from Baja California throughout the year (Wooster and Reid 1963; Wickham 1975) to Vancouver Island (Ingraham 1967; Reed and Halpern 1976). In fall and winter, the countercurrent is strong and reaches to the surface, inshore of the California Current; the flow is then called the Davidson Current (Hickey 1979). During the summer, persistent northwesterly winds occur along the California coast and blow the surface water southward, covering the countercurrent, which remains as an undercurrent at depths of 200 to 500 m (Chelton 1982). The area influenced by the countercurrent extends up to 500 km offshore from the California coast at depths below 200 m and has been described as the California Undercurrent Domain because of its broad seaward extent under the California Current (Dodimead et al. 1963; Favorite et al. 1976).

This paper describes an index of low-frequency variations of the countercurrent, based on a 10-year time series of frequent hydrographic observations and calculations of dynamic height anomalies at a deep station in Monterey Bay, California. Sea-level, ship-of-opportunity XBT, and surface-drifter data are compared with the index for agreement with the hypothe-

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sized variations of flow of the countercurrent. Available biological data are examined for consistency with the flow index.

The fluctuations of the alongshore currents off California are as yet poorly understood but appear to have an important role in changes in distribution and abundance of a variety of marine species. Not only are the changes in currents themselves important in changing the distribution of pelagic organisms, but associated changes in the depth of the density structure may also be significantly related to changes in concentrations of dissolved nutrients and biological productivity. The intensity of upward transport of nutrients from below the thermocline by wind mixing changes markedly with changes in thermocline depth. Bernal (1981) and Chelton (1981) found that long-period variations of zooplankton in the California Current are correlated with fluctuations of temperature in the eastern tropical Pacific. They suggested that zooplankton variations may be related to variations of nutrients advected from the north by the California Current, combined with a reduction of upwelling of nutrients caused by increased thermocline depth. The occurrence off California of organisms of southern origin is also related to increases in water temperature that appear to be associated with increases in the transport of coastal countercurrents (Radovich 1961).

MONTEREY BAY HYDROGRAPHIC DATA

A unique set of time-series hydrographic observations is available in Monterey Bay, about 100 miles south of San Francisco (Bretschneider and McLain 1983). The data were collected at station H-3, located near the mouth of the Monterey submarine canyon, where water depth is more than 900 meters (Figure 1). Hydrographic observations in Monterey Bay were begun in the 1930s by Skogsberg (1936) and continued in the 1950s by Stanford University's Hopkins Marine Station (HMS) as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The sampling program in Monterey Bay was designed to obtain more frequent monitoring of ocean fluctuations than was possible on large-scale CalCOFI surveys (Bolin and Abbott 1963). During the first years of the program, samples were collected at station H-3 to 100 m, but later sampling was limited to the upper 50 m of the water column. In 1968 the sampling depth was increased to over 500 m.[1] HMS sampling at H-3 ceased in December 1973, but sampling was continued at the same location by Moss Landing Marine Laboratories from July 1974 to June 1978 (station 2203).[2] In addition, several expendable bathythermograph (XBT) casts have been taken at nearly the same sampling location to depths of over 400 m by the Naval Postgraduate School, Monterey, California. Salinity values were estimated for each XBT profile so that XBT casts could be used to fill gaps in the time series of hydrographic stations (Bretschneider and McLain 1983). These data were merged to form a time series; 1968 data were deleted because their temperature-salinity curves appeared erratic. The final time series contains 241 hydrographic profiles taken in the 10-year period from 1969 to 1978 and provides good time resolution with nearly biweekly sampling. The data were well distributed seasonally, with 16 to 23 profiles for each month of the year.

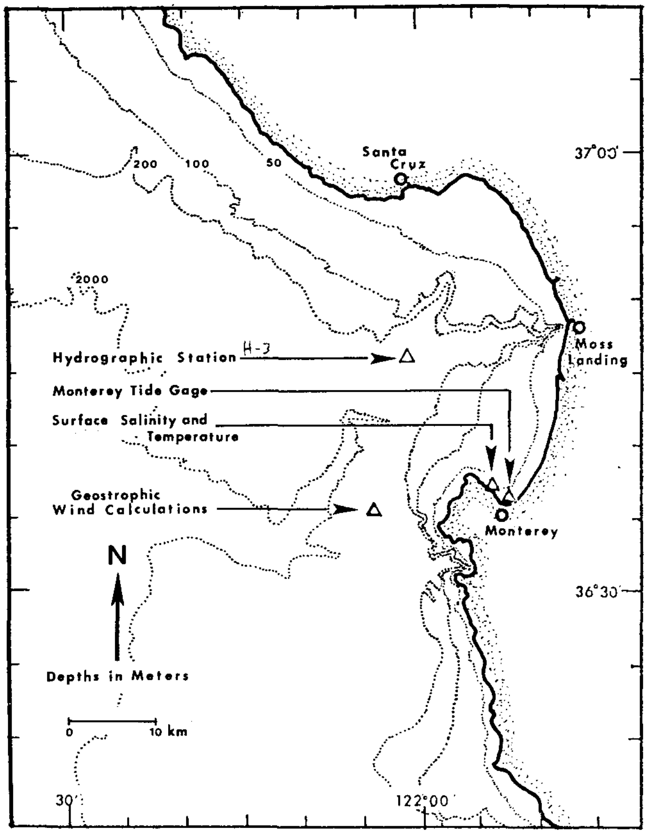

Figure 1. Map of the Monterey Bay, California, region showing location of data sources.

Hydrographic data from station H-3 are subject to short-period disturbances associated with internal waves in Monterey canyon (Broenkow and McKain 1972). Errors in the observations of temperature and salinity, local eddies, or other local environmental phenomena probably also contribute short-term noise

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[1] Hopkins Marine Station, CalCOFI Hydrographic Data, Collected on approximately biweekly cruises on Monterey Bay, California. Annual Reports for years 1968 to 1973 (mineo.). Hopkins Marine Station, Pacific Grove, California 93950.

[2] CalCOFI hydrographic data reports, Monterey Bay, July 1974-June 1978. Tech. Publications 75-1, 76-1, 77-1, 78-1, and 79-1. Moss Landing Marine Lab., Moss Landing, California 95039.

in the data. However, the frequency of sampling to at least 500 m at station H-3 over a multiyear period is unique along the central California coast, and—for ocean monitoring purposes—overrides deficiencies in the data caused by high-frequency noise.

Three distinct seasonal phases of Monterey Bay hydrography were proposed by Skogsberg (1936) and amplified by Bolin and Abbott (1963). These are the upwelling period of summer, a calm warm "oceanic" period in fall, and the Davidson Current period in winter. In January and February, surface water has a high temperature and low salinity (roughly 13°C and 33.2°/oo). As upwelling begins in spring, deep water rises, and the surface water cools and becomes more saline, reaching typical values of 9°C and 34.0°/oo in summer. Warming occurs in the oceanic period in fall, and the surface salinity decreases in winter. At depth (200 to 400 m), conditions are more stable, and the annual temperature-salinity excursions are reduced from their surface values.

The average seasonal pattern of varying oceanographic conditions in Monterey Bay is strongly modified in certain winters by changes in the vertical thermal structure (Figure 2). The 8° and 10°C isotherms were as much as 100 m deeper than their mean depths in winters of 1969-70 and 1972-73, and 20-50 m deeper in the winters 1976-77 and 1977-78. The average depth of the 8°C isotherm lies at depths of 250 and 300 m from August to January, but the 8°C isotherm was at depths of 300-420 m from August to at least November 1969 (deep data in early 1970 are missing) and from July 1972 to February 1973. The 10° and 12°C isotherms were 50-70 m deeper than normal in these two winters, but the anomalous deepenings of these isotherms did not start until October, two months later than that of the 8°C isotherm. The three isotherms were also deeper than normal in the winters of 1976-77 and 1977-78, although not as markedly so as in 1969-70 and 1972-73. Again in these winters, anomalous deepening of the 10° and 12°C isotherms lagged that of the 8°C isotherm. In almost every case, all three isotherms returned to normal depths nearly simultaneously in April or May. Isotherm depths were near normal in the winters of 1970-71, 1971-72, and 1974-75, and were consistently shallower than normal in the winter of 1975-76.

The anomalous deepenings of the deep isotherms may have occurred in two waves, with an initial depression in summer and a second depression the following winter. Anomalous depressions of isotherms were observed in summer 1969 and 1972. Although deep data in the following winters are sparse, second waves of isotherm depression the following winters appear to have occurred. Double depressions were observed in 1976-77 and 1977-78 but were of lesser magnitude than those in 1969-70 and 1972-73.

The anomalous depressions of isotherms were associated with above-normal surface temperatures in late winter. The surface water remained above 12°C until February to April during the winters when the

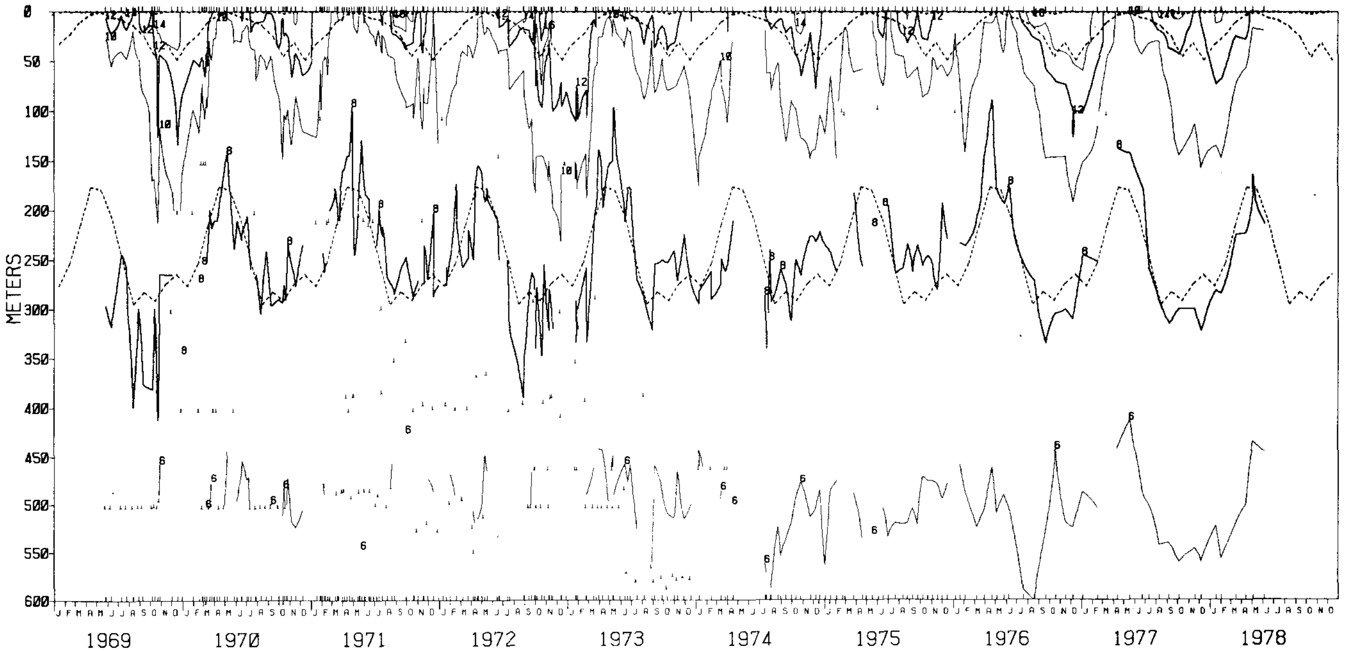

Figure 2. Time series vertical section of temperature (degrees Celsius) at station H-3. Dotted lines show long-term monthly means of 8°, 12°, and 16°C isotherms. Small, inverted "T" marks show greatest depth of data at each hydrographic cast.

8°C isotherm was anomalously deep, but when the 8°C isotherm was near or shallower than normal, the surface water cooled to below 12°C by October or November. (A slight exception to this was in the winter of 1977-78, when the surface water was below 12°C for a short period in November and December 1977 but then again warmed and remained above 12°C until April 1978.)

Salinity at station H-3 (Figure 3) has generally similar interannual variations. Depressions of the 34°/oo isohaline by 200 m or more occurred in late 1969 and in winter 1972-73. Lesser deepenings of 50-100 m occurred in the winters of 1976-77 and 1977-78. The 34°/oo isohaline was at near-normal depths in the winters of 1970-71, 1974-75, and 1975-76, and shallower than normal in winter 1973-74.

Wooster and Jones (1970) described the California Undercurrent as a poleward flow along the coasts of California and Baja California and recognizable by a coastward deepening of isopycnals and poleward transport of warm, saline water. They suggest that the undercurrent can be recognized by the presence of water of greater than about 34.0°/oo on the 150 cl/ton (sigma-t = 26.54) surface. To look for undercurrent water off Monterey, we plotted salinity on constant density surfaces (Figure 4). On the 26.50 sigma-t surface, there were no large increases in salinity during the period of record, and thus pulses of equatorial water were not observed off Monterey. (Isolated anomalously high temperature values of near 10°C occurred in the hydrographic cast data at 300-400-m depths in December 1969 and December 1972. These values are interesting because they occurred at times when unusually high temperatures might have been observed, but they were deleted as erroneous because XBT data from the same months and depths did not show similar high values.)

Low surface salinities were observed at station H-3 in early 1970 and early 1978 (Figure 4), probably as a result of onshore Ekman transport of low salinity offshore water. Chelton (1981) described the low salinities observed on the CalCOFI survey during winter 1977-78 and showed that the low salinity could not have resulted from precipitation alone. Reid et al. (1958) showed a core of low-salinity water (less than 33.0°/oo) on the surface 200-400 km off central California. Saur (1980) showed that, based on surface salinity observations made by ships of opportunity between San Francisco and Honolulu during 1966-74, a core of low-salinity surface water occurs off San Francisco throughout the year and tends to move onshore in spring and offshore in autumn. Onshore transport in winter (Figure 8) could force this low-salinity surface water onto the coast and could have caused the salinity minima observed at station H-3 in February 1970 and March-April 1978. Saur's data on surface salinity also agree well with station H-3 data for 1969-72. Bolin and Abbott (1963) show similar surface salinity minima in Monterey Bay in January 1956 and March 1958, following similar periods of strong onshore transport (Figure 8), although they suggest that the low salinities are primarily due to precipitation. Broenkow and

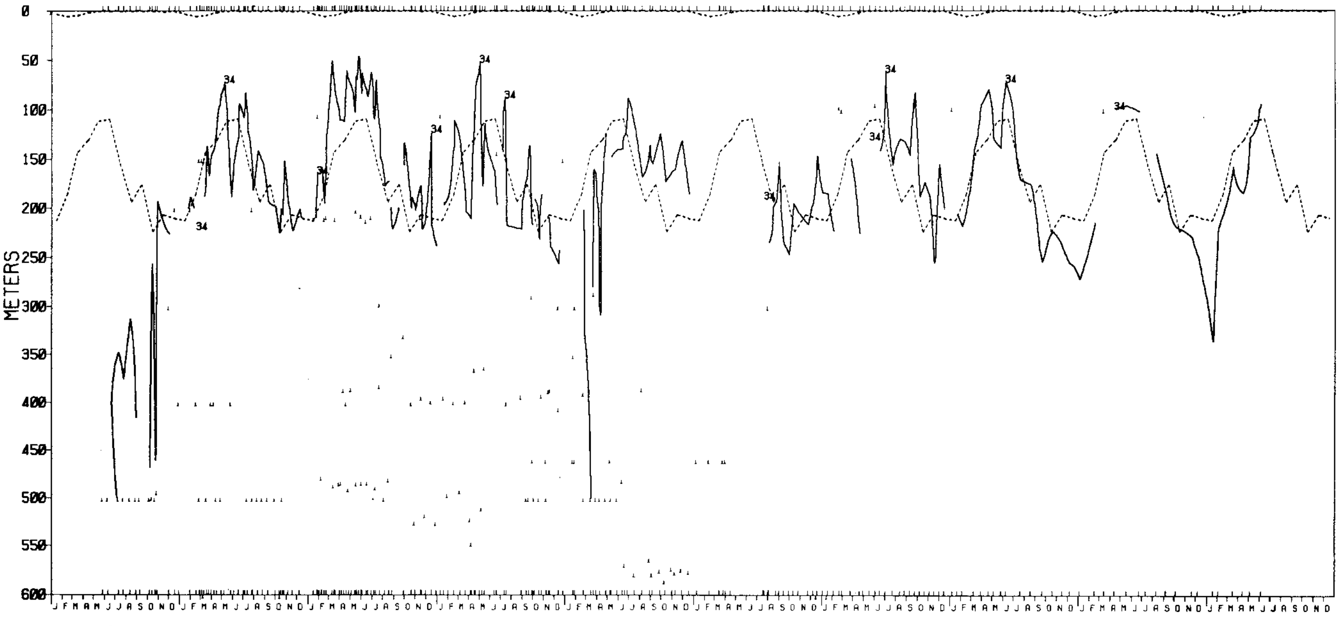

Figure 3. Time series vertical section of salinity (parts per thousand) at station H-3. Dotted lines show long-term monthly means of depth of 33 and 34.00‰ isohaline.

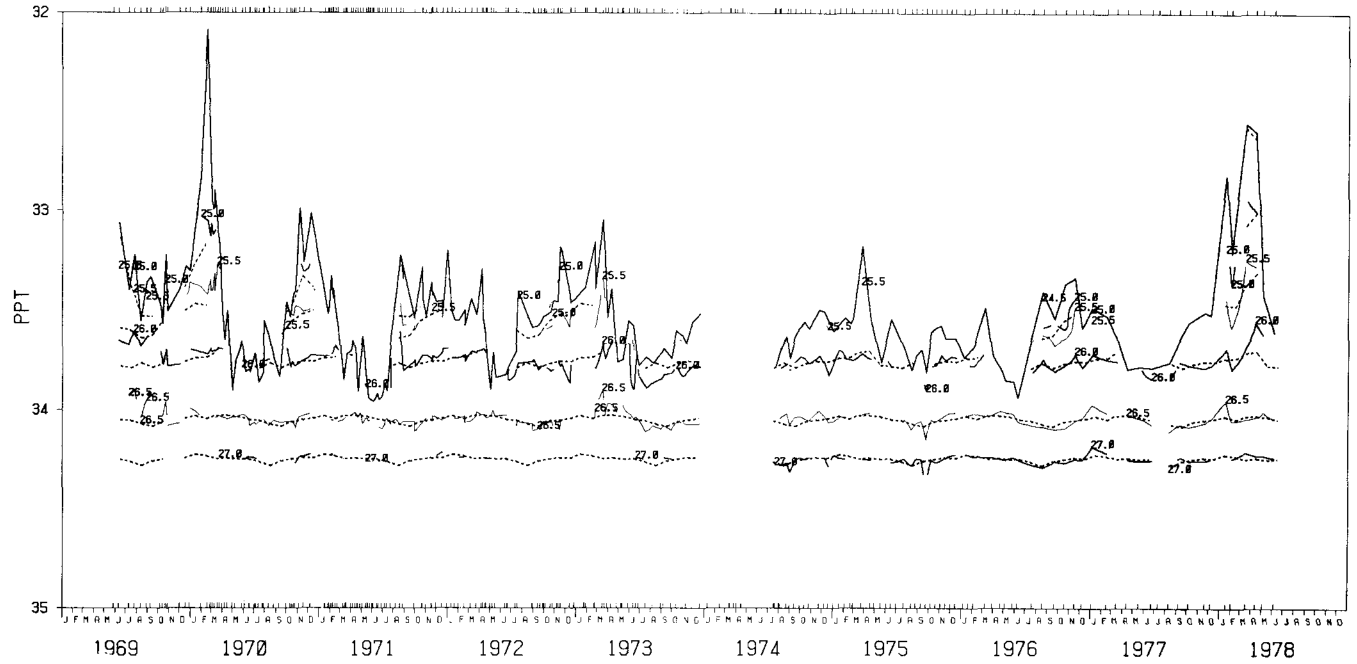

Figure 4. Time series of salinity (parts per thousand) on sigma-t surfaces at station H-3. Dotted lines show long-term monthly means.

Smethie (1978) suggest that lower salinities observed in Monterey Bay in the winter of 1972-73 relative to the winter of 1971-72 were due to more persistent southerly winds in 1972-73 and that the low salinities were associated with storms and consequent heavy rainfall and land runoff.

Dynamic height anomalies were computed for each of the hydrographic profiles at station H-3 and plotted as time series (Figure 5). Although the hydrographic casts generally extended to 500 m or more, we chose 400 m as the reference depth to allow use of the XBT observations. The mean seasonal cycle of 0/400-db dynamic height (shown as dotted lines in Figure 5) had a minimum in May or June and double maxima in

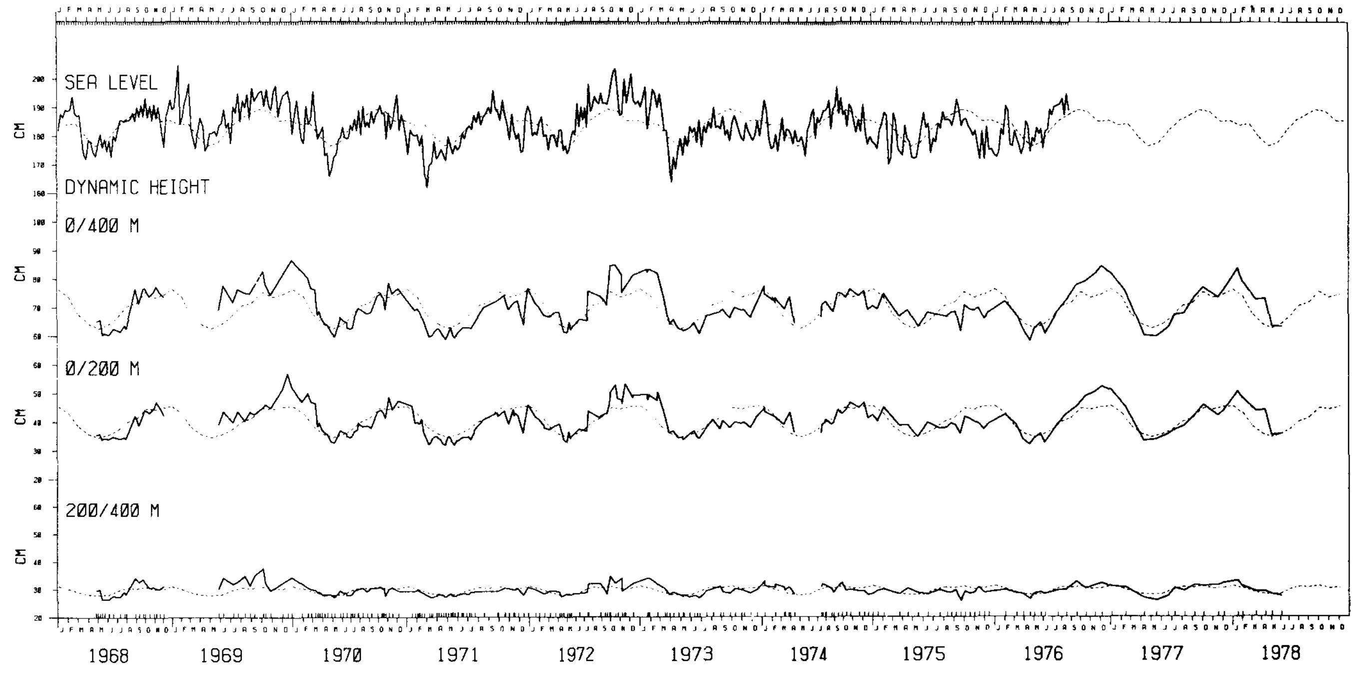

Figure 5. Time series of unadjusted weekly mean sea level (cm) at Monterey, California, and 0/400-db, 0/200-db, and 200/400-db dynamic height (dyn cm) at station H-3. Dotted lines show long-term monthly means.

September and December. The two maxima of the mean seasonal cycle of dynamic height in fall and winter are caused by the double wave of isotherm depressions mentioned previously. Because of the relative greater effect of temperature than salinity in determining density in this region, depression of the thermal structure (and consequent increased dynamic height) overrides the effect of depression of the salinity structure (in reducing dynamic height). Large year-to-year fluctuations occurred in the record of 0/400-db dynamic height with above-normal values of dynamic height in the winters of 1969-70, 1972-73, and to a lesser extent in the winters of 1976-77 and 1977-78. Below-normal values of dynamic height occurred in the winters of 1973-74 and 1975-76.

Most of the fluctuations of the 0/400-db dynamic height were caused by changes in the upper 200 m of water, as is seen by comparing time series of two components of the 0/400-db height; 0/200-db and 200/400-db heights. The 0/200-db dynamic height has a seasonal cycle that is similar to that of the 0/400-db dynamic height with double maxima, in September and December, and a minimum in April. The 0/200-db dynamic height had deviations from its mean seasonal cycle that were similar to the 0/400-db dynamic height deviations: the maxima of the 0/400-db dynamic height in the winters of 1969-70, 1972-73, 1976-77, and 1977-78 are also seen in the 0/200-db series. In contrast to the fairly regular seasonal cycle of the 0/200-db series, the 200/400-db series of dynamic height has little seasonal variation and has minor maxima in the winters of 1969-70 and 1972-73 and a minimum in summer 1977. The maxima in the winters 1969-70 and 1972-73 are associated with the depressions of the thermal structure to depths below 200 m.

Sea level at Monterey had interannual fluctuations similar to the 0/400-db dynamic height (Figure 5). The data plotted are weekly means of hourly sea-level elevations at the Monterey tide gage and were not adjusted for atmospheric pressure fluctuations. The sea-level data show high-frequency fluctuations of 10-20-day period that may be due to pressure changes. Fluctuations of longer period appear to be correlated well between the two series.

The interannual fluctuations of dynamic height at station H-3 and sea level at Monterey are apparently due to large-scale, coast-wide variations in the alongshore currents. If the anomalous depressions of isotherms and related anomalous increases of dynamic height occur primarily near shore, and conditions offshore are more stable from year to year, the anomalous thermal conditions would cause anomalous increases in the slope of the sea surface toward the coast and, hence, anomalous increases in poleward alongshore currents. Thus the time series of dynamic height and related sea-level variations can provide an index of the interannual changes in the flow of the California Countercurrent. Not only can the series of dynamic heights show interyear differences of poleward transport, but on a finer time scale the series may even indicate shorter period changes. The apparent correspondence between dynamic height and sea-level changes on monthly time scales may confirm this.

No long time series of observations of transport of the countercurrent are available for direct comparison with the dynamic height index. The only data on alongshore currents available are from hydrographic surveys, current meters, ships of opportunity, and drifter studies. Many of these data are of short duration and are scattered in time and thus cannot be easily used to resolve interyear differences. We shall examine each of the data sources for comparison with the hypothesized fluctuations of the countercurrent flow, based on the time series of 0-400-db dynamic height from station H-3.

RATIONALE FOR COUNTERCURRENT INDEX

A rationale for a relation between interannual fluctuations of dynamic height at station H-3 and strength of the California Countercurrent can be made based on the data collected on the CalCOFI hydrographic surveys that have been conducted along the coasts of California and Baja California since the early 1950s. Published charts of 0/500-db and 200/500-db dynamic height for particular CalCOFI surveys show that during periods of higher than normal dynamic height at station H-3, intensified poleward flow occurred along the coast.

Direct comparison of time series of CalCOFI and station H-3 data are not possible because the CalCOFI survey data are available much less frequently than station H-3 data. The CalCOFI surveys were not made at regular time intervals but instead were made nearly monthly in some years, quarterly in other years, and not at all in still other years. We compared annual means and seasonal cycles of dynamic height from the two sources. We recognize that different individual years are included in each set of monthly means but neglect the errors introduced. The data for CalCOFI lines 67 and 70 off central California for years 1958-78 were obtained.[3] The data on annual means of dynamic height at station H-3 are based on at least 12 hydrographic casts per month, but annual means of the CalCOFI data are limited by inadequate sampling in certain months, as pointed out by Chelton (1980). For example, there were several months in which no

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[3] L. Eber, Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, CA 92037.

observations were available and several others when only one observation was made.

The annual and seasonal ranges of the monthly means are shown in Figure 6. The annual mean dynamic heights on line 70 off Point Sur, south of Monterey, show that the dynamic height normally slopes downward from the coast to a trough 30-40 km offshore (near station 55) and then rises in an offshore direction. By geostrophy, the downward slope from the coast is associated with northward alongshore flow, and the upward slope offshore beyond the trough is associated with southward flow. Chelton (1980) has fit the annual variations of CalCOFI survey data with two harmonics and plotted monthly maps of dynamic height along the California coast. Chelton's maps show a trough off Monterey, parallel to the coast from September to February and located 100-200 km offshore.

The magnitude of the range of annual variations of dynamic height is greatest at the coast and decays in an offshore direction (Figure 6). Since station H-3 is well inshore of the trough and since inshore variability is greater than that in the trough, fluctuations of dynamic height at station H-3 reflect fluctuations of the slope of dynamic height normal to the coast and hence variations of the countercurrent. Huyer (1977) found that off Newport, Oregon, there was a minimum of seasonal variation of steric height about 80 km from the coast.

The trough of dynamic height weakens and moves inshore in summer. This can be seen in monthly distributions of 0/500-db dynamic heights along lines 67, off Monterey Bay, and 70, off Point Sur (Table 1). Nearshore observations are not available from these lines, and thus data from station H-3 are assumed to represent inshore variations along the lines. Mean dynamic height is computed for each station and month, even if only a single observation was available for that location. The number of observations ranges from 1 to 15, with generally greater sampling on line 70 than line 67. (There were 131 observations on line 67, and 211 on line 70.) On lines 67 and 70, the trough of dynamic height (indicated in Table 1 by dynamic heights of less than 80 cm) is generally located near stations 53 or 55 but moves inshore and disappears in June or July. In summer, because of northwesterly winds, alongshore surface wind stress off Monterey is large, with peak values in May or June (Nelson 1977). Wind stress causes upwelling along the coast, and the thermal structure slopes upward toward the coast. The nearshore surface current becomes southerly, weakening the countercurrent and causing the California Current to move inshore and override the countercurrent. These processes cause a redistribution of mass so that the trough of dynamic height moves inshore and disappears in summer.

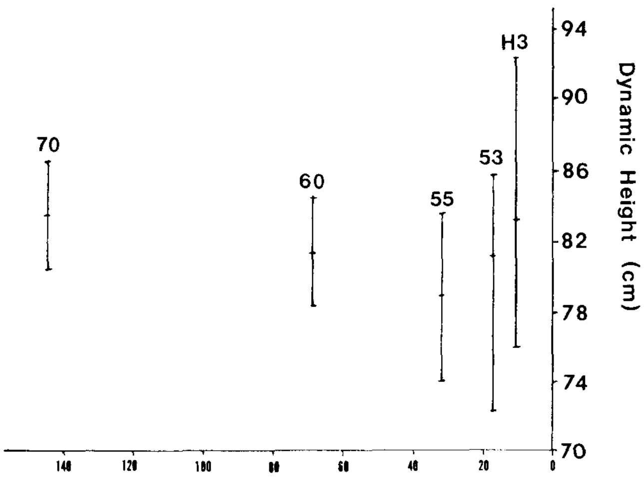


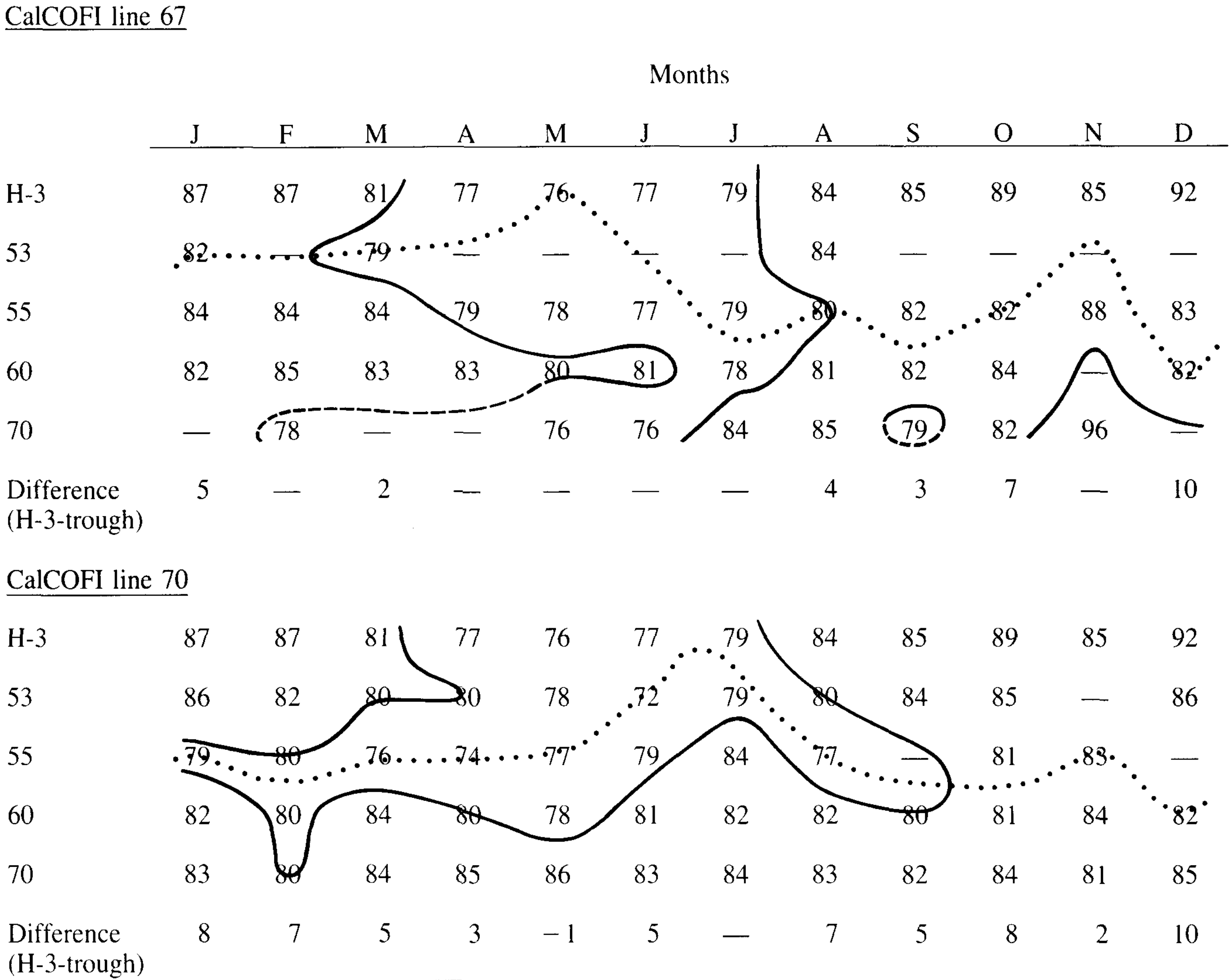
Figure 6. Annual means and seasonal ranges of 0/500-db dynamic height (dyn cm) at station H-3 and along CalCOFI line 70.

An index of countercurrent transport can be made by calculating the difference of dynamic height at station H-3 and the trough minimum. This difference (Table 1) is greatest from October to February, with peak values in December, suggesting that maximum countercurrent flow occurs in December. This is in agreement with plots of Hickey (1979), which show strongest northward alongshore flow from November to January.

COMPARISON WITH TIME SERIES SEA-LEVEL DATA

Reid and Mantyla (1976) have shown that in the North Pacific south of about 40°N, monthly mean sea levels are typically highest in late summer and early fall and lowest in winter as a consequence of the annual heating and cooling cycle. North of about 40°N, however, the seasonal cycle shifts phase, and sea levels are highest in winter and lowest in summer. This phase shift cannot be explained by seasonal heating and cooling. Reid and Mantyla showed that the high sea levels of winter are instead a consequence of the circulation of the subarctic cyclonic gyre of the North Pacific Ocean. The California Countercurrent can be considered a southern arm of the cyclonic gyre along the California coast. The countercurrent has strongest flows in winter, causing sea level to slope upward toward the coast and accounting for the phase shift south of 40°N. Sturges (1974) accounted for high sea levels and dynamic heights near Neah Bay, Washington, in terms of stronger northward along-

TABLE 1
Monthly Mean 0/500-db Dynamic Height (cm) at Station H-3 and at Stations on CalCOFI Lines 67, off Monterey Bay, and 70, off Point Sur



CalCOFI line 67

	Months											
	J	F	M	A	M	J	J	A	S	O	N	D
H-3	87	87	81	77	76	77	79	84	85	89	85	92
53	82	—	79	—	—	—	—	84	—	—	—	—
55	84	84	84	79	78	77	79	80	82	82	88	83
60	82	85	83	83	80	81	78	81	82	84	—	82
70	—	78	—	—	76	76	84	85	79	82	96	—
Difference (H-3-trough)	5	—	2	—	—	—	—	4	3	7	—	10

CalCOFI line 70

	J	F	M	A	M	J	J	A	S	O	N	D
H-3	87	87	81	77	76	77	79	84	85	89	85	92
53	86	82	80	80	78	72	79	80	84	85	—	86
55	79	80	76	74	77	79	84	77	—	81	83	—
60	82	80	84	80	78	81	82	82	80	81	84	82
70	83	80	84	85	86	83	84	83	82	84	81	85
Difference (H-3-trough)	8	7	5	3	−1	5	—	7	5	8	2	10

Tables are contoured, and dotted line indicates trough of dynamic height. Difference of monthly mean dynamic height at H-3 and trough is also shown.

shore currents in winter. Similarly, Marthaler (1976) compared monthly mean sea level at Newport, Oregon, with currents observed with current meters on the continental shelf off Newport during 43 different months. He found that sea level and alongshore currents were strongly correlated, with best correlations from November to May or June when northward flows were strongest.

Sea level at Monterey is closely correlated with dynamic height at station H-3 for the years of common record (Figure 5; Bretschneider and McLain 1983). Sea level at other stations along the West Coast from Los Angeles to Neah Bay, Washington, (Figure 7) had similar year-to-year variability in the dynamic height at station H-3. Periods of above-normal sea level generally occurred in the latter portions of certain years: 1951, 1957, 1958, 1963, 1965, 1969, 1972, 1976, and 1977. Below-normal sea levels occurred in 1948, 1949, 1955, 1956, 1973, and 1975. Because of the similarity of sea level and dynamic height in years when both data series are available, sea level can also be used as an index of alongshore currents off central California (Chelton 1981). This relation allows inexpensive monitoring of alongshore currents from shore stations on an interannual time scale rather than by expensive ship surveys.

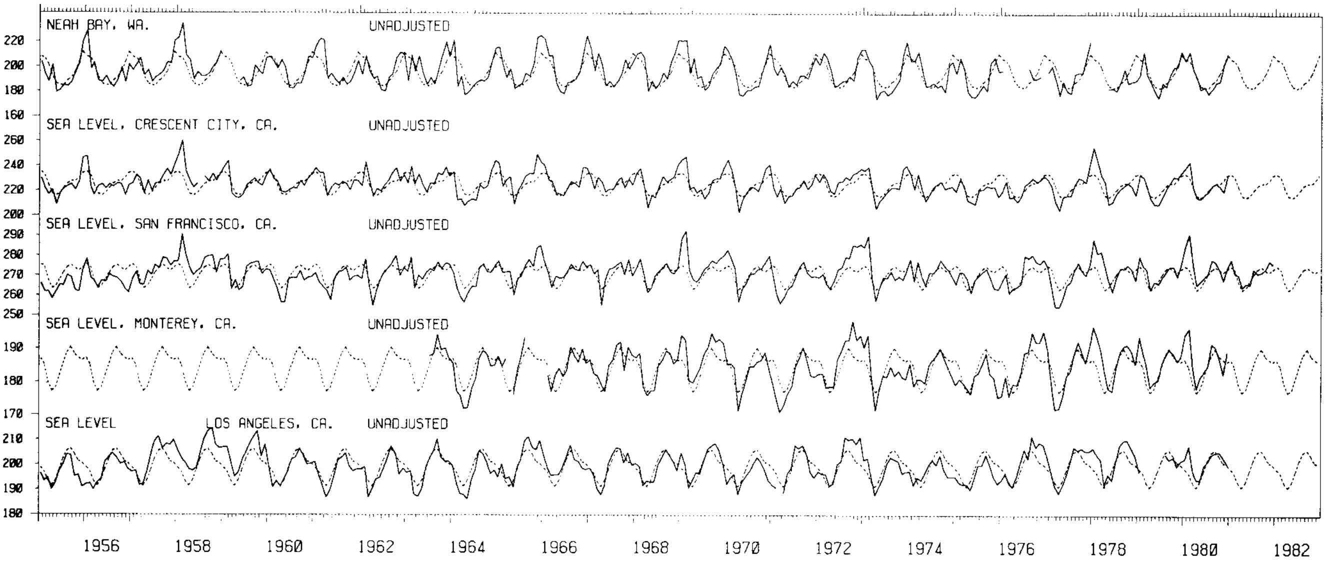


Figure 7. Time series of sea level (cm) at selected West Coast tide gage stations. Data have not been adjusted for atmospheric pressure effects. Dotted lines show long-term monthly means.

COMPARISON WITH SHIPS-OF-OPPORTUNITY XBT DATA

Approximately biweekly sections of sea-surface temperature, salinity, and subsurface temperature have been made since 1966 by expendable bathythermograph (XBT) from ships of opportunity on the route from San Francisco to Honolulu (Saur et al. 1979). The XBT drops were made at approximately 120-km intervals along the route, with sections repeated at approximately 2-week intervals. Price (1981) has computed dynamic heights from these XBT data and has computed an index of strength of the countercurrent. Price used climatological hydrographic data to compute long-term mean temperature-salinity relationships and thus to estimate salinity from observed temperature data. This method of monitoring ocean currents has the advantages of relatively low cost (compared to repeated hydrographic observations from research vessels) and good time resolution but suffers from limited depth range and possible inaccuracies in the estimation of salinity. The XBT drop closest to the coast was often 100 km or more offshore, and thus the observations may have often missed the countercurrent. In spite of the problems, Price's index of the flow of the countercurrent (called V4) shows fair agreement with estimates of countercurrent flow from station H-3 dynamic height data and with sea-level data at both Monterey and San Francisco. All series show high values in late 1969 and in late 1972-early 1973, and low values in 1968, 1970, late 1973, and 1974. Price's index shows a very strong double peak in 1972-73; this may be related to the double waves of isotherm depression seen at station H-3.

COMPARISON WITH HYDROGRAPHIC AND DRIFTER DATA

The available hydrographic and sea-level data indicate significant interannual fluctuations of alongshore currents. The periods of strong flow are discussed below and compared to available hydrographic survey and surface drifter observations.

1957-59

High sea levels (Figure 7) were observed from 1957-59, suggesting a period of anomalously strong northward alongshore currents. Reports presented at the Rancho Santa Fe Symposium in 1958 described numerous unusual oceanographic and biological events observed in 1957 and 1958; these were attributed to anomalous northward coastal flow. Schwartzlose (1963) noted very strong northward transport of drift bottles along the coast in 1958. Tully et al. (1960) described anomalous increases in water temperature off British Columbia in 1957 and 1958.

1969-70

The computed dynamic height values from station H-3 were above normal in July and August 1969, peaked in December, and declined to relatively low values by May 1970. Schwartzlose and Reid (1972) considered that the Davidson Current was well developed in November 1969. Drift bottle recoveries indicated that coastal water was flowing northward from southern California at a minimum speed of 13 km/day. Recovery records for CalCOFI drift bottle studies (Crowe and Schwartzlose 1972) showed considerable northward flow in both October and November 1969 from central California. Several drifters released off central California during these months were recovered in southeastern Alaska, and numerous recoveries came from Oregon and Washington. The magnitude of northerly flow noted during these months was comparable to that observed during November 1957 and January 1958.

1972-73

Wickham (1975) made hydrographic and drogue surveys off Monterey in early August of 1972 and 1973. His data show that water between the surface and 500 m was warmer, more saline, and had a greater northward velocity during August 1972 than August 1973. Water in August 1972 appeared to have "southern" characteristics similar to water observed by Molnar (1972) inshore of a transition zone south of Point Arguello during June 1972. Water offshore of this transition zone had "northern" characteristics similar to water found off Monterey in June. Wickham (1975) further suggested that water observed near Monterey in August 1972 was southern water advected northward from the region of Point Arguello at a speed of at least 5 cm/sec. This is in agreement with the station H-3 data, which show that an intrusion of relatively warm water into Monterey Bay began sometime in June or July 1972 (Figures 3 and 5).

Additional evidence of intensification of the countercurrent in June-July 1972 appears in the hydrographic and current studies of Broenkow and Smethie (1978). Based on hydrographic data from station H-3 between 1971 and 1973, they concluded that local upwelling events, evidenced by a shallowing of near-surface isotherms, generally corresponded to peaks in local northerly winds. They noted an exception to this relationship in July 1972, however, when a temperature maximum occurred despite the presence of northerly winds.

In a surface study, Blaskovich (1973) released drift cards monthly in Monterey Bay between September 1971 and April 1973. He found southward flow from March to May1972, but from June to September 1972 most recoveries were made on the eastern shore of Monterey Bay, indicating a lack of typical summer southward flow. In another drifter study conducted in the Monterey Bay area between November 1971 and April 1973, Griggs (1974) found a good correlation between southward surface drift and northerly winds from March to May 1972. The relationship broke down in June, July, and September 1972, when drifter recoveries demonstrated substantial northward surface flow despite the presence of northerly winds.

Evidence that the intensification of the countercurrent in 1972 was not confined to central California waters can be found in the results of a drift-bottle study conducted from early March to early August 1972 off northern Oregon (Rothlisberg 1975). Northward surface drift persisted from March to mid-April. Currents in late April were transitional, with a large southerly component, and recoveries in May indicate that southward flow had become dominant. In spite of strong northerly winds from May through August, however, a reversal to northward flow was indicated by recoveries from June and July releases.

Broenkow and Smethie (1978) concluded from the station H-3 hydrographic data that northward flow in the winter of 1972-73 was stronger than that of the previous winter. This result was also shown by drifter releases during the winters of 1971-72 and 1972-73, which indicated northward flow in both winters but long-distance drifts only during winter 1972-73. Blaskovich (1973) reported the recovery of a drift card in Oregon that was released in October 1972 at Monterey, as well as an Oregon recovery and a Washington recovery from November 1972 releases. Paradoxically, another card released in October 1972 found its way south to San Simeon, a distance of 150 km. Griggs (1974) does not give detailed accounts of individual drifter movements, but recoveries during December 1972 and February 1973 indicated that a more extensive northward flow occurred during this period than from November 1971 to February 1972. Griggs, like Blaskovich, found both long-distance southern and northern movement during October 1972.

1976-77

Anomalously high dynamic heights at station H-3 in 1976-77 would indicate that intensification of northward alongshore flow may have started in June 1976 and reached its maximum influence by the end of December. Comparative data are unavailable off central California, but Tsuchiya (1980) summarized the results of nine nearshore cruises off southern California from 1974-77. Tsuchiya found that during October 1976 to January 1977, the water in the upper 300 m was warmer and more saline than normal. He related the change to a large-scale warming of the eastern North Pacific, but an intensification of northward flow along the coast at the time may also have been a cause.

A decline of dynamic height values to lower than normal occurred in summer 1977, suggesting a period of stronger than normal southward flow. The dynamic height data indicate that an intensification of the countercurrent began in fall 1977 and apparently peaked in

January 1978 (one month later than in the previous winter) before declining to minimum values in May 1978. A cooperative United States-Poland oceanographic survey was conducted along the west coast of the United States during August and September 1977 (Ingraham and Love 1978). Geostrophic currents derived from the survey data indicate that surface flow was generally southward all along the coast, but flow at 150 m (computed relative to 500 db) was generally northward except in the vicinity of the Columbia River. Ingraham and Love considered these observations to be evidence that a substantial northward flow existed at depth during late summer 1977 over the outer continental shelf and slope. Gardner (1982) found evidence of Pacific equatorial water on the continental shelf north of Vancouver Island in April and November 1977, with greater amounts in November.

CAUSES OF COUNTERCURRENT FLUCTUATIONS

Several processes act in concert to drive alongshore currents. Hickey (1979) has described the countercurrent in terms of wind stress and the curl of the wind stress. Wind stress seems the more important. Several studies off Oregon (e.g., Cutchin and Smith 1973; Huyer et al. 1978) have shown that currents over the continental shelf observed with moored current meters are highly correlated with sea level at nearby tide gages and that both respond rapidly to changes in forcing by alongshore winds.

Sharp drops of both dynamic height at station H-3 and sea level at Monterey occurred in early 1970, 1973, and other years. This suggests that the transition between northward and southward flow in spring may be rapid. Huyer et al. (1979) describe sharp flow reversals off Oregon during March of both 1973 and 1975. They refer to these current reversals as a ''spring transition'' and suggest that such reversals occur each spring and represent a relatively permanent change from winter (northward flow) to summer (southward flow) conditions on the shelf. The time series of dynamic height at station H-3 (Figure 5) suggests that such pronounced reversals do not occur every year and may be weak or oscillatory, as in 1971, 1974, and 1975. Spring reversals following winters of above (below)-normal sea level and dynamic height tend to be more (less) intense than normal.

Whereas the mean seasonal cycle of dynamic height at station H-3 suggests that southward flow occurs during the first half of the year and northward flow during the second half of the year, reversals of the direction of flow are common within both periods. These can be seen as sharp reversals of dynamic height at station H-3 and can be explained by assuming that on large space scales, water to the north of H-3 is colder than that to the south. Northward flow (or anomalously weak southward flow) would then cause increased water temperature (averaged over the upper 400 m) and consequently, increased dynamic height (assuming also that salinity effects are small). Conversely, southward flow (or anomalously weak northward flow) would cause decreased water temperatures and dynamic heights. Thus reversals of the time slope of dynamic height at coastal locations such as station H-3 can reflect reversals of coastal flow.

Evidence that fluctuations in the dynamic height reasonably depict actual current reversals is available from drifter movements in 1972. The dynamic height data suggest that a sharp reversal in currents occurred between mid-September and mid-November 1972. The implied strong northward flow followed by strong southward flow is substantiated by the long-distance transport of drifters, both to the north and south, reported to have occurred in October 1972 by Blaskovitch (1973) and Greggs (1974).

Sverdrup transport set up by curl of the wind stress over the region is a second process driving the countercurrent but is less well understood than wind stress itself. Nelson (1977) has computed and plotted monthly maps of wind stress curl off the West Coast based on historical ships' wind observations. Nelson's maps show fine seasonal detail (about 110-km resolution) but because of scarcity of historical data, they do not show interyear variations. Chelton (1980) computed similar maps of wind stress curl, based on analyzed fields of surface pressure, which can be computed monthly but have lower spatial resolution (about 300-km resolution) than Nelson's maps and are subject to poor resolution of surface pressure gradients along coasts because of coastal mountains (Bakun 1973). Both Nelson's and Chelton's maps show general negative wind stress curl offshore and a band of positive curl along the coast, a situation that would produce poleward alongshore currents.

Nelson's maps show several peaks of positive wind stress curl along the coast: 42°N south of Cape Blanco, 38°N near Point Reyes, 34°N south of Point Conception, 31°N off northern Baja California, and 27°N south of Punta Eugenia. Chelton's maps show only one of these areas—the major feature south of Point Conception. To examine the effect of Sverdrup transport on alongshore currents, we computed time series of monthly wind stress curl at these locations along the coast for the years 1946-80 from monthly mean surface pressure fields developed by FNOC and using methods of Bakun (1973, 1975). The time series of wind stress curl did not appear to be correlated with the dynamic height series and hypothesized alongshore currents. This result is similar to that of Hickey (1979), who found little correlation of alongshore currents with wind stress curl, and with Bretschneider and McLain (1983) who found no correlation of Sverdrup transport with dynamic height at station H-3. Wind stress curl may, however, contribute a long-term net tendency for poleward alongshore currents because of the long time periods required for spin-up of a curl-driven current (Chelton 1982).

In addition to wind stress and wind stress curl, a third process that drives alongshore currents is local forcing by the component of Ekman transport toward the coast and resultant depression of the isotherms near the coast. Cairns and Lafond (1966) described short-period fluctuations in shallow water off San Diego, caused by onshore Ekman transport. The process seems of greater importance on longer time and space scales. Southerly winds and resulting onshore transport are relatively infrequent off California but become increasingly common in winter with distance to the north so that onshore transport and downwelling occur each winter along the coasts of the Pacific Northwest and the Gulf of Alaska (Bakun 1973). Figure 8 shows the time series of the component of Ekman transport normal to the coast, again computed by the methods of Bakun. Off California at latitudes 36°N and 39°N, there were anomalously strong onshore Ekman transports during the winters of 1957-58, 1960-61, 1969-70, 1972-73, 1977-78, and 1979-80. Anomalously strong onshore transport would cause anomalous depression of the thermal structure and consequently cause anomalously high sea level and dynamic height along the coast. Northward flow would result from upward slope of the sea surface toward the coast. Thomson (1972) proposed onshore Ekman transport as an explanation for annual variations in the northward penetration of relatively warm water off the British Columbia coast during 1955-56. Douglas and Wickett (1978) explained above-normal bottom-water temperatures on the continental shelf off Vancouver Island in February-March 1978 as a result of anomalously strong onshore Ekman transport.

A fourth process that drives alongshore currents on interannual time scales is remote forcing by propagation of a depression of the thermocline polewards along the coast from the Eastern Tropical Pacific. McCreary (1976) and Hurlburt et al. (1976) modelled the effect of a weakening of the trade winds over the equatorial Pacific and a resultant depression of the thermocline along the coast of Peru. They showed that the depression would be propagated both to the north and south along the coast as a coastally trapped Kelvin wave. Associated with the wave are poleward coastal jets formed by quasi-geostrophic adjustment to the depressed pycnocline along the coast. Enfield (1981) reviewed the available literature on this process, and Mysak et al. (1982) looked for effects of baroclinic waves in physical and biological time series data along the coast.

A major realization of this process occurred in 1972 when a strong El Niño occurred off Peru, and warm water intruded into the area and depressed the thermocline. Wyrtki (1975) presented monthly maps of the topography of the 15°C isotherm surface off Peru, and Enfield (1981) presented temperature sections off Ecuador and Peru during the event. Their data show

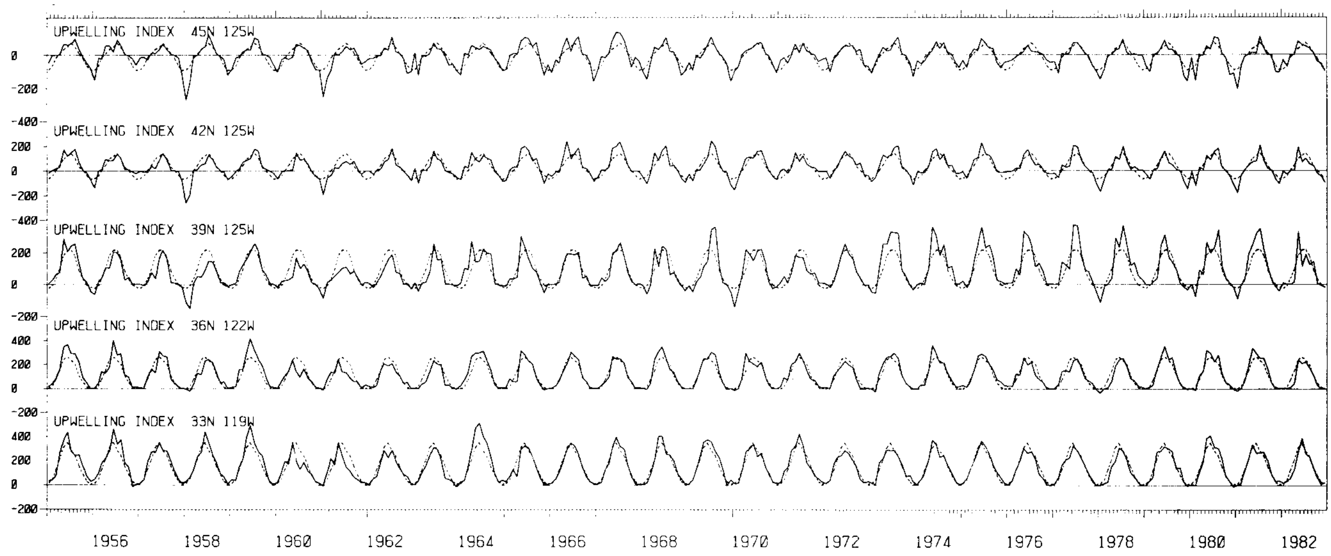


Figure 8. Time series of component of Ekman transport normal to the coast (m^3/sec/100 m of coastline) at selected locations along the West Coast. Data computed by methods of Bakun (1973, 1975). Dotted lines show long-term monthly means.

that the 15°C isotherm is often within 20 m of the surface, or surfaces off the Peruvian coast with coastal temperatures less than 15°C. During the 1972 event, however, the 15°C isotherm was depressed along the coast to depths of 20-100 m in February-March, 60-120 m in August-September, and 150-250 m by December.

The anomalous depression of the thermal structure was observed to propagate both to the north and south. Wyrtki (1975) described changes observed to the south in the depth of the 26.4 sigma-t surface off northern Chile during the 1972 event. During normal years, this surface is between 50 and 100 m along the Chilean coast and deepens to 150-200 m at about 300 km offshore. During June to August 1972, the surface was depressed to depths of 200-300 m all along the coast of northern Chile. It was deepest near the coast and rose to depths of less than 150 m about 200 km offshore, implying a poleward alongshore current.

The propagation of the wave northward from the equator is poorly documented because of lack of hydrographic observations during late 1972 off North America. The waves enter the Gulf of California and dominate conditions there (Baumgartner et al. 1979). High-frequency waves (of 10-30-day period) may be trapped by the Gulf of California and not continue up the Pacific coast of Baja California (Enfield 1981). The data series off Monterey suggests that waves of lower frequency continued up the coast and caused maximum depression of the thermocline in Monterey Bay in December 1972.

The propagating wave can be seen in monthly mean sea-level data. Bretschneider and McLain (1979) showed that sea level at stations from Chile to Alaska had coherent fluctuations at low frequencies over long stretches of coast. These fluctuations were apparently associated with El Niño phenomena in the Eastern Tropical Pacific. Enfield and Allen (1980) explained the coherence by poleward-propagating coastally trapped Kelvin waves. Bretschneider and McLain (1983) presented time-distance isogram plots of anomaly of monthly mean sea level at stations along the coast from Peru to Alaska for 1963 to 1974. Their figures show that in January 1972, a period of anomalously high sea level developed off Peru and persisted throughout the year. The region of anomalously high sea level expanded northwards and reached California by July or August 1972. A second, stronger pulse reached San Francisco in October to December 1972. These waves were apparently related to the double wave of isotherm depression observed at that time at station H-3. Enfield (1981) explained the double waves of isotherm depression and associated peaks of high sea level off Peru as oceanic events related to relaxation of winds over the mid-Pacific, subsequent recovery, and on successive reflections of Kelvin and Rossby waves off the eastern and western ocean boundaries.

The four processes—wind stress, Sverdrup transport, onshore Ekman transport, and propagation of disturbances from the tropics—do not act in unison but have independent effects that may act in different combinations each year. Many of the years of high sea level and dynamic off-California height were years of El Niño events in the Eastern Tropical Pacific (e.g., 1958, 1963, 1972, and 1976) while others (e.g., 1957-58, 1960-61, 1969-70, 1972-73, 1977-78, and 1979-80) had winters of local onshore transport (Figure 8). Years such as 1973 and 1975 had normal or below-normal values of both dynamic height and sea level and were years in which neither El Niño nor anomalously strong Ekman onshore transport occurred. In 1976, there was an El Niño in the Eastern Tropical Pacific that apparently created a coastal Kelvin wave, which caused the observed depression of the isotherms at station H-3 and the hypothesized increased countercurrent flow the winter of 1976-77. In contrast, in 1977 there were normal conditions in the tropics, but strong onshore Ekman transport at 36°N in December 1977 and January 1978 apparently caused the depression of isotherms at station H-3 the winter of 1977-78. In some years, such as 1958 and 1972, both processes occurred and reinforced one another.

The characteristic time scales of these processes differ, and thus it may be possible to distinguish between them. Onshore Ekman transport is related to atmospheric fluctuations and persists only one or two months, whereas the effects of propagating coastal waves persist for several months or longer. Evidence for this is seen in 1976 when the peak of dynamic height was long-lasting and probably related to a propagating coastal wave. In 1977, when onshore transport apparently caused the anomalously high dynamic height, the peak lasted only a month or so.

The timing of the peaks of dynamic height may give clues to the processes causing them. Hickey (1979) suggested that the speed of the undercurrent has two seasonal maxima, one in summer and the second in winter, but she cannot easily relate the maxima to variations of wind stress and wind stress curl. Alternately, the double maxima of speed of the undercurrent may result from (1) the double maxima of isotherm depression in years of strong coastal wave propagation, (2) a combination of a summer peak caused by coastal propagating waves and a winter peak caused by onshore Ekman transport, or (3) some combination of these processes.

Hickey (1979) also suggested that the intensity of the summer maximum of the undercurrent increases toward the south, whereas the winter maximum decreases toward the south. She could not, however, explain these relations from distributions of wind stress and wind stress curl. These relations would be consistent with an explanation of the summer maximum related to poleward-propagating coastal waves (which originate to the south) and the winter maximum related to onshore Ekman transport (which is a local process along the coast).

EFFECTS OF THE COUNTERCURRENT ON MARINE ORGANISMS

Fluctuations in strength of the countercurrent have had notable effects on the distribution and abundance of various marine organisms. Many of these effects are poorly understood and documented, but available observations of unusual distributions of organisms do agree fairly well with the hypothesized fluctuations of the countercurrent. Only a few examples can be given here, and much research remains to be done on these effects. Radovich (1961) described many such unusual occurrences during the "warm-water" years 1957-59 and earlier, particularly in 1926, 1931, and 1941. He recognized that some of the occurrences were more closely associated with changes in the flow of the countercurrent than with increases in water temperature.

Phytoplankton

Bolin and Abbott (1963) described fluctuations of the countercurrent and associated phytoplankton catches off central California for the years 1954 to 1960, and Abbott and Albee (1967) updated the series for 1961 to 1966. Garrison (1979) provided additional data for the years 1976 and 1977. All the authors found significant year-to-year variations, with plankton organisms characteristic of low latitudes more prominent in the warm years. They suggested the importance of advection effects in causing the changes. Also, a general northward extension of subtropical and tropical phytoplankton during the warm years was noted by Balech (1960).

Zooplankton

Blackburn (1979) described fluctuations in the distribution of the salp *Doliolum denticulatum* off California during 1969. He noted that the earlier work of Berner and Reid (1961) had shown that the distribution of *Doliolum* was unusual in 1957 and 1958 in that some *Doliolum* remained inshore off southern California during the winter of 1957-58, whereas in 1949-55, they had not. Blackburn also noted that the distributions in 1969 were more similar to those in 1957-58 than to those in 1949-55. This supports the conclusion that both 1957-58 and 1969 were years with strong northward intrusions of southern water. Other species of invertebrates that have well-documented northern extensions of their range during warm-water years are the sand crab, *Emerita analoga,* (Efford 1970) and two euphausiids, *Euphausia eximia* and *Nyctiphanes simplex* (Brinton 1960).

Hubbard and Pearcy (1971) studied the distribution of salps in plankton collections off Oregon in the years 1961-64. They found that during these years several salps of probable southern origin, particularly *Thalia democratica,* occurred only in late 1963. This was a period of slightly higher than normal sea level and, although no dynamic height data are available from station H-3, probably stronger-than-normal countercurrent.

Gardner (1982) observed the occurrence of several subtropical zooplankton species in samples taken along the British Columbia coast in April and November 1977. He noted more widespread occurrence of the subtropical forms in November than April and associated their occurrence with a warm-water intrusion.

During 1978, salps were observed in large numbers off British Columbia and southeastern Alaska and were associated with other unusual observations (Lasker 1978; McLain and Ingraham 1980). As has been mentioned, onshore transport the previous winter caused intensified northward flow in 1978 and may explain these observations.

Pelagic Red Crab

Pelagic red crab, *Pleuroncodes planipes,* are normally found off the central and southern coast of Baja California (Mais 1974). The range of the species extended north as far as Monterey during the warm period from mid-1957 to early 1960 (Berner 1960; Glynn 1961; Longhurst 1967). Longhurst examined CalCOFI data from 1955-60 and distinguished two periods (1955-57 and 1958-60) with dissimilar latitudinal distributions of red crab. A northward extension of their range began in June and July 1957 in the area between Point San Eugenia and Cape Colnett, Baja California. By October 1957, crab were found near Ensenada, and in December they appeared off San Diego. In 1958 the main population probably moved no farther than San Diego, but isolated groups may have moved as far north as Monterey. In late 1958, northward movement began again, and by early 1959, crab were widely distributed north to San Pedro. Massive strandings occurred at San Pedro in 1959; by early 1960, the northward extension seemed to have ceased. Glynn (1961) reported massive strandings of red crab at Monterey in January 1960. CalCOFI data indicate that a general retreat of the northward range extension began in January 1960 (Longhurst 1967). By the end of 1961 the northern limit and center of abundance had shifted southward to about the same latitude as in mid-1957. Longhurst concluded that some factor other than temperature was responsible for this unusual northward movement. He believed that some alteration in circulation allowed crab to be swept north by coastal countercurrents.

Subsequent to the warm years (1957-60), red crab were found on Monterey beaches in the winters of 1969-70 and 1972-73 (Hardwick and Spratt 1979). The appearance of red crab north of their usual range in these winters had also been observed on Fisheries Resources Sea Surveys of the California Department of Fish and Game. The following observations were extracted from reports of those surveys.

Sea surveys to assess biomass of northern anchovy, *Engraulis mordax,* were conducted several times a year off southern California and Baja California from 1964-78. In 1979 and 1980, the number of surveys was reduced. On the surveys in November-December 1969, red crab were found consistently north of their usual range—as far north as La Jolla, California. By February 1970, crab were absent from northern Baja California and southern California waters. Because red crab were found on Monterey beaches during this period, some crabs must have moved through southern California waters undetected.

The Fisheries Resources Sea Surveys reported that large quantities of red crab were again found off Los Angeles in February 1973. "Quantities far exceeded previous observations including the warm-water years of 1957-58." Red crab maintained a presence off southern California through August 1973. By October 1973 their occurrence was unusual, a few still being found near San Diego.

Unusual observations were made in January 1977 when crab were found north to Cape Colnett, Baja California. Red crab appeared again a little farther north at Ensenada in January-February 1978. In February 1979 no unusual observations were noted, but by April 1979 the Sea Surveys reported the "most extensive influx of this species since 1973 occurred. They were taken on 10 scattered stations from San Diego to Santa Cruz Island." In February 1980, crabs were found from Point Dume southward.

In many of these studies, the organisms were not only found north of their usual range, but those on the northern edges of the range extensions were found inhabiting water cooler than where they are normally found. Because of this, theories developed to explain this extension involve northward forcing by the coastal countercurrents rather than southern populations simply expanding into favorable environmental conditions.

Sockeye Salmon

Adult sockeye salmon normally return to the Fraser River by rounding the south end of Vancouver Island via the Strait of Juan de Fuca; fewer than 20% of the run return around the north end of Vancouver Island via Queen Charlotte Sound. Royal and Tully (1961) reported that in 1958, however, the fish returned in large numbers around the north end of the island, causing reduced availability to fishermen in the Strait of Juan de Fuca. Tully et al. (1960) suggested that the northward shift was associated with anomalous oceanographic conditions during 1957 and 1958. Wickett (1977) listed peak fractions of fish returning around the north end of Vancouver Island as 35% in 1958, 24% in 1966, 25% in 1967, 34% in 1972, and 22% in 1974. Blackbourn[4] provided more recent values of 56% in 1978, 33% in 1979, 70% in 1980, and 69% in 1981. The very anomalous and persistent northward displacements of sockeye migration routes in recent years correlate roughly with onshore Ekman transport off northern California (39°N in Figure 8) the previous winter and may be related to flow of the countercurrent.

CONCLUSIONS

Fluctuations of dynamic height computed from frequent hydrographic data at station H-3 in Monterey Bay during 1969-78 agree well with sea-level data at Monterey on interannual and even monthly time scales.

A trough of dynamic height exists some 20-40 km off the coast in winter and weakens and moves inshore in summer. Interannual variations of dynamic height in the trough are of smaller magnitude than the variations at station H-3 and thus to a first approximation, fluctuations of the slope of dynamic height normal to the coast can be approximated by the fluctuations of dynamic height at the coast. Thus the interannual fluctuations of dynamic height and sea level at the coast can be used as an index of alongshore currents. By geostrophy, increased (decreased) dynamic height and sea level are associated with anomalously strong (weak or even reversed) northward flow.

The cause of the interannual variations of dynamic height and sea level appear to be due to two major processes: (1) remote forcing by poleward-propagating coastal trapped waves from the tropics

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that depress the thermal structure along the coast in some years by 50-100 m, and (2) local forcing by anomalous onshore Ekman transport in winter. Both processes are accompanied by coastal jets, which appear as anomalously strong alongshore currents. Interannual fluctuations of wind stress are certainly important in forcing alongshore currents, but fluctuations of wind stress curl do not appear related to interannual changes of coastal sea level nor of dynamic height at station H-3.

Interannual fluctuations of the countercurrent appear to affect many different organisms, including phytoplankton, zooplankton, and sockeye salmon. Many of the effects are only poorly documented and understood and thus deserve further investigation.

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DESCRIPTION OF EARLY STAGES OF WHITE SEABASS, *ATRACTOSCION NOBILIS*, WITH NOTES ON DISTRIBUTION

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ABSTRACT

Eggs, larvae, and juveniles of *Atractoscion nobilis*, reared in the laboratory, are described and compared with those of *Cynoscion* species. Eggs of *A. nobilis* are among the largest reported for a sciaenid species (1.24-1.32 mm diameter), and the larvae have a distinctive morphology and pigment pattern that contrasts sharply with that of *Cynoscion* species. The larvae are robust, with long pectoral and pelvic fins and have a solid pigment sheath of melanophores and xanthophores that initially covers the head and trunk and expands to cover the body completely. The only other sciaenid with similar developmental stages is *Sciaena umbra* of the eastern Atlantic, Mediterranean, and Black Sea. Late-stage larvae of *Larimus fasciatus* of the western Atlantic have large, heavily pigmented paired fins, but the body pigment is not a solid cloak as in *A. nobilis*.

Atractoscion larvae occurred in only 104 samples of all CalCOFI collections made between 1950 and 1978. Larvae occurred from Santa Rosa Island, California, to Santa Maria Bay, Baja California, with highest concentrations in the Sebastian Viscaino Bay and San Juanico Bay regions. Most of the larvae occurred from May to August, with a peak in July.

RESUMEN

Se describen los huevos, larvas y juveniles de *Atractoscion nobilis* cultivadas en el laboratorio, y se comparan con especies de *Cynoscion*. Entre las especies de Sciaenidae, los huevos con mayores dimensiones corresponden a *A. nobilis* (1.24-1.32 mm. de diámetro), y sus larvas muestran una morfología bien definida, con el pigmento distribuido de forma diferente a la que presentan las especies de *Cynoscion*. Las larvas son robustas, con aletas pectorales y pélvicas largas, y llevan pigmento que incluye melanoforos y xantoforos. Esta capa de pigmento cubre inicialmente la cabeza y tronco, extendiéndose hasta cubrir completamente el cuerpo. *Sciaena umbra* es otro Sciaenidae con fases de desarrollo similar, y habita el Atlántico oriental, Mar Mediterráneo y Mar Negro. Las últimas fases larvales de *Larimus fasciatus* del Atlántico occidental, son de gran tamaño, con aletas pares densamente pigmentadas, pero la pigmentación del cuerpo no es una capa continua como en *A. nobilis*.

De todas las colecciones de CalCOFI efectuadas entre 1950 y 1978, únicamente 104 muestras contenían larvas de *Atractoscion*. Estas larvas se distribuían desde la Isla Santa Rosa, California, hasta Bahía Santa María, Baja California (México), y las mayores concentraciones de larvas aparecían en las zonas de las Bahías Sebastián Vizcaíno y San Juanico. La mayor parte de las larvas se obtuvieron en el período de Mayo hasta Agosto, con máximos en Julio.

INTRODUCTION

The white seabass, *Atractoscion nobilis*, is the largest sciaenid inhabiting the waters off California and western Baja California and, because of its size and high food quality, has been a prized sport and commercial species. Vojkovich and Reed (1983) summarize the decline of the fishery, despite numerous management regulations imposed since 1931, and emphasize the need for information about early life history.

The taxonomic status of the white seabass has been unclear since the original description of Ayres (1860), who placed it in the genus *Johnius*. Gill (1863) established the genus *Atractoscion* to include *A. aequidens* of the southern African and Australian coasts, and the white seabass. Jordan and Evermann (1898) made *Atractoscion* a subgenus of *Cynoscion*, and Trewavas (1977) re-established the genus *Atractoscion* to include *A. aequidens* and *A. nobilis*, based primarily on the fact that these two species lack the adult canine teeth typical of other *Cynoscion* species.

The purpose of this paper is to describe the early life history of *A. nobilis* and to present data on seasonal distribution of larvae from CalCOFI collections. Also, the early stages of *A. nobilis* are compared with those of *Cynoscion* to provide additional taxonomic characters of cynoscionine fishes.

MATERIALS AND METHODS

Specimens used in the description came from four sources. The original identification was based on a

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single larva taken from a reared batch of sciaenid eggs, mostly *Cheilotrema saturnum,* collected by plankton net at the surface off Tourmaline Canyon, San Diego, on July 6, 1978. The 8.3-mm larva was sampled on July 31, 25 days after collection. Temperature range of the 100-l rearing tank was 18.7-21.7°C, and the larva was fed a diet of the rotifer *Brachionus plicatilis* and nauplii of *Artemia salina.* A second source of specimens was a batch of eggs provided by the aquarium at Scripps Institution of Oceanography. On June 13, 1980, the eggs appeared in a tank containing two white seabass that had been collected as one-year-old fish and maintained in the tank for two years. The eggs were transported to the Southwest Fisheries Center and placed in a 100-l rearing tank. Hatching occurred after 3 days, and yolk was exhausted on about day 6, at which time *B. plicatilis* was added to the tank. The larvae did not feed, and all were dead on day 10. Temperature range in the tank was 16.5-20.0°C.

The principal sources of larvae were from two spawnings of captive adult *A. nobilis* maintained under modified environmental conditions at the Southwest Fisheries Center by Roger Leong (pers. comm.). The first spawning was on March 18, 1982, and, for a period of 8 days, specimens were supplied to us by Carol Kimbrell. The second spawning was on April 12, 1982, and larvae were reared by Carol Kimbrell according to procedures described in Hunter and Kimbrell (1980). Specimens were supplied to us daily, and some were photographed, after anesthetization in MS-222, to record live color pattern. All specimens were preserved in 4% Formalin.

One series was assembled to describe changes in morphology and pigment pattern, and another to describe head-spine formation and ossification of meristic elements. For comparative purposes, two series of *Cynoscion acoupa maracaiboensis* were also assembled from specimens supplied by Dr. Raymond Olivares, University del Zulia, Maracaibo, Venezuela. Techniques and terms used in the description follow those outlined in Moser and Ahlstrom (1970, 1978) and Ahlstrom et al. (1976).

Distributional data were obtained by examining all ichthyoplankton samples containing sciaenids taken by CalCOFI from 1950 to 1978, and by identifying and measuring specimens of *A. nobilis.*

DESCRIPTION (Figures 1-4)

Distinguishing Features

Eggs are larger (1.24-1.32 mm diameter) and have a larger oil globule (0.30-0.36 mm diameter) than those of the six other sciaenid species off California (Watson 1982, *Genyonemus lineatus;* Moser et al., other species[1]). Egg diameter of the other sciaenids is less than 1.0 mm, and oil globule diameter is less than 0.26 mm. Larvae hatch at a larger size (ca. 2.8 mm) and are larger at yolk depletion (3.7 mm) than in the other species, which hatch at 1.4-1.8 mm and are 2.4-3.0 mm at yolk depletion. First-feeding larvae are distinguished by a melanistic sheath that covers the head and trunk to slightly posteriad of the anus. *Menticirrhus undulatus* is similar but less intensely pigmented, is less robust, and is smaller at comparative states of development. Beyond initial feeding stages *A. nobilis* larvae become deep-bodied, and develop a large broad head and a solid pigment cloak that gradually covers the entire body. After notochord flexion the paired fins become enlarged and heavily pigmented, and a characteristic banding pattern develops on the body.

Eggs

The eggs of *A. nobilis* are among the largest known for Sciaenidae. For 25 eggs measured from the June 13, 1980, spawning the diameter range was 1.24-1.32 mm ($\bar{x}$ = 1.27 ± 0.02 SD), with an oil globule diameter range of 0.30-0.36 mm ($\bar{x}$ = 0.33 ± 0.02 SD). In the developing embryo the oil globule is located posteriad in the yolk sac. Melanophores begin to appear on the embryonic axis within the first day, and the embryo develops a solid sheath of melanophores on the head and trunk before hatching. Melanophores on the oil globule are concentrated on the inner surface.

Morphology

At hatching the larva is relatively undifferentiated and has a large ovoid yolk sac (ca. 0.9 × 1.5 mm). During the yolk-sac period relative snout-anus length and overall body depth decrease as the yolk is depleted (Table 1), and at the termination of the yolk-sac stage the gut begins to coil. The pectoral fin buds appear about midway through the yolk-sac period and have a well-differentiated base and blade by the end of the period.

During the preflexion and flexion stages relative snout-anus length, head length, head width, snout length, and body depth increase while relative eye diameter decreases gradually (Tables 1, 2). At notochord flexion, larvae have attained their highly characteristic morph—a massive head with large jaws, a pronounced convex dorsal profile, and a deep, robust trunk region that tapers gradually to a narrow caudal peduncle. In postflexion larvae there is a con-

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[1] Manuscript (in preparation) on early stages of sciaenid species off California.

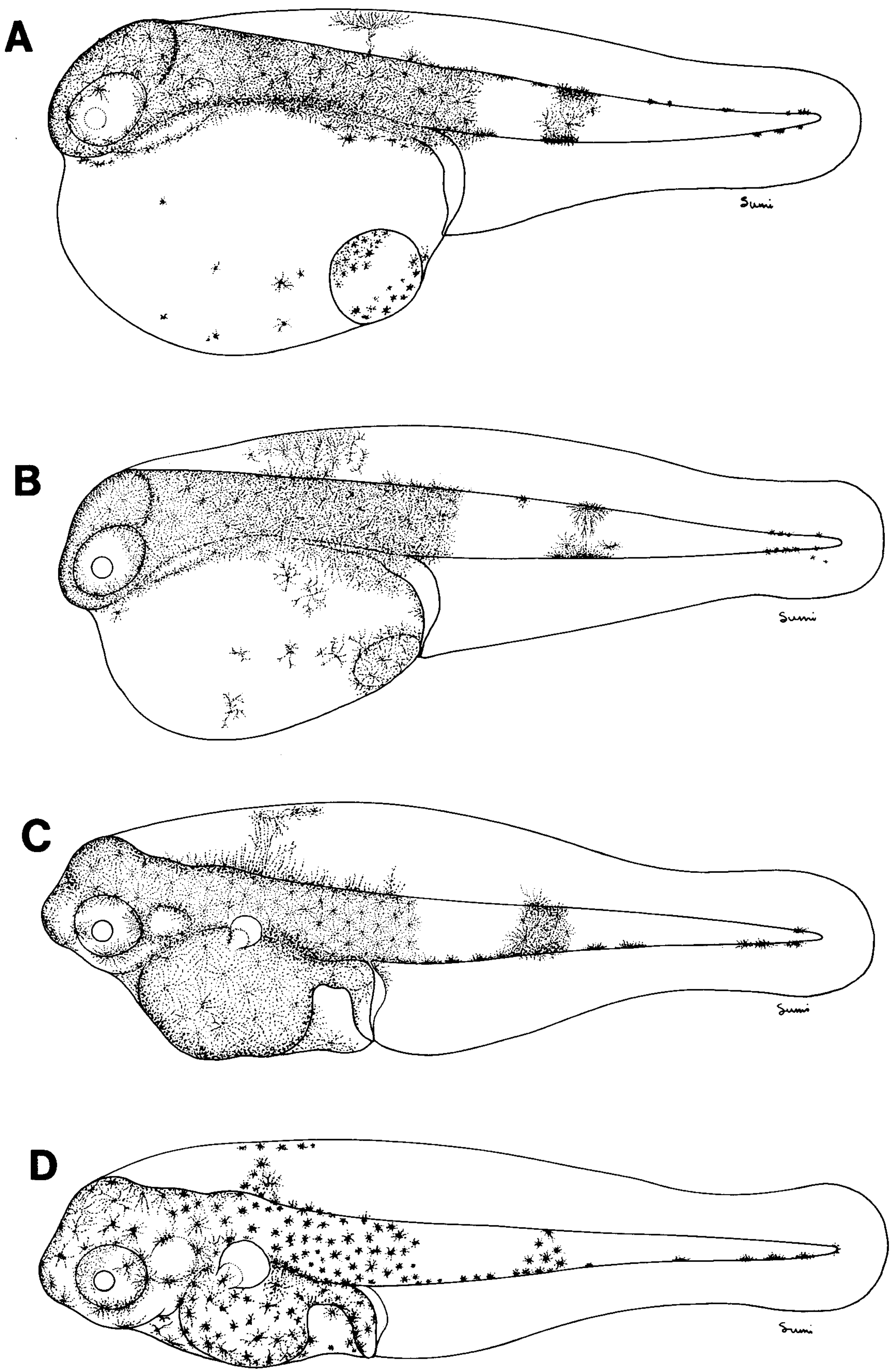

Figure 1. Yolk-sac larvae of *Atractoscion nobilis* from July 13, 1980, spawning. *A.* 2.8 mm, day 3; *B.* 3.2 mm, day 3; *C.* 3.5 mm, day 4; *D.* 3.7 mm, day 5.

TABLE 1
Measurements (mm) of Early Stages of *Atractoscion nobilis*

Body length	Age (days)	Snout-anus distance	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Yolk sac length	Yolk sac depth	Oil globule diameter
2.8	3	1.6	0.76	0.42	0.10	0.27	1.1	—	—	—	1.5	0.90	0.36
3.2	3	1.7	0.70	0.47	0.15	0.30	0.94	—	—	—	1.3	0.86	0.36
3.5	4	1.6	0.75	0.46	0.13	0.32	0.81	—	0.15	—	0.81	0.57	0.35
3.7	5	1.6	0.78	0.55	0.18	0.34	0.71	—	0.27	—	0.57	0.50	0.26
3.5	7	1.6	0.91	0.65	0.17	0.32	0.81	0.19	0.30	—	—	—	0.15
3.7	7	1.7	0.90	0.74	0.16	0.37	0.96	0.22	0.31	—			
4.0	8	1.8	1.0	0.79	0.22	0.40	1.0	0.25	0.35	—			
4.2	10	1.9	1.2	0.81	0.28	0.41	1.0	0.26	0.42	—			
4.5	10	2.1	1.2	0.88	0.25	0.44	1.2	0.28	0.44	—			
4.7	10	2.3	1.3	0.90	0.28	0.48	1.3	0.29	0.48	—			
5.1	14	2.4	1.4	1.0	0.35	0.49	1.5	0.29	0.52	—			
5.2	15	2.6	1.3	1.0	0.3	0.53	1.5	0.35	0.52	0.08			
5.5	15	2.6	1.5	1.2	0.38	0.55	1.7	0.36	0.60	0.08			
5.7	15	2.8	1.7	1.2	0.50	0.62	1.8	0.40	0.62	0.11			
5.9	15	2.9	1.7	1.2	0.50	0.64	1.9	0.46	0.60	0.10			
6.0	18	2.9	1.8	1.4	0.51	0.67	2.0	0.52	0.62	0.13			
6.2	18	3.1	2.0	1.5	0.48	0.68	2.1	0.46	0.65	0.20			
6.5	22	3.5	2.0	1.5	0.54	0.67	2.2	0.63	0.75	0.33			
6.8	22	4.0	2.3	1.6	0.50	0.83	2.6	0.80	0.76	0.49			
7.0	25	4.0	2.4	1.7	0.58	0.84	2.6	1.0	0.75	0.72			
7.4	25	4.2	2.6	1.9	0.66	0.89	2.8	1.2	0.81	0.88			
7.8	25	4.6	2.8	1.8	0.64	0.88	2.8	1.2	0.78	0.85			
8.2	25	5.1	3.0	1.9	0.62	0.94	2.9	1.4	0.80	1.0			
8.8	30	5.4	3.1	2.1	0.86	1.0	3.6	1.9	0.84	1.5			
9.2	30	5.6	3.2	2.4	0.95	1.0	3.5	1.8	0.83	1.7			
9.6	30	6.1	3.3	2.6	0.90	1.1	3.8	2.1	1.0	1.8			
10.0	29	6.4	3.4	2.5	0.92	1.0	3.6	2.0	0.84	1.7			
10.5	37	7.2	3.8	2.5	1.1	1.2	3.9	2.6	0.92	—			
10.7	37	7.2	4.0	2.6	1.0	1.2	3.8	3.0	1.0	2.0			
11.3	37	7.1	4.2	2.6	1.1	1.3	4.1	3.0	1.0	2.4			
11.7	37	7.8	4.2	2.7	1.1	1.3	4.2	2.9	1.0	2.3			
12.0	37	7.8	4.4	2.9	1.2	1.3	4.4	3.0	0.94	2.5			
12.2	37	7.8	4.3	2.9	1.2	1.3	4.2	3.3	1.0	2.7			
12.8	44	8.3	4.5	3.0	1.2	1.4	4.5	3.5	1.0	2.7			
13.1	36	9.2	5.0	2.9	1.2	1.5	4.8	3.6	1.0	2.9			
13.9	36	9.3	5.1	3.0	1.2	1.5	4.8	3.7	1.1	2.9			
14.9	44	10.3	5.2	3.5	1.3	1.7	5.2	4.2	1.1	3.6			
15.5	52	10.8	5.6	3.3	1.5	1.8	5.2	3.8	1.1	3.3			
15.8	48	11.3	6.3	3.3	1.9	1.5	4.9	4.2	1.1	3.7			
17.1	44	11.7	5.8	3.8	1.8	1.5	6.1	4.8	1.2	3.8			
17.2	49	11.8	7.2	3.4	1.5	1.9	6.3	5.3	1.1	4.3			
17.7	42	12.2	6.2	3.4	1.6	1.9	5.5	4.5	1.2	3.8			
18.7	48	13.3	7.5	4.0	1.9	2.1	6.3	5.3	1.2	3.8			
20.2	46	13.8	7.5	4.2	1.4	1.8	6.8	5.5	1.3	5.2			
20.5	46	14.2	7.3	4.2	1.6	2.0	6.7	5.6	1.3	4.8			
22.8	46	16.2	8.5	5.0	1.9	2.3	7.5	5.8	1.3	5.3			
23.0	46	16.2	7.8	4.5	2.0	2.2	7.6	6.0	1.4	5.3			
27.3	57	19.3	8.8	5.0	1.9	2.5	8.8	6.7	1.6	6.2			
38.1	76	26.6	13.8	6.0	2.7	3.5	10.7	8.0	1.9	6.3			
38.4	76	26.3	13.0	5.4	2.7	3.3	10.8	—	2.0	6.3			
53.6		37.1	17.2	7.2	4.2	3.7	14.0	9.7	2.5	10.0			
64.7		45.1	20.3	8.8	5.0	4.3	17.0	11.3	2.5	11.7			
75.2		51.9	22.8	10.0	5.3	5.2	20.2	12.7	3.2	13.3			
82.0		57.3	24.6	9.5	7.0	5.3	22.2	—	3.4	13.6			
98.4		69.5	30.3	13.0	6.7	5.8	24.7	—	4.2	15.3			

Specimens between dashed lines are undergoing notochord flexion. Specimens between solid lines are reared juveniles. Specimens below solid line are juveniles from Scripps Institution of Oceanography fish collection.

tinued relative increase in snout-anus length. Relative head length and body depth are slightly greater than in the previous stage. Relative snout length remains constant, but relative head width and eye diameter continue to decrease slightly. There is a gradual deepening of the body during this stage, to become somewhat slab-sided, and the entire dorsal profile becomes strongly arched, tapering abruptly at the caudal pedun-

TABLE 2
Morphometry of Larvae and Early Juveniles of *Atractoscion nobilis*

	Snout-anus distance	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral base depth	Pelvic fin length
	Body length	Body length	Head length	Head length	Head length	Body length	Body length	Body length	Body length
Preflexion									
$\bar{x}$ ± SD	47.6 ± 4.06	25.1 ± 2.69	69.9 ± 7.43	20.2 ± 3.26	38.5 ± 3.58	26.6 ± 5.18	6.0 ± 0.33	8.6 ± 1.90	—
(range)	(43.2 – 57.1)	(21.1 – 28.6)	(55.3 – 82.2)	(13.2 – 25.0)	(34.2 – 43.6)	(19.2 – 39.3)	(5.4 – 6.3)	(4.3 – 10.2)	—
N	11	11	11	11	11	11	7	9	0
Flexion									
$\bar{x}$ ± SD	50.8 ± 3.75	29.7 ± 2.77	74.4 ± 3.81	26.0 ± 2.95	36.0 ± 2.86	32.8 ± 2.75	8.2 ± 1.81	10.8 ± 0.61	3.0 ± 2.07
(range)	(47.3 – 58.8)	(25.0 – 33.8)	(69.6 – 80.0)	(21.7 – 29.4)	(31.6 – 40.8)	(28.8 – 38.2)	(6.5 – 11.8)	(10.0 – 11.6)	(1.5 – 7.2)
N	8	8	8	8	8	8	8	8	8
Postflexion									
$\bar{x}$ ± SD	64.2 ± 4.02	35.8 ± 1.15	66.7 ± 5.63	25.9 ± 2.21	31.4 ± 1.58	36.4 ± 1.80	23.0 ± 4.61	8.8 ± 1.14	18.3 ± 4.23
(range)	(56.8 – 70.2)	(24.0 – 38.2)	(58.0 – 78.8)	(20.7 – 29.7)	(29.4 – 35.0)	(33.5 – 40.9)	(14.3 – 28.2)	(7.1 – 10.9)	(10.3 – 24.2)
N	19	19	19	19	19	19	19	19	18
Reared Juveniles									
$\bar{x}$ ± SD	69.7 ± 1.20	36.8 ± 2.65	53.4 ± 6.73	22.6 ± 2.57	27.6 ± 2.18	32.4 ± 2.58	26.4 ± 2.49	23.5 ± 1.90	22.2 ± 3.11
(range)	(68.3 – 71.5)	(33.9 – 41.9)	(41.5 – 65.5)	(18.7 – 25.9)	(24.0 – 31.0)	(28.1 – 36.6)	(21.0 – 28.3)	(20.8 – 26.7)	(16.4 – 25.7)
N	12	12	12	12	12	12	11	11	11
Field-Collected Juveniles									
$\bar{x}$ ± SD	69.7 ± 0.63	30.9 ± 0.85	42.1 ± 2.10	24.6 ± 2.42	21.2 ± 1.34	26.3 ± 0.79	17.5 ± 0.60	24.4 ± 1.99	17.3 ± 1.27
(range)	(69.0 – 7.06)	(30.0 – 32.1)	(38.6 – 43.9)	(2.21 – 28.5)	(19.1 – 22.8)	(25.1 – 27.1)	(16.9 – 18.1)	(22.1 – 25.8)	(15.5 – 18.7)
N	5	5	5	5	5	5	3	3	5

Values given for each body part are expressed as percentage of body length or head length.

cle. In reared juveniles relative head width and body depth decrease as the body becomes terete.

Fin Formation/Meristics

Ossification of the principal caudal fin rays begins at the initiation of notochord flexion (ca. 5.6 mm); however, the full complements of 9+8 principal and 8+7 procurrent rays have not begun ossifying until larvae reach about 7.1 and 14.5 mm, respectively (Table 3). Notochord flexion is complete at about 7.0 mm SL. Ossification of rays begins in the other fins about midway through notochord flexion. The full complement of IX-X + I, 19-23 dorsal rays is ossifying just after notochord flexion is complete. Anal fin formation is similar, with the soft rays ossifying first and the full count of I-II, 8-10 present just after flexion. Both fins become lobate in postflexion larvae and early juveniles, as does the caudal fin.

Ossification of rays in the paired fins begins at about 6.0 mm, midway through notochord flexion (Table 3). The full complements of 15-18 pectoral and I,5 pelvic rays are present in early postflexion larvae. The fins enlarge rapidly in the postflexion stage. Average relative pectoral fin length is three times

TABLE 3
Meristics from Cleared and Stained Larvae of *Atractoscion nobilis**

Day	Body length	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Principal caudal fin rays	Procurrent caudal fin rays	Vertebrae	Branchiostegal rays	Pelvic rays
10	4.5	—	—	—	—	—	—	2	—
14	5.0	—	—	—	—	—	3	6	—
15	5.6	—	—	3	4 + 4	—	8	7	—
18	5.8	—	—	6	6 + 6	—	16	7	—
22	6.1	VIII + I,12	—,2	6	7 + 7	—	19	7	—,3
22	6.7	VIII + I,15	—,6	7	8 + 7	—	21	7	I,3
24	7.1	IX + I,18	I,8	12	9 + 8	0 + 1	20	7	I,5
25	7.6	IX + I,20	I,9	13	9 + 8	1 + 1	25	7	I,5
27	9.4	IX + I,22	II,10	16	9 + 8	4 + 4	25	7	I,5
37	9.9	X + I,22	II,10	18	9 + 8	6 + 6	25	7	I,5
35	11.0	X + I,21	II,9	17	9 + 8	7 + 7	25	7	I,5
42	13.5	X + I,19	II,10	17	9 + 8	7 + 7	25	7	I,5
42	14.5	X + I,23	II,10	17	9 + 8	8 + 7	25	7	I,5

*Counts of paired structures taken on left side.

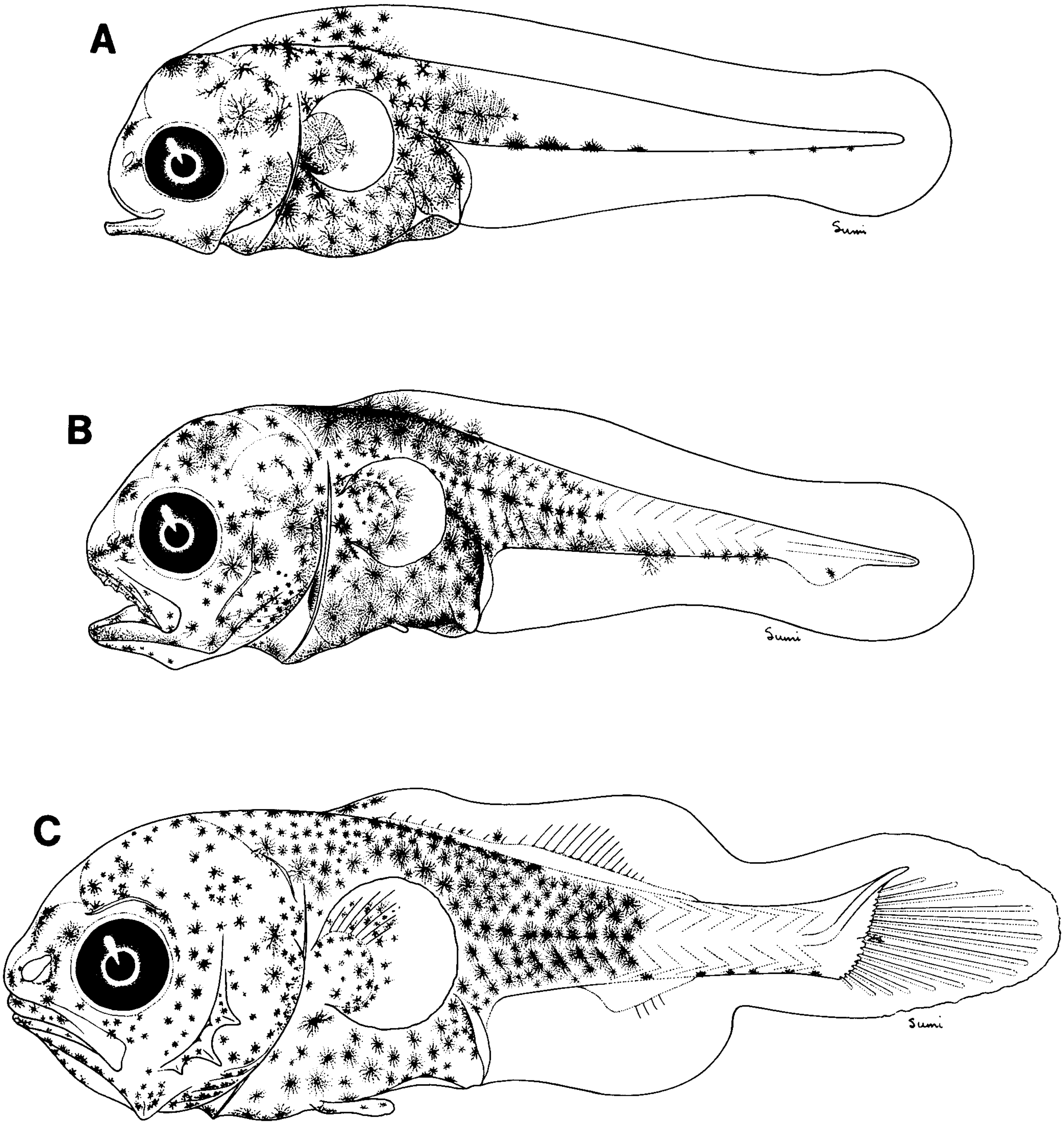

Figure 2. Larvae of *Atractoscion nobilis* from April 12, 1982, spawning. *A.* 3.7 mm, day 8; *B.* 5.1 mm, day 14; *C.* 6.5 mm, day 22.

greater in postflexion larvae than in flexion larvae, and relative pelvic fin length is six times greater. Both fins become lobate to somewhat fan-shaped in postflexion larvae (Figure 3).

Larvae begin to develop an array of head spines just before notochord flexion. The spines of the opercular series of bones appear first, with the preopercle developing the greatest number of spines (Table 4, Figures 3, 4). The posttemporal spines also develop early; the bone becomes trough-shaped, with spines forming on the anterior and posterior upturned edges. Anterior to the posttemporal bone, two scale bones develop in the region of the epiotic, one directly dorsal to the other. They too are trough-shaped and develop spines on the upturned edges. The frontal bone develops a supraocular crest bearing a series of spines. A longitu-

TABLE 4
Development of Head Spines (Left Side) in Larvae of *Atractoscion nobilis*

Bone	Location	Number of spines												
		Day												
		10	14	15	18	22	22	24	25	27	37	35	42	42
		Body Length (mm)												
		4.5	5.0	5.6	5.8	6.1	6.7	7.1	7.6	9.4	9.9	11.0	13.5	14.5
Preopercle	Anterior series	1	2	2	3	4	5	6	5	4	5	15	14	11
	Posterior series	—	2	3	3	3	4	5	5	6	10	8	12	8
Opercle		—	—	1	1	1	1	1	1	2	2	2	2	2
Subopercle		—	—	—	2	1	2	2	2	2	2	3	1	2
Interopercle		—	—	—	1	1	1	1	1	3	4	4	7	4
Posttemporal		—	—	—	—	—	—	—	1	6	10	7	7	6
Frontal	Supraocular	—	—	—	—	—	—	—	—	6	8	3	2	3
Pterotic		—	—	—	—	—	—	—	—	1	4	3	1	4
Scale Bone	Dorsal epiotic region	—	—	—	—	—	—	—	—	1	3	2	2	2
Scale Bone	Ventral epiotic region	—	—	—	—	—	—	—	—	1	4	4	3	3
Lacrymal		—	—	—	—	—	—	—	—	3	4	4	3	—
Dermospherotic		—	—	—	—	—	—	—	—	—	2	2	2	2
Circumorbitals		—	—	—	—	—	—	—	—	—	—	—	+	+

dinal crest develops on the pterotic, and bears up to 4 spines. The lacrymal bone develops 3-4 spines on its ventral margin at about 9.0 mm SL and, soon after, a small trough-shaped dermosphenotic (6th circumorbital) bone with 2 spines develops at the dorso-posterior margin of the orbit. At the end of the larval period 4 other circumorbitals develop around the posterior margin of the orbit, and each develops several spines.

Beginning at about 9.0 mm SL, scales, each with a single spine, appear on the opercle. They increase in number to almost cover the opercle at the end of the larval period.

Pigmentation

White seabass larvae develop two distinctive forms of pigmentation within a single pattern. Both melanophores and xanthophores begin to appear with equal prominence in the embryo; they increase in number and overlay each other almost exactly, to form a bicolored pattern. The following description applies to both melanophores and xanthophores, except as noted.

At hatching the entire head and trunk are pigmented solidly to slightly posteriad of the yolk mass (Figure 1). A postanal band is present on the tail, and, rearward of this, the dorsal and ventral midlines of the tail have melanophores only. This is the only place where both types of pigment cells are not present together. Above the trunk a tuft of pigment extends upward into the finfold and expands at the finfold margin. The oil globule is covered with pigment cells, and pigment is scattered over the yolk. As the yolk sac is depleted the gut mass becomes solidly pigmented, as does the pectoral fin base and, of course, the eye. At the end of the

TABLE 5
Measurements (mm) of Postflexion Larvae of *Cynoscion acoupa maracaiboensis*

Body length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length
7.3	4.2	2.4	0.6	0.56	2.2	—	—	0.16
7.6	4.3	2.8	0.6	0.64	2.5	0.80	0.40	0.72
7.8	4.4	2.7	0.6	0.64	2.7	0.88	0.44	0.68
8.1	4.8	2.9	0.7	0.70	2.7	0.92	0.52	0.76
8.9	5.6	3.3	0.8	0.80	2.9	1.2	0.64	0.88
9.3	6.2	3.4	0.9	0.72	2.8	0.80	0.64	0.72
10.3	6.9	3.7	1.0	0.80	3.2	1.5	0.80	1.1
10.5	7.0	4.1	0.96	1.0	3.2	1.84	0.64	1.2
13.5	9.4	5.3	1.3	1.1	4.2	—	0.76	2.1
14.2	9.5	5.2	1.1	1.3	4.4	3.1	0.84	2.1
$\bar{x}$ ± SD	6.29 ± 5.10	36.3 ± 2.09	8.8 ± 0.81	23.2 ± 1.56	31.8 ± 1.51	12.4 ± 4.56	6.1 ± 1.12	10.0 ± 3.74
(range)	(56.4 – 69.8)	(32.3 – 39.5)	(7.6 – 9.9)	(20.3 – 24.8)	(29.6 – 34.4)	(6.0 – 21.7)	(3.8 – 7.8)	(2.2 – 15.4)
N	10	10	10	10	10	10	10	10

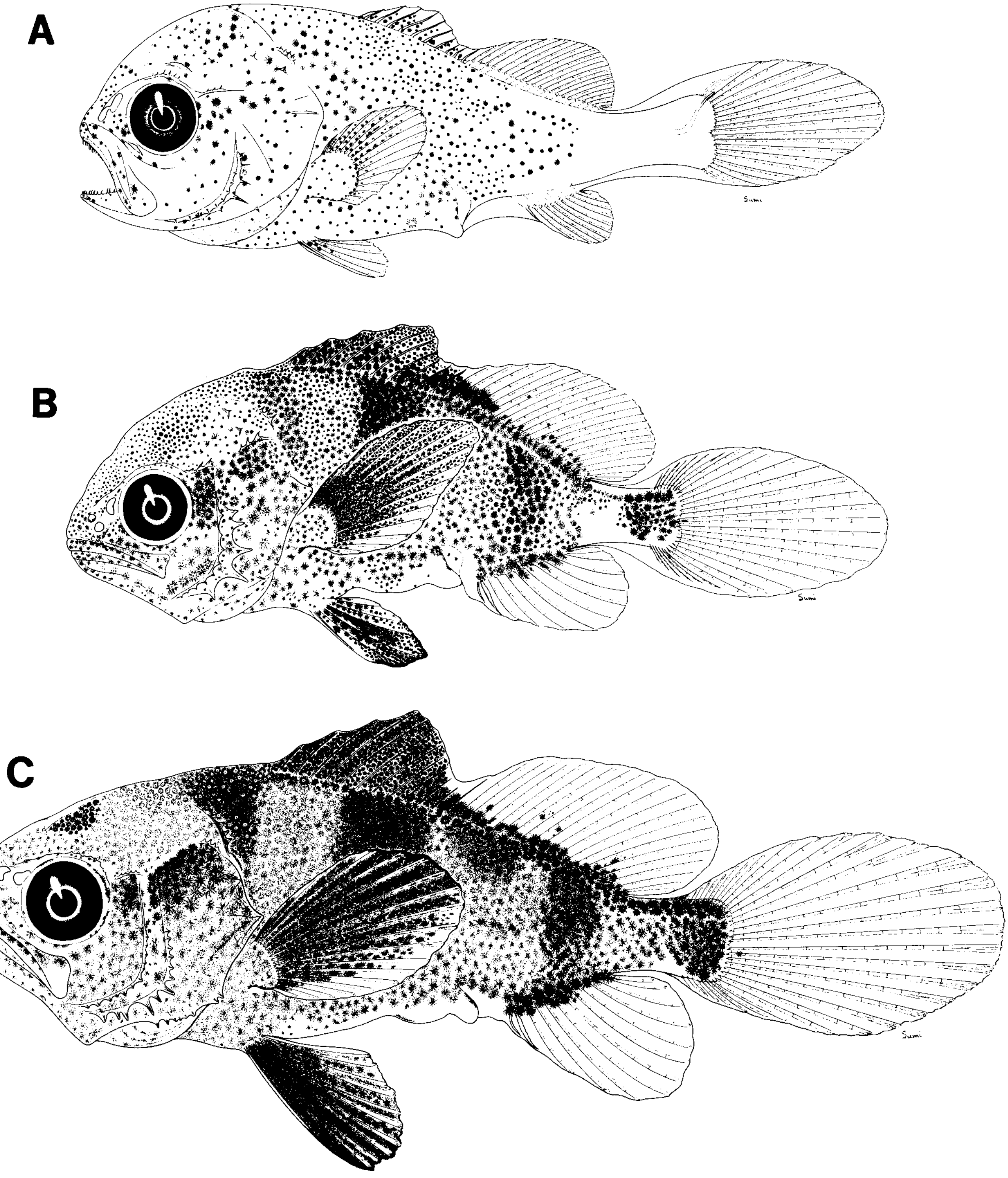

Figure 3. Larvae of *Atractoscion nobilis*. *A*. 8.3 mm, specimen reared from planktonic egg collection July 6, 1978, day 25. Note contracted state of melanophores; *B*. 10.7 mm, from April 12, 1982, spawning, day 37; *C*. 14.9 mm, from April 12, 1982, spawning, day 44.

yolk-sac period a postanal band is still present, but the dorsal midline melanophores are absent.

At the end of the first week (ca. 3.7 mm) the postanal band disappears. The postanal ventral midline series remains, with the melanophores of the anterior half of the series larger than those of the posterior half. The melanophores of the body cloak lying over the horizontal septum posterior to the pectoral fin appear larger and stand out as a line. Pigment begins to form on the pectoral fin blades.

Figure 4. Juveniles of *Atractoscion nobilis*. *A*. 33.5 mm SL, day 72, from April 12, 1982, spawning. *B*. 64.5 mm SL, day 103, from January 26, 1983, spawning.

During the remainder of the preflexion period the body sheath extends posteriad to almost midway on the tail, and pigment increases on the pectoral fin. During notochord flexion the body sheath progresses posteriad; pigment increases on the pectorals; and pigment begins to appear on the developing anterior dorsal fin and the pelvic fin.

In postflexion larvae the body sheath continues to expand posteriad, and the rapidly enlarging paired fins become heavily pigmented, as does the spinous dorsal fin. At about 10.0 mm SL, only the caudal peduncle and the caudal, soft dorsal, and anal fins remain unpigmented. A pigment patch appears at the base of the caudal fin (at ca. 10 mm), over the hypurals, and expands to meet the body sheath; thus the body is completely covered by ca. 15 mm. Pigment extends onto the bases of the soft dorsal and anal fins, but the caudal fin remains unpigmented until after the larval period.

Vertical pigment bands are usually present in *A. nobilis* as small as 10.5 mm SL (Figure 3B). The nape band and a band under the middle of the first dorsal fin (spines 5-9) are the first to appear. These are soon followed by a band under the middle of the second dorsal fin (rays 13-16), and at this stage the heavily pigmented caudal fin base also has the appearance of a band (Figure 3C). Some late-flexion larvae have a band under the anterior portion of the second dorsal fin (rays 3-7). Four intermediate bands or saddles develop between these 5 primary bands in juveniles, but these are fainter and narrower than the primary bands (Figure 4).

TABLE 6
Development of Head Spines (Left Side) in Postflexion Larvae of *Cynoscion acoupa maracaiboensis*

Bone	Location	Number of spines								
		Body length (mm)								
		6.9	7.5	8.3	8.4	9.8	10.3	10.7	13.5	14.2
Preopercle	Anterior series	3	4	4	6	4	5	4	7	8
	Posterior series	3	4	4	5	4	4	4	4	5
Opercle		—	—	—	1	2	2	2	2	2
Subopercle		1	1	2	1	1	2	1	1	3
Interopercle		1	1	1	1	1	1	1	1	2
Posttemporal		1	1	2	1	3	5	2	6	8
Frontal	Supraocular	2	3	3	4	6	6	6	10	11
Pterotic		—	—	—	—	—	1	—	2	3
Scale Bone	Dorsal epiotic region	—	—	—	—	—	—	1	2	2
Scale Bone	Ventral epiotic region	—	—	—	—	—	—	—	3	3
Lacrymal		—	—	1	—	1	1	1	1	—
Dermosphenotic		—	—	—	—	1	1	—	1	1
Circumorbitals		—	—	—	—	—	—	—	—	+

Comparison with Related Genera

Early life stages of *A. nobilis* differ markedly from those of 5 species of *Cynoscion* described in the literature: *C. acoupa maracaiboensis*[2]; *C. leiarchus* (Sinque 1980); *C. nebulosus* (Hildebrand and Cable 1934; Fable et al. 1978; Powles and Stender 1978); *C. nothus* (Hildebrand and Cable 1934; Powles and Stender 1978); *C. regalis* (Welsh and Breder 1923; Pearson 1941; Powles and Stender 1978); *C. striatus* (Weiss 1981). Egg diameters—known for *C. acoupa* (0.79-0.89 mm), *C. nebulosus* (0.70-0.85 mm), and *C. regalis* (0.80-1.05 mm)—are smaller than in *A. nobilis*. *Cynoscion* species, with the exception of *C. nebulosus*, are lightly pigmented at hatching, and first-feeding larvae have melanophores along the dorsal and ventral midlines, over the dorsal surface of the gut, and on the head, usually at the opercular region. With the exception of *C. nebulosus*, dorsal midline pigment is soon lost, and pigment is added to the head and over the body in patches that form vague bars in postflexion larvae. In *C. nebulosus* the dorsal and ventral midline pigment intensifies with development, as does a prominent lateral pigment line that extends along most of the body and forward as internal head pigment. This becomes a prominent irregular stripe in postflexion larvae and in juveniles.

As in *Atractoscion*, *Cynoscion* larvae develop a large bulbous head with large jaws; however, the snout and gut are shorter in *Cynoscion*. The body is rounded in cross section and tapers gradually posteriad from the head, contrasting with the deep, robust body form of *A. nobilis*. Larvae of *C. nebulosus* differ from other *Cynoscion* in having a more slender profile.

Series of postflexion larvae of *C. acoupa maracaiboensis* were measured and cleared and stained to compare morphometrics, head-spine development, and meristics with *A. nobilis* (Tables 5-7). Relative snout length, eye diameter, pectoral and pelvic fin length are markedly smaller in *C. acoupa*. Spines de-

TABLE 7
Meristics of Postflexion Larvae of *Cynoscion acoupa maracaiboensis*

Body length (mm)	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Principal caudal fin rays	Procurrent caudal fin rays	Vertebrae	Branchiostegal rays	Pelvic rays
6.9	XIII + I,18	I,8	—	9 + 8	—	25	7	I,4
7.5	X + I,19	II,8	15	9 + 8	3 + 3	25	7	I,5
8.3	IX + I,21	II,8	12	9 + 8	3 + 3	25	7	I,5
8.4	X + I,22	II,8	17	9 + 7	6 + 5	25	7	I,5
9.8	X + I,19	II,8	16	9 + 8	6 + 5	25	7	I,5
10.3	X + I,19	II,8	17	9 + 8	6 + 5	25	7	I,5
10.7	X + I,20	II,8	16	9 + 8	7 + 6	25	7	I,5
13.5	X + I,20	II,8	17	9 + 8	9 + 8	25	7	I,5
14.2	X + I,19	II,8	18	9 + 8	10 + 9	25	7	I,5

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[2] Olivares, R. MS. Observaciones preliminares sobre el desarollo de huevos y larvas vitelinas de la Curvina de Lago. *Cynoscion acoupa maracaiboensis* (Pisces: Sciaenidae).

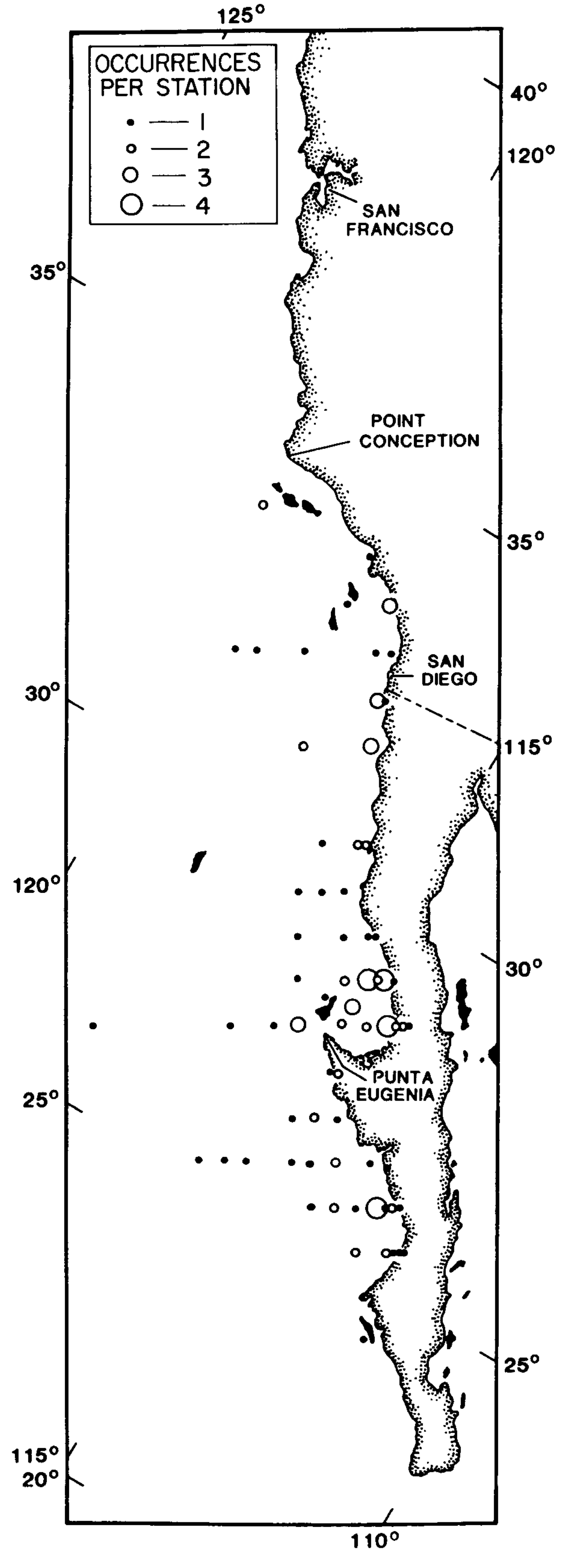

Figure 5. Occurrences of *Atractoscion nobilis* larvae in all CalCOFI samples taken from 1950 to 1978.

velop on the same bones, but there are fewer spines on the preopercle and lacrymal compared with *A. nobilis*.

To our knowledge the only species of sciaenid with early stages similar to *A. nobilis* is *Sciaena umbra* from the eastern Atlantic, Mediterranean, and Black Sea (Montalenti 1937; Dekhnik 1973). Egg diameter is 1.15-1.30 mm, with an oil globule diameter of 0.23-0.30 mm (Dekhnik 1973). Larvae are 2.5-2.6 mm at hatching and develop a body form and pigment pattern very similar to that of *A. nobilis*. Late-stage larvae of the western Atlantic species, *Larimus fasciatus*, have large, heavily pigmented paired fins, but the body pigment is not a solid cloak as in *A. nobilis* (Hildebrand and Cable 1934).

DISTRIBUTION

Atractoscion nobilis larvae occurred in only 104 of all CalCOFI tows made during 1950-78. Of these, 98 occurrences were recorded in tows made in April-August in a coastal zone with a seaward limit to station 60. Only 2 occurrences were on stations seaward of station 60—station 120.90 on cruise 5106 and station 130.65 on cruise 5906. Latitudinal limits were from CalCOFI station 83.55 near the northern Channel Islands to station 143.26 near Santa Margarita Island and Magdalena Bay, Baja California (Figure 5). Fifteen percent of the white seabass occurrences were in southern California waters, and the remaining 85% were along Baja California, with 50% north and 35% south of Punta Eugenia. The highest concentrations of larvae were found in the inshore regions of Sebastian Viscaino Bay and San Juanico Bay, Baja California. *A. nobilis* larvae were collected from January-October, but 92% of the occurrences and 95% of the individuals were taken from May-August. The peak month was July, with 55% of the occurrences and 60% of the individuals.

The size-frequency distribution of the white seabass larvae collected during the CalCOFI sampling program was narrow, with a mean length of 3.4 mm ± 1.10 SD and a range of 1.6-7.2 mm in the 122 larvae measured. Latitudinal trends in spawning season could not be determined with this limited length-frequency data.

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THE FEEDING HABITS AND DISTRIBUTION OF JUVENILE-SMALL ADULT CALIFORNIA HALIBUT *(PARALICHTHYS CALIFORNICUS)* IN COASTAL WATERS OFF NORTHERN SAN DIEGO COUNTY

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ABSTRACT

The stomach contents of 336 California halibut 109-689 mm standard length (SL) were examined. Halibut were trawled from 6-m, 18-m, and 30-m depths off San Onofre and near Oceanside from March 1981 to March 1982. The relative influences on diet of depth of capture, predator body size, and the seasonal abundances of major prey types were examined. Major prey by frequency of occurrence were northern anchovy *(Engraulis mordax)* and large mysids, notably *Neomysis kadiakensis*. Northern anchovy dominated by weight; mysids dominated in terms of numbers consumed. Halibut <25 cm SL ate mostly mysids and some larval fishes; halibut >30 cm SL ate mostly northern anchovy and other juvenile and adult fishes. Fish of intermediate (25-30 cm SL) size consumed both prey types in roughly equal frequency. Prevalence of anchovy in the diet tracked the seasonal (summertime) increase of anchovy in nearshore waters. Extent of feeding on mysids reflected mysid abundance much less perfectly. Depth of capture influenced diet little, except indirectly, since relatively small halibut tended to predominate at the shallowest depth sampled.

Otter trawl, bag seine, and ichthyoplankton data suggest that the California halibut spawns in nearshore coastal waters, utilizes embayments as nursery grounds while a young juvenile (age-group 0 and yearling), and inhabits shallow, open coastal waters during late juvenile and later life-history stages.

RESUMEN

Se examinó el contenido estomacal de 336 *Paralichthys californicus* (Halibut de California) de 109-689 mm de longitud normal. Estos peces capturaron en arrastres efectuados a 8, 18 y 30 m de profundidad, frente a San Onofre y en las cercanías de Oceanside (California) durante el período de Marzo 1981 a Marzo 1982. Se relaciona la influencia de la profundidad de captura y la talla del depredador,con la dieta y abundancia de la presa en la región. El alimento que aparecía con mayor frecuencia en el estómago era la anchoa *(Engraulis mordax)*, y Misidáceos grandes, principalmente *Neomysis kadiakensis*. La anchoa dominaba en peso y los Misidáceos en número. *Paralichthys californicus* de menos de 25 cm de longitud normal se alimentaba frecuentemente de Misidáceos junto con algunas larvas de peces, y los de más de 30 cm devoraban con preferencia anchoas y otros peces, tanto adultos como jóvenes. Los peces de tallas intermedias (25-30 cm de longitud normal) consumían ambos tipos de presa con igual frecuencia. La predominancia de la anchoa en la dieta marcaba el incremento de este pez en la regioń costera durante el verano. La captura de Misidáceos indicaba con menor precisión la abundancia de estos crustaceos. La profundidad habitada por *Paralichthys californicus* influye, aunque indirectamente, en la dieta, ya que los ejemplares pequeños tienden a predominar en los estratos menos profundos.

Los datos obtenidos con redes de arrastre y de cerco, así como los análisis del ictioplancton, indican que *Paralichthys californicus* efectua la puesta en aguas costeras, utilizando los bancos como zonas de cria y habitando ahí los jóvenes hasta de un año de edad, mientras que los estados más avanzados de la fase juvenil y adultos habitan aguas someras y costeras no protegidas.

INTRODUCTION

The California halibut *(Paralichthys californicus)* is a species of major economic importance in California. However, its sport and commercial catches have steadily declined since catch records have been kept (Frey 1971). In recent years, the southern California partyboat fishery (MacCall et al. 1976) and the statewide partyboat and commercial catches (e.g., see Oliphant 1979) have remained at low levels. Possible explanations for this decline are naturally occurring population fluctuation, overexploitation of adult stocks by commercial fishing, alteration of nursery grounds, a northern shift in the center of population density (Frey 1971), or, most probably, some combination of the four explanations. A more complete understanding of the feeding habits and other details

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of the life history of this important sport and commercial species could help avert further declines in its abundance.

Food habits data are fragmentary for the various life history stages of California halibut. The foods of adult halibut have been generally described by Frey (1971) for fish caught in trawls throughout California waters; by Quast (1968) and Feder et al. (1974) for halibut in or near giant kelp *(Macrocystis)* beds off southern California; and by Ford (1965) for fish on the La Jolla intercanyon shelf near San Diego. Haaker (1975) and Barry and Cailliet (1981) described the food habits of juvenile halibut in Anaheim Bay, Orange County, and Elkhorn Slough, Monterey County, respectively.

This study together with that of Roberts et al. (1982) provides the first comprehensive food habits data for the juveniles and small adults of this species in southern California coastal waters. Specifically, we characterize the diet of California halibut in terms of body size, depth of capture, seasonal variation, and their interrelationships. We further relate halibut diet to the abundance of major prey estimated during the same annual period.

METHODS

Methods of Capture

California halibut were collected at two longshore locations off San Onofre and about 18 km downcoast, near Oceanside, at 6-m, 18-m, and 30-m bottom depths (Figure 1). Standard (7.5 m) otter trawls with 1.3-cm stretch mesh cod-end liners (Mearns and Allen 1978) were used. During a major yearlong collection period from March 1981 through March 1982, 243 night trawls were made; an additional 34 daytime trawls were made during April and May 1981. Incidental food habits data for halibut captured after March 1982 are included for comparison but were not rigorously analyzed.

Stomach Analysis

The alimentary tract of each halibut collected was fixed in 10% Formalin immediately following capture. Fish were macroscopically sexed, measured (SL in mm), and weighed (0.1 g, wet weight) in the laboratory.

The viscera were fixed for a minimum of 4 days, soaked in tap water for 24-48 hrs, and stored in 70% ethanol prior to further examination.

Prey items in the stomachs were identified to the lowest possible taxa and sex/maturity classes. All prey items were assigned reconstructed wet weights; several methods were used. Clothier (1950) was used to identify fish skeletal remains. Fish prey were assigned reconstructed (undigested) wet weights derived from standard length-wet-weight regressions. Partial remains of fish prey, identified to species, were assigned lengths by comparing key vertebral measures to reference specimens. Mysids were assigned reconstructed weights based on sex and maturity criteria rather than length classes (L. Gleye, Marine Ecological Consultants of Southern California, unpubl. data.).

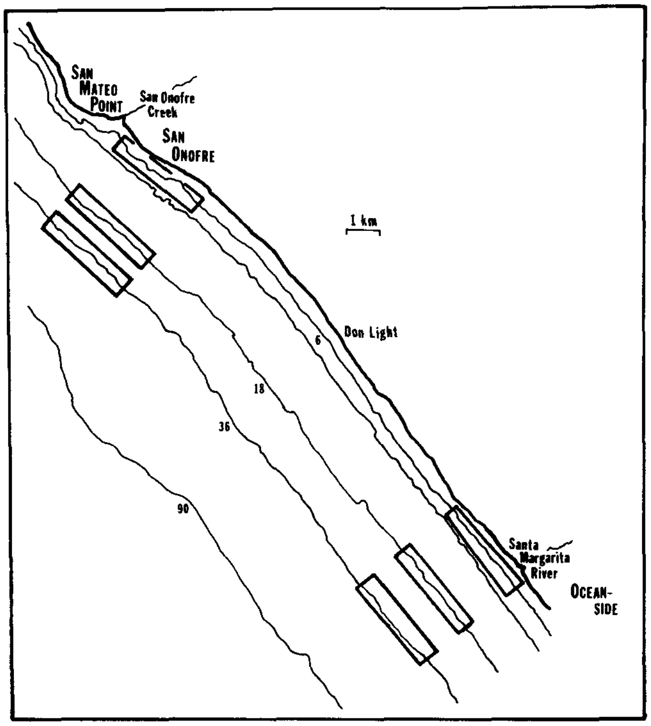

Figure 1. Chart of the nearshore waters between San Clemente and Oceanside, California, showing the locations off San Onofre and near Oceanside at which California halibut were trawled. Depth contours are meters below MLLW.

Statistical Analysis of Diet

Major prey categories were tabulated by percent frequency of occurrence (% FO), percent reconstructed weight (% W), and percent number (% N) using all halibut stomachs collected from March 1981-March 1982. An index of relative importance (IRI; Pinkas et al. 1971) was calculated based on these parameters. Prey categories accounting for less than 0.4% of the total IRI were pooled to form a single group. Prey categories were then ranked by their IRI.

Day samples (16 stomachs with food) were pooled with night samples (26 stomachs) for halibut collected in April and May 1981. There was no statistical difference ($P > 0.1$) between total stomach contents of these day and night sample fish in mean percentage digested (estimated by eye to the nearest 25%). There also was no diel difference in mean reconstructed weight of prey standardized by halibut weight (all $P >$

0.1). Stomach samples of fish from both longshore locations were pooled, since there was no difference ($P > 0.2$) between them in the mean weight of either of two major prey taxa (northern anchovy, mysids) scaled for halibut weight.

Interrelations among halibut size, depth of capture, and % FO of two major prey (anchovy, mysids) were examined with a threeway test of independence (G-test; Sokal and Rohlf 1969:601). The analysis was restricted to halibut captured at the 6-m and 18-m depths. Too few halibut were caught at the 30-m depth to be included in the analysis. Seasonal variation in diet also could not be simultaneously examined because of insufficient sample sizes. Halibut were divided into two length classes (≤245 and >245 mm SL) in order to minimize the number of cells containing zeros. These length classes also roughly reflect the size at which a major dietary shift occurs (see Results). Stomachs in which anchovies and mysids co-occurred were excluded from this analysis, because the added variability obscured the distinction between occurrence of the two types.

Estimates of Prey Abundance

The relative abundance (mean monthly CPUE) of northern anchovy *(Engraulis mordax)* was estimated from lampara seine hauls made at 5-16-m depths in the San Onofre-Oceanside area from March 1981 through March 1982 (E. DeMartini, unpubl. data). Abundances of mysids were estimated based on epibenthic sled samples from 6-m, 8-m, 12-m, 15-m, 23-m, 30-m, and 37-m depths in the San Onofre-Oceanside area on four daytime cruises (June, September, December 1981; March 1982) by Marine Ecological Consultants of Southern California (S. Watts, pers. comm.). For additional description of sampling gears see Roberts et al. (1982). Mysid abundance was expressed as numbers per m^2 area integrated throughout the water column from surface to seabed. Two rare species of mysids not present in our halibut stomach samples were excluded from the mysid abundance estimate.

RESULTS

Prey Eaten

Northern anchovy and mysids were the two most important prey types when ranked by IRI (Table 1). Northern anchovy had the greatest total frequency of occurrence in halibut stomachs and constituted nearly 82% by weight of all prey. Two mysid species, *Neomysis kadiakensis* and *Metamysidopsis elongata*, plus northern anchovy accounted for >90% of the total IRI. Each of the remaining prey taxa accounted for <0.4% of total IRI. Of the 336 California halibut captured (size range 124-476 mm SL), 155 (46%) had empty stomachs. There were no marked differences in the number of empty stomachs among the depths, seasons, and halibut body sizes examined. Large adult halibut seemed to specialize on fishes larger than northern anchovy. For example, the largest halibut (689 mm SL) that we captured during the major, yearlong part of the study had consumed two adult white croaker, *Genyonemus lineatus*. Another large adult halibut (820 mm SL) captured in May 1982 had consumed two adult hornyhead turbot, *Pleuronichthys verticalis*.

TABLE 1
Major Prey Categories of California Halibut, *Paralichthys californicus*, Ranked by IRI*

	IRI (%)	% W	% N	% FO[1]
Northern anchovy	3675 (54.0)	81.6	7.1	41.4
Small mysids[2]	1608 (23.7)	0.3	59.1	27.1
Large mysids[3]	1066 (15.7)	1.6	29.6	34.2
Other fish species[4]	440 (6.5)	16.0	3.0	23.2
Caridean shrimp	9 (0.1)	0.4	0.8	7.2
All other prey	2 (0.0)	0.1	0.4	3.9

[1] Sums to >100% caused by co-occurrences of prey categories in stomachs.
[2] All mysid species, including *Neomysis* spp immatures and juveniles.
[3] *Neomysis* spp adults only.
[4] Includes unidentifiable fish remains.
*(Index of Relative Importance: Pinkas, Oliphant, and Iverson 1971). Components of the IRI—percent of total weight (%W), percent of total number (%N), and percent frequency of occurrence (%FO) of prey in halibut stomachs—are also given. Data represent 336 stomachs (155 empty) of halibut trawled at 6-m, 18-m, and 30-m depths from off San Onofre and near Oceanside from March 1981 through March 1982.

Factors Influencing Prey Eaten

Both halibut body size (S, either ≤245 mm or >245 mm SL) and depth of capture (D, 6 or 18 m) are related to the percent frequency of occurrence (% FO) of two (northern anchovy, mysid) major prey types (Table 2). The size of halibut influenced the type and frequency of prey consumed. Larger juvenile and small adult (>300 mm SL) halibut fed primarily on northern anchovy; small juvenile (<245 mm SL) halibut fed on mysids and larval fish; and intermediate halibut fed on both northern anchovy and mysids to a large extent (Figure 2).

Halibut captured at 6 m were smaller than fish captured at 30 m (Table 2; Figure 3). However, the prey type (mysids or anchovy) in stomachs and the depth of capture were independent for halibut of all sizes pooled (Table 2). This indicates that the relative frequency of the two prey consumed is primarily dependent on the size of halibut, regardless of depth.

Monthly variation in the % FO of mysids in stomachs did not appear to track the monthly variation in mysid abundance (Figure 4). For example, the % FO

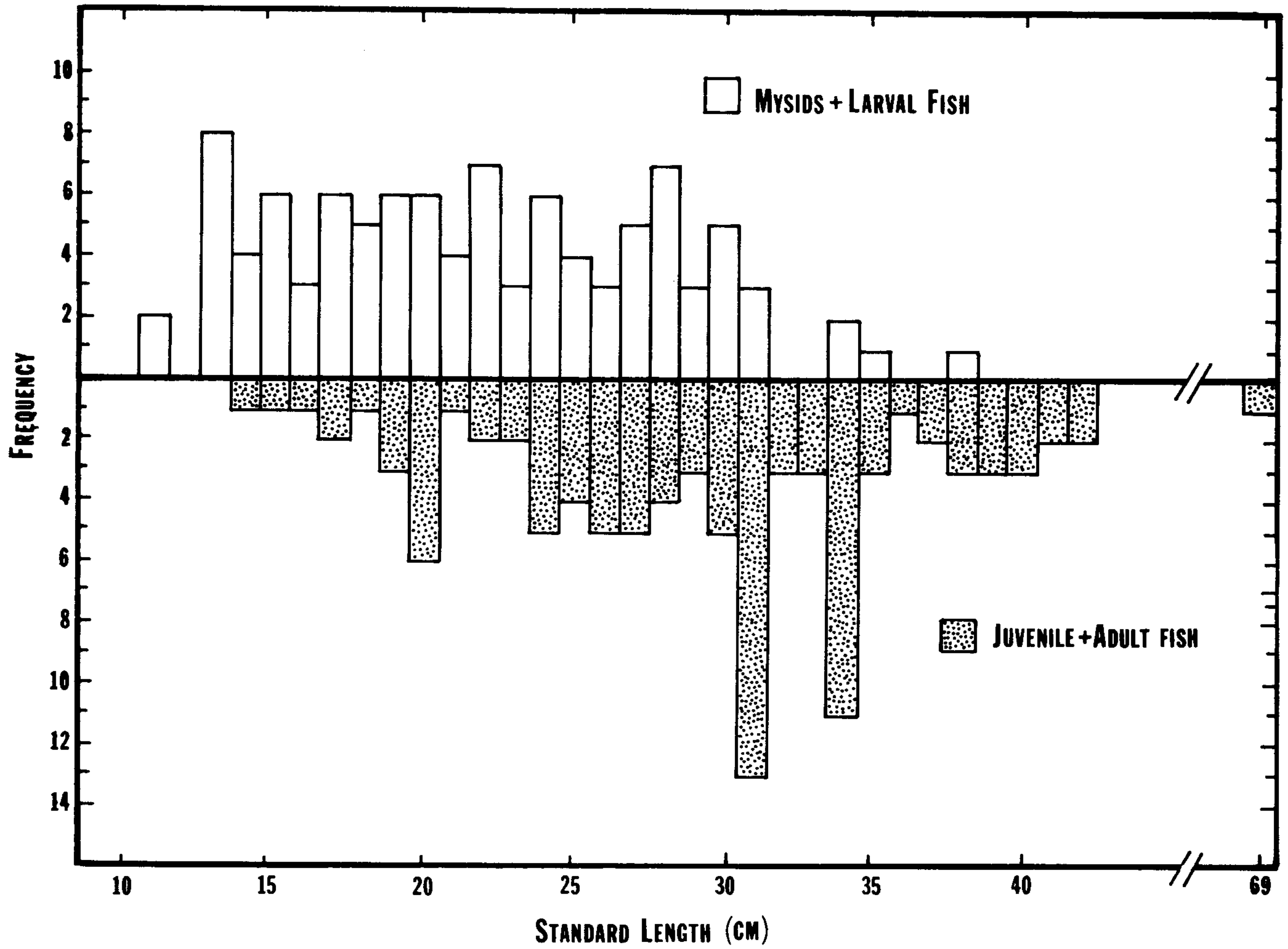

Figure 2. Bar histogram chart of the absolute frequency of occurrence of two major prey categories (mysids and larval fishes; juvenile and adult fishes) found in the stomachs of California halibut of various body sizes that were trawled at 6-m, 18-m, and 30-m depths from off San Onofre and near Oceanside during March 1981 through March 1982. Total number of prey occurrences (201) exceeds the number of stomachs containing these major prey because of co-occurrences of prey categories.

TABLE 2
Results of Threeway Test of Independence for California Halibut

Halibut size (mm SL)	Trawl depth (m)	Prey frequency of occurrence Mysids	Prey frequency of occurrence Anchovy
≤245	6	21	12
≤245	18	25	0
>245	6	1	6
>245	18	24	44

Factors	Type of test	G-value	df	Alpha-level
SxDxP	Independence	83.3	4	0.005
SxDxP	Interaction	17.3	1	0.005
SxP	Independence	29.2	1	0.005
SxD	Independence	36.8	1	0.005
PxD	Independence	0.1	1	0.9>P>0.5

Factors analyzed were size (S—either ≤245 mm or >245 mm SL); depth of capture (D—either 6 or 18 m); and frequency of occurrence of two major prey categories (P—either mysids or northern anchovy) in stomachs. Stomachs in which mysids and anchovy co-occurred were excluded from the analysis. Halibut captured at the 30-m depth were too few to be included in the analysis.

of mysids in the stomachs of halibut <245 mm SL was higher during June 1981 than September 1981, even though mysids (primarily *Metamysidopsis elongata*) were twice as abundant during September.

The % FO of northern anchovy in stomachs of halibut >245 mm SL, however, closely tracked the abundance of anchovy. For example, both the % FO in stomachs and the CPUE of anchovy were elevated from June 1981 to September 1981 (Figure 4).

DISCUSSION

General Aspects of Diet

The major prey (mysids, small fishes) of juvenile and small adult California halibut, *Paralichthys californicus*, of coastal waters resemble the foods of juvenile and small adult summer flounder *(Paralichthys dentatus)*, a morphologically similar congener found in North Atlantic bays and estuaries (Powell and

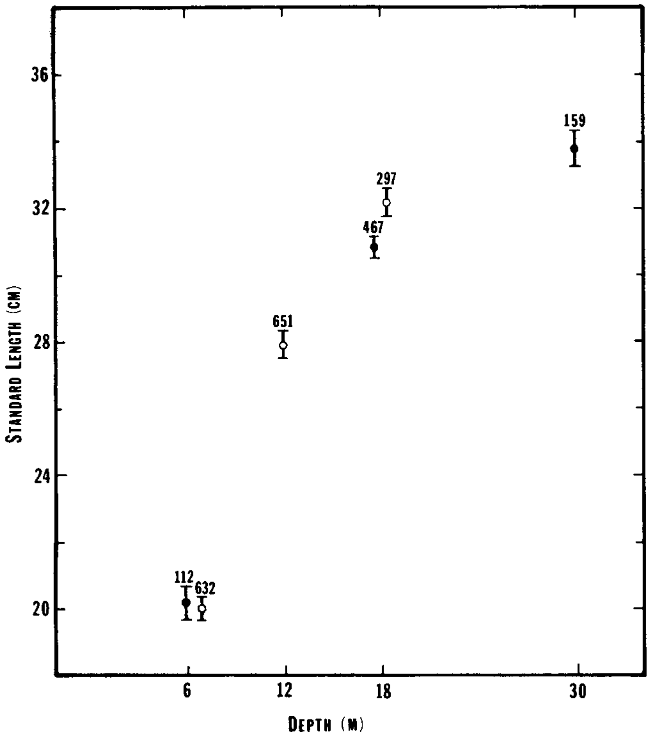

Figure 3. Mean body sizes (standard length in mm) of California halibut trawled at 6-m, 12-m, 18-m, and 30-m depths from the area between San Onofre and Oceanside. Two standard errors of means and sample sizes are noted. Length data for halibut present in trawls (1.3-cm stretch mesh cod-end liner) made by Lockheed Ocean Sciences Laboratory at 6-m, 12-m, and 18-m depths during 1978, 1979, 1980, and 1981 (see Southern California Edison Company 1979, 1980, 1981, and 1982) are represented by the hollow circles. Length data collected by the authors for trawls made from April 1980 through March 1982 are noted by the solid circles.

Schwartz 1979; Poole 1964; Smith and Daiber 1977). The diet of California halibut in coastal waters, however, differs from that of juvenile halibut from Anaheim Bay (Haaker 1975). These differences in prey eaten probably reflect differences in prey abundance (availability) in the two habitats. For example, gobies are an important prey of small juvenile halibut in Anaheim Bay (Haaker 1975), and gobies are known to be abundant in Anaheim Bay (MacDonald 1975). Conversely, gobies are not abundant in the shallow (<30 m) coastal waters between San Onofre and Oceanside (E. DeMartini, unpubl. data), and they did not occur in our sample halibut.

Northern anchovy are a major prey of adult California halibut (Frey 1971). Our data demonstrate that northern anchovy also are an important food for juvenile and small adult halibut in the coastal waters of southern California. Most (96%) of our sample halibut that ate anchovies had eaten immature stages (<10 cm SL; Hunter and Leong 1981). Of all anchovy prey, 97% and 94% by number and weight, respectively, were immature fish.

Mysids also are important in the diet of juvenile halibut in coastal waters, although they seem insignificant in Anaheim Bay (Haaker 1975). Ford (1965) found mysids in the stomachs of 8 halibut (average 305 mm TL, equal to 263 mm SL; Haaker 1975) out of 36 collected from coastal waters near San Diego, 45-65 km downcoast of our sampling areas. Moreover, small juvenile halibut appear to selectively feed on the larger, rarer mysids available. Although large mysids *(Neomysis* spp adults) were about 28 times less abundant than small mysids, they represented nearly one-third of the total numbers of mysids consumed by our sample halibut (Table 1). Large mysids occurred more frequently than small mysids in halibut stomachs with food and accounted for about 5 times the total weight of small mysids (Table 1). Slower rates of digestion for large mysids might have caused us to overestimate the importance of large mysids. However, we feel this influence was minor, since most mysids of all sizes encountered in stomachs were relatively undigested. The generally faster digestion and gut evacuation rates for mysids versus fish, though, probably caused some unavoidable underestimation of the importance of mysids in halibut diet.

Influences of Body Size, Depth, and Season on Diet

Changes in diet with increased body size have been demonstrated for small juvenile California halibut in Anaheim Bay (Haaker 1975) and for the juveniles and small adults of two congeners in North Carolina estuaries (Powell and Schwartz 1979). Halibut in Anaheim Bay (Haaker 1975) and the two Atlantic *Paralichthys* spp (Powell and Schwartz 1979) switch to a more piscivorous diet as they grow larger. Our data show that juvenile-small adult halibut in coastal waters also switch to a more piscivorous diet with increased body size (Figure 2; Table 2).

The body length (~25 cm SL) at which halibut in coastal waters begin to shift to a more piscivorous diet roughly corresponds to the length (9 inches or about 23 cm TL; Frey 1971) at which male halibut begin to mature. Females begin to mature at a much larger size (17 inches or 43 cm TL; Frey 1971). Hence our samples characterize the diet for fish of a range of maturity states of both sexes: 61% of our halibut were adult males, 15% adult females, and 24% immatures—the latter probably mainly juvenile females. Sample sizes were insufficient, however, to analyze diet by sex as well as body size. Only one of our sample halibut exceeded the current minimum legal size (22 inches or 559 mm TL) of sport-caught halibut (Figure 2).

Clark (1930, 1931) notes that young California halibut occur in shallow water, while larger fish frequent greater depths except for an onshore spawning migra-

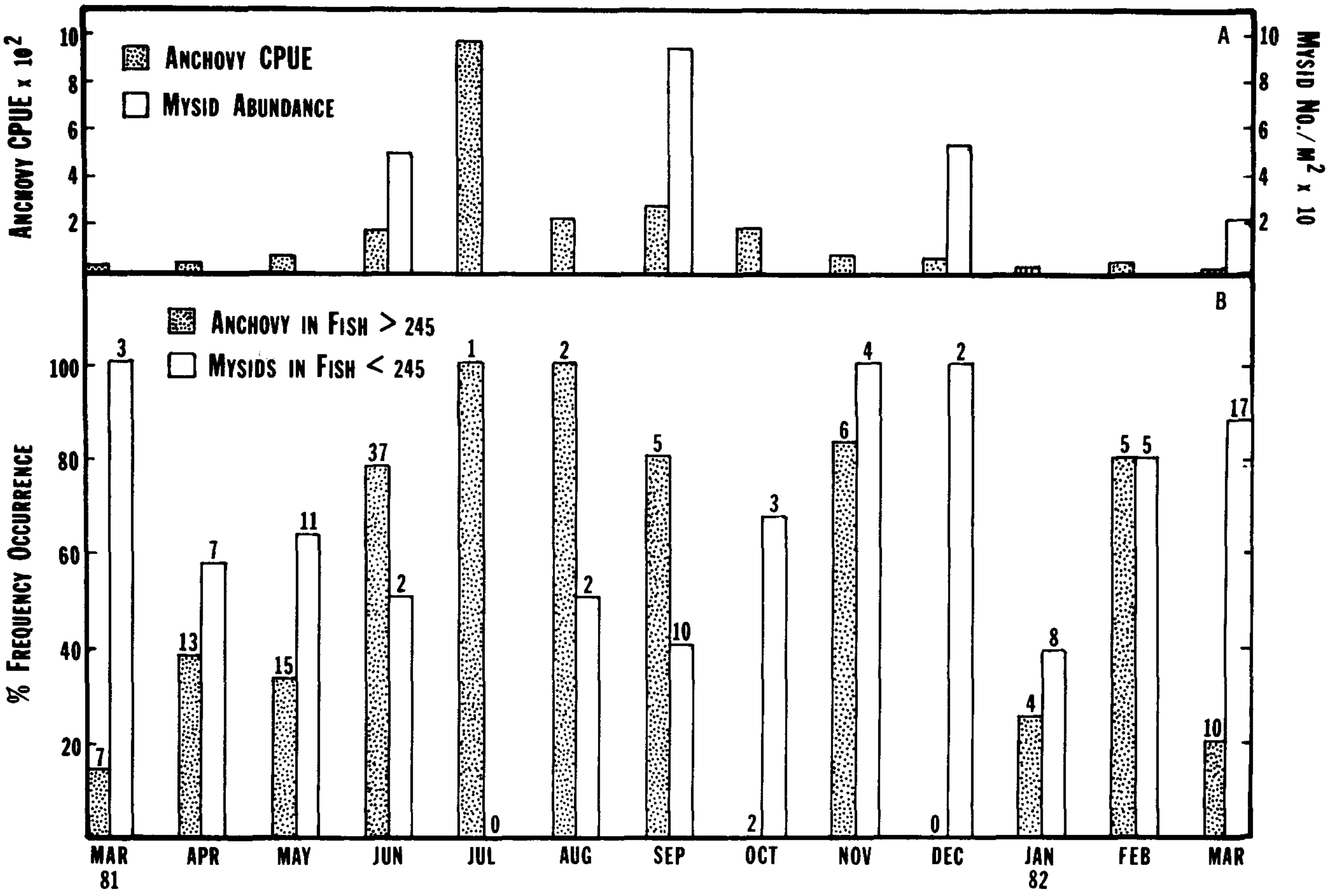

Figure 4. *(A)* Relative abundance (CPUE) of northern anchovy and abundance (number per m^2) of mysids in the San Onofre-Oceanside region at the various sampling depths and longshore locations pooled. Mysid data are restricted to species that occurred in our halibut stomach samples. *(B)* Relative frequency (% FO) of anchovy and mysid prey present in stomachs of halibut from all depths of capture and both longshore locations pooled. Numbers of stomachs with food are noted by month and by halibut length class ($\leq$245 or >245 mm SL).

tion. Our data show that juveniles smaller than about 10 cm SL do not occur in shallow (<30 m) coastal waters. Age I+-sized fish (15-25 cm SL) and II+ (30-45 cm SL) and older-sized fish (Haaker 1975; Innis 1980) segregate by depth, with older juveniles and young adults occurring deeper than younger juveniles (Figure 3). Undoubtedly, our trawls grossly undersample adult-sized halibut at all depths, and this accounts for our inability to detect the seasonal onshore spawning migration of adults (see Barry and Cailliet 1981).

The % FO of northern anchovy and mysids in the stomachs of juvenile-small adult halibut of all sizes pooled is independent of depth (Table 2). Differences in diet (mysids vs northern anchovy) between small juvenile ($\leq$245 mm) and larger (>245 mm) halibut, however, are dependent on depth (Table 2). Small juveniles inhabited shallow (6 m) depths and consumed mysids, while larger fish frequented deeper waters and ate mostly northern anchovy. Northern anchovy were eaten more frequently by juvenile and small adult halibut during summer-fall, despite the fact that mysids were also relatively abundant then. At this time anchovy were more abundant nearshore, and this is typically the case (see Huppert et al. 1980). These data corroborate the preliminary observations of Roberts et al. (1982) and are consistent with a major prediction of Optimal Foraging Theory—namely, that more-preferred, often larger prey are eaten regardless of the relative abundance of less-preferred prey (Hughes 1980). Our data lend further support to Roberts et al. (1982), who also suggested that the differences in diet between juvenile and small adult halibut might be due to prey selection and that small juveniles may inhabit shallow coastal waters because mysids, their preferred prey, are more abundant there.

In summary, northern anchovy and mysids are the major prey of juvenile and small adult California halibut in the coastal waters of the San Onofre-Oceanside region. The relative importance of these two prey varies with size of halibut and season. Anchovies are most important during summer-fall. Smaller juvenile halibut tend to inhabit shallower coastal waters and consume mysids more frequently than anchovies, despite the insignificant relation between depth per se and the relative frequency of mysids versus anchovies eaten.

Implications of Size-Specific Depth Distributions

Our data indicate that California halibut <10 cm SL are largely absent from shallow (6-30-m depth) coastal waters off northern San Diego County (Figures 2,3). Moreover, only 2% of 1580 halibut trawled at 6-m, 12-m, and 18-m depths in another coastal monitoring study off northern San Diego County were <10 mm SL (Table 3). These data contrast sharply with a majority of other studies done in Elkhorn Slough, Mugu Lagoon, Anaheim Bay, and Newport Bay (Table 3), which show that juvenile halibut <10 cm SL are an abundant size group during certain times of year. None of the few California halibut captured in the surfzone (<5-m depths) using a bag seine in the San Onofre-Oceanside region were <205 mm SL (Table 3). Mostly large juvenile halibut were caught in a subsequent study, analogous to the latter, made in the same area and at La Jolla near San Diego (Table 3).

On the basis of these data we tentatively conclude that juvenile halibut <10 cm SL reside primarily in embayments and not in shallow coastal waters. Haaker's (1975) data for Anaheim Bay suggested this. There is an obvious need for further studies of juvenile halibut distribution designed specifically to test this hypothesis. We feel, though, that surfzone sampling using 1.3-cm stretch mesh bag seines (Table 3) should have collected greater numbers of small juveniles between 5-10 cm SL, if young-of-the-year were abundant in surfzone regions.

California halibut apparently spawn in nearshore coastal waters (Frey 1971; Gruber et al. 1982). The planktonic larval stages (≤ ~1 cm SL; J. R. Hunter, H. G. Moser, W. Watson, pers. comm.) occur throughout the water column, primarily over 12-45-m bottom depths within 1.9-5.4 km of shore in the San Onofre-Oceanside region (A. Barnett, Marine Ecological Consultants of Southern California, unpubl. report); and larger larvae occur closer to shore (A. Barnett, unpubl. data). Halibut larvae are most abundant in this region during March-September (A. Barnett, unpubl. report), which agrees with the February-July spawning season noted by Frey (1971).

We do not yet know whether halibut larvae metamorphose in nearshore coastal waters and then migrate into embayments, or transform to juveniles within embayments after somehow reaching these areas while in the plankton. The former seems more likely based on the early life history of other *Paralichthys* spp. A western Atlantic congener, *Paralichthys dentatus*, spawns in offshore coastal waters, and larvae probably metamorphose nearshore before entering estuaries (Smith 1973). Juvenile *P. dentatus* are restricted in their distribution to estuaries (Smith 1973).

TABLE 3

Summary of Gear and Sampling Designs, Sampling Effort, and Catches of Juvenile-Small Adult California Halibut for Various Studies Made in Central and Southern California Waters

Sample type(s)	Mesh size (cm)	Region sampled	Collection period	No. samples (effort)	No. halibut ≤10 cm	No. halibut >10 cm	Source
Otter trawl	1.3	Elkhorn Slough, Monterey Bay	Oct 78-May 80	146	7	64	Barry and Cailliet (1981); J.P. Barry, pers. comm.
Bag seine	1.0	Mugu Lagoon, Ventura County	Feb 77-Nov 81	228	975	278	C. Onuf, pers. comm.
Otter trawl	2.5 0.6	Anaheim Bay, Orange County	Jan-Apr 70 May 70-Feb 71	~ 48 ~120	~ 44 ~487	~182 ~ 603	Haaker (1975, Fig. 41)
Otter trawl, bag seine	0.8, 0.3	Newport Bay, Orange County	Mar 74-Sep 75	129, 24	18	111	L.G. Allen, pers. comm.
Otter trawl, bag seine	0.8, 0.3		Jan 78-Jan 79	48, 48	11	52	
Otter trawl	1.3	San Mateo Pt.—Don Light, north San Diego County; coastal waters (6, 12, & 18 m)	Mar 78-Dec 81	831	34	1546	SCE (1979, 1980, 1981, 1982)
Bag seine	1.3	San Onofre—Oceanside surfzone (≤5-m depth)	Jun-Dec 76; Mar-Apr 77	68	0	5	Tetra Tech (1977)
Bag seine	1.3	San Onofre—Oceanside, La Jolla surfzone (≤5-m depth)	Nov 78-Jul 79	175	2	13	E. DeMartini (unpubl. data)

Halibut catches are divided into individuals ≤10 cm and >10 cm SL. All mesh-size data are stretch measurements for the bag or cod-end liner sections, as appropriate. Apparent differences among embayments in the relative proportions of halibut ≤10 and >10 cm undoubtedly reflect both differences in gear and variable recruitment in the different years of study.

Paralichthys olivaceus has a similar early life history in Japan (Minami 1982).

Shallow waters of the open coast serve as a nursery ground for many species of nearshore fishes in the Southern California Bight (Sherwood 1980). The California halibut may be one of a minority of species for which embayments are essential during the early juvenile stage.

We feel that the major alteration and destruction of bays and estuaries in southern California (e.g., see Reish et al. 1980) undoubtedly has eliminated many of the nursery grounds that are necessary during the early life history of the California halibut.

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SATELLITE REMOTE SENSING OF THE HABITAT OF SPAWNING ANCHOVY IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Images of sea-surface temperature and phytoplankton pigments in the Southern California Bight were processed from satellite data obtained during four intensive CalCOFI anchovy egg surveys from 1980 to 1982. Mesoscale patterns of water masses and fronts in the images can explain the distribution of northern anchovy spawning as indicated by first-day eggs. In general, spawning in the northwestern region of the bight is excluded from a cold-water mass south of Point Conception, whereas spawning to the south is confined to coastal waters with moderately high phytoplankton pigment levels. The satellite-measured parameters may indicate critical factors for larval survival. Such satellite images can be used to improve the sampling efficiency of egg surveys.

RESUMEN

Mediante satélites se han obtenido imágenes de la temperatura de la superficie del mar y de pigmentos del fitoplancton, para la zona del seno del sur de California. Estos datos han sido procesados conjuntamente con la información obtenida durante cuatro exploraciones de CalCOFI (1980-1982) para recolectar huevos de anchoa (*Engraulis mordax*).

El contorno de la distribución de masas de agua y frentes en estas imágenes, puede informar sobre la distribución de la actividad de puesta de la anchoa, señalada por la presencia de huevos de un dia en las colecciones. En general, la puesta en la parte noroeste del seno está aislada de la masa de aguas frías al sur de Punta Concepción, mientras que la zona de puesta al sur está confinada a las aguas costeras con niveles relativamente elevados de pigmentos fitoplanctónicos.

Los parámetros medidos por el satélite pueden ser indicadores de factores críticos para la supervivencia de las larvas. Las imágenes proporcionadas por los satélites podrían utilizarse para perfeccionar la eficacia en el muestreo de huevos de anchoa.

INTRODUCTION

Intensive anchovy egg surveys of the CalCOFI region inshore of station 60 have been conducted once or twice yearly since 1980. The Southern California Bight (Figure 1) is the center of distribution of the large central stock of northern anchovy and has been sampled most intensively. The spatial distribution of early stage eggs, indicating recent spawning, corresponds closely to the distribution of adults in night midwater trawls during the spawning season (Figure 2). Temperature and salinity were the only environmental parameters measured routinely on these surveys, although nutrients, phytoplankton pigments, and primary productivity have been measured on some CalCOFI cruises. Vertical egg tows were made at stations 7.4 km apart on transect lines separated by 37 km. This sampling plan gives considerably higher resolution of spatial distribution patterns than does the regular 37- (74-)km CalCOFI station (line) spacing.

Sensors carried on earth-orbiting satellites since 1978 provide high-resolution images of sea-surface temperature and phytoplankton pigment concentration. Accurate estimates of these parameters, corrected for atmospheric scattering and absorption, can be derived from multispectral radiance data. Temperature data are derived from the thermal infrared channels of the Advanced Very High Resolution Radio-

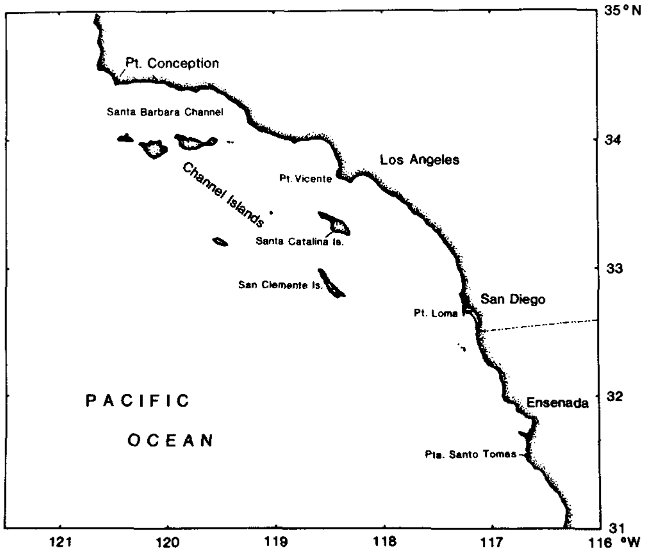

Figure 1. Map of the Southern California Bight.

[Manuscript received February 25, 1983.]

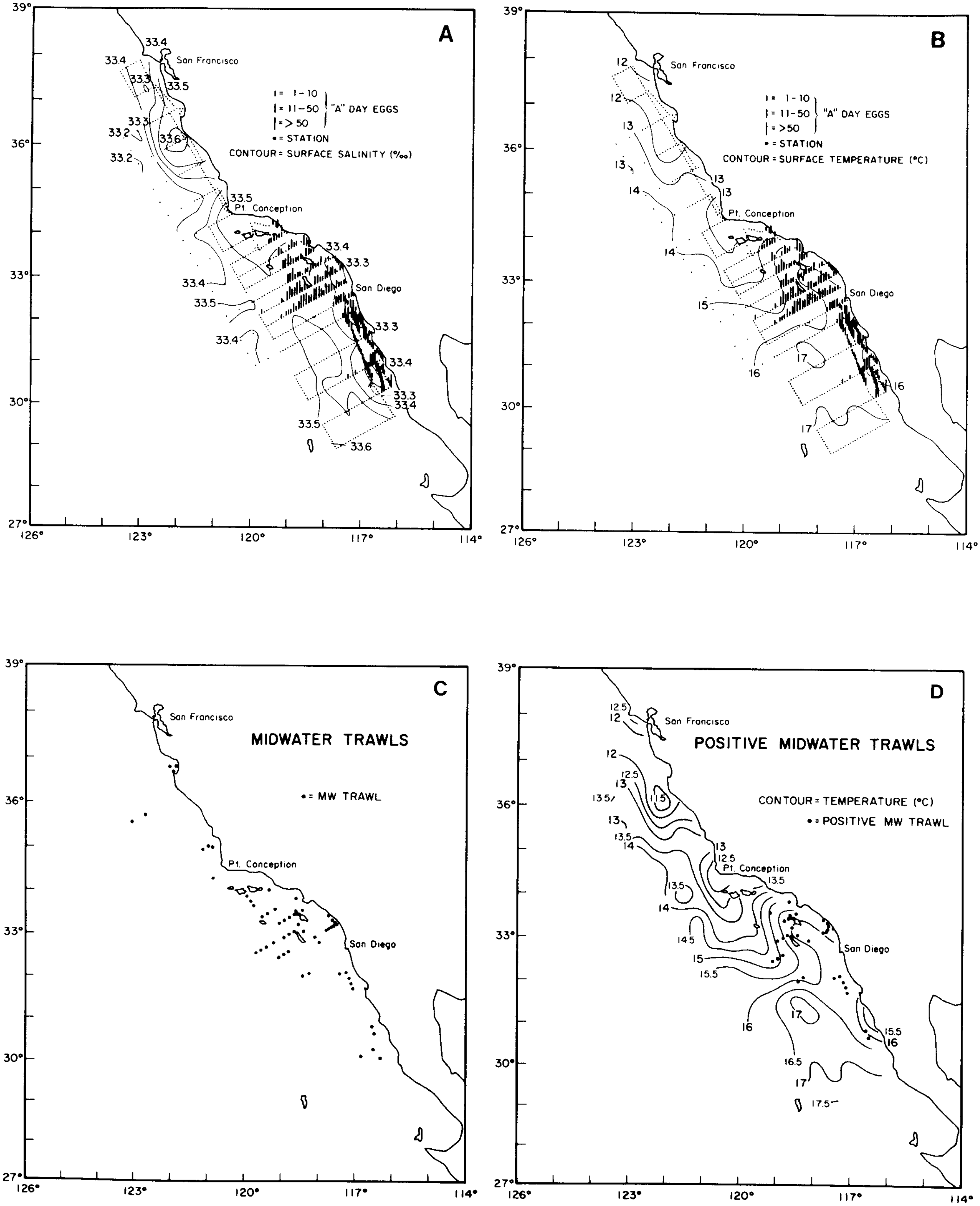

Figure 2. Distribution of anchovy eggs and adults in relation to salinity and temperature, CalCOFI cruise 8003: (*A*) A-day eggs and surface salinity; (*B*) A-day eggs and surface temperature; (*C*) all midwater trawls taken from March 27 to April 12, 1980, by R/V *David Starr Jordan;* (*D*) midwater trawls with adult anchovy catches and surface temperature. From Lasker et al. (1981).

TABLE 1

1980-82 CalCOFI Egg Survey Dates and Stations in the Southern California Bight, and Dates and Times of Corresponding AVHRR and CZCS Images

CalCOFI cruise	Southern California Bight stations		AVHRR image	CZCS image
	Dates	N		
8003	20 Mar-10 Apr 1980	359	7 Apr, 1850 PST	8 Apr, 1113 PST
8004	12 Apr-29 Apr 1980	286	—	—
8102	16 Feb- 6 Mar 1981	429	21 Feb, 1955 PST	23 Feb, 1124 PST
8104	31 Mar-12 Apr 1981	373	5 Apr, 2029 PST	4 Apr, 1144 PST
8202	27 Jan-27 Feb 1982	543	29 Jan, 1334 PST	29 Jan, 1109 PST

meter (AVHRR) currently on NOAA-7 and formerly on TIROS-N and NOAA-6. Phytoplankton pigment data are derived from the visible channels of the Coastal Zone Color Scanner (CZCS) on Nimbus-7.

Synoptic images of California coastal waters obtained daily or twice daily and with a resolution of ~1 km give us a much different view of the CalCOFI survey region than is provided by a ship taking hydrographic samples at 37-km intervals on a month-long cruise. This report demonstrates that satellite images define environmental features and boundaries on a scale that helps explain the spatial patterns of spawning activity observed on intensive egg surveys in the Southern California Bight.

DATA AND METHODS

Five intensive egg surveys were completed in 1980-82 (Table 1). Anchovy eggs from vertical egg tows (333-μm-mesh conical net of 25-cm diameter from a depth of 70 m for 1 min) were sorted and staged. Net tows were standardized so that sample counts are equivalent to eggs per 0.05 m^2. Counts of A-day eggs (0-24 hours old) were assumed to represent recent spawning at the station location. Positive egg stations were sorted by egg count into three classes of approximately equal size.

AVHRR infrared data were obtained for the most cloud-free day during each survey, from satellite passes archived at the Scripps Satellite Oceanography Facility (SSOF). Radiance data were converted to temperature using an SSOF radiometric calibration procedure based on Lauritson et al. (1979). Correction for atmospheric water vapor and aerosols, without concomitant sea-truth or atmospheric data, is possible using empirical regressions of ship temperatures on satellite temperatures in two or three thermal infrared bands. The NOAA-6 AVHRR had only two such channels, and the 3.7-μm channel was plagued by excessive noise that steadily increased during the operational lifetime of the satellite. Two-channel correction of the full-resolution NOAA-6 images (8003, 8102, and 8104) was therefore not possible. The 8202 image was corrected with a "split-window" algorithm[1] using channels 4 (10.9μm) and 5 (12.0μm) of the NOAA-7 AVHRR.

Ship-bucket temperatures, obtained at egg tow stations on the same day as the satellite pass, were used to correct the NOAA-6 images. Additive corrections for cold biases of −1.87°, −1.96°, and −1.77°C in the 8003, 8102, and 8104 images yielded root-mean-square differences of 0.50°, 0.52°, and 0.32°C ($n=27$, 16, and 32 stations). Since corrections based upon linear regression of ship temperatures on satellite temperatures produced only slight improvements (rms differences = 0.36°, 0.32°, and 0.32°C), the simple additive correction was used. Removal of a residual bias of −0.18°C from the corrected 8202 image yielded an rms difference of 0.23°C ($n=35$).

The Visibility Laboratory of Scripps Institution of Oceanography performed preliminary processing of CZCS data. Band 1 (blue) and band 3 (yellow-green) radiances were corrected for Rayleigh and aerosol scattering by Visibility Lab versions of the CZCS Nimbus Experimental Team's atmospheric algorithm (Smith and Wilson 1981). This algorithm was modified between the dates when the 8003 and 8102 images were processed. The 8104 image was corrected only for Rayleigh scattering, but there was little aerosol contamination visible in the corrected image. Blue/green ratios were converted to phytoplankton pigment concentration (chlorophyll plus phaeopigments) with the pigment algorithm of Smith and Baker (1982). Absolute levels of phytoplankton pigments in the images presented here are not comparable because of the application of different atmospheric correction algorithms and the lack of sea-truth data.

RESULTS

Frequency distributions of ship-bucket temperature measured at stations in the Southern California Bight, and the percentage of positive stations in each temperature interval, are illustrated in Figure 3. Little or no spawning occurred at stations <13.5°C. The warmest

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[1] McClain, E. P. 1981. Split-window and triple-window sea surface temperature measurements from satellites. Preprint. Mini-symposium on Applications of Aerospace Remote Sensing in Marine Research, ICES Statutory Meeting, Woods Hole, Mass., 6-10 October 1981.

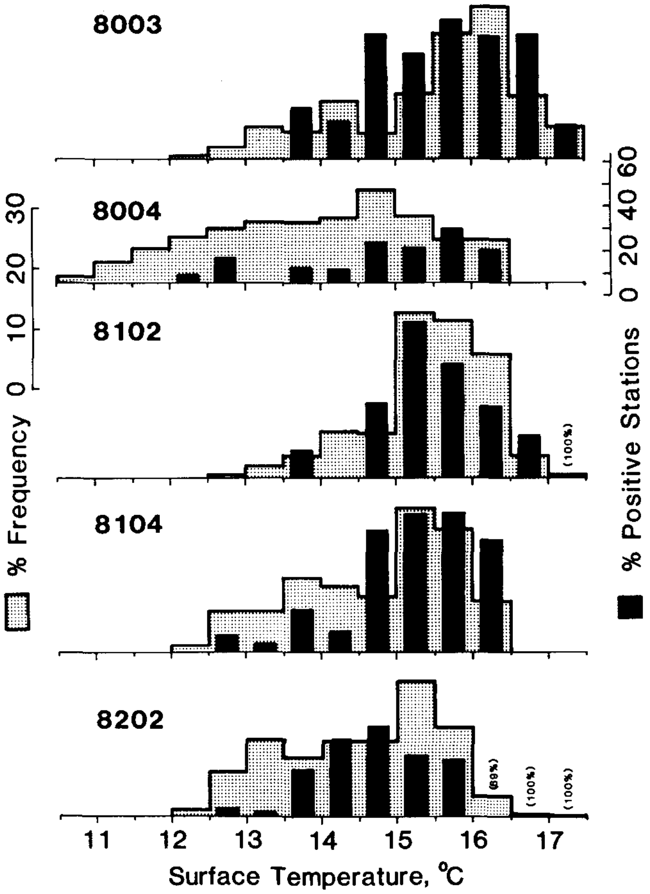

Figure 3. Frequency distributions of CalCOFI stations by surface temperature, and frequency of positive A-day anchovy egg catches within each temperature interval, for five intensive egg surveys. Large percentages of small numbers of stations are in parentheses. Only stations within the Southern California Bight, from line 80 to line 101.6 and no farther offshore than station 60, were included. Extra transects added on cruise 8202 were omitted.

mean surface temperature was observed on cruise 8003 (15.2°C), when spawning occurred most frequently at 14.5-17°C. Mean temperature decreased to 14.4°C during cruise 8004. Spawning was reduced considerably, with eggs found at only 29 of 286 bight stations, and this cruise will not be considered further.

Mean surface temperatures on cruises 8102 (15.1°C) and 8104 (14.7°C) were slightly lower than on 8003, but the modal temperature range of successful spawning did not change. The 1982 egg survey was earlier in the year than 8003 and 8102. Mean surface temperature in the bight was only 14.3°C. The modal spawning temperature range was about 0.5°C colder than in 1980 and 1981, whereas the frequency of successful spawning within that range was generally lower.

The satellite images are enhanced so that low temperatures and high phytoplankton pigment levels appear light, while high temperatures and low pigment levels appear dark. All four pairs of images (Figures 4-7) show the same basic mesoscale features:

1. A plume of cold water upwelled off Point Conception and to the north, and then advected to the south by the California Current. This water has relatively high phytoplankton pigment concentrations.
2. A narrow band of cool water caused by local upwelling along the coast to the east and south of the plume. Occasionally, small plumes extend farther offshore from prominent capes such as Point Vicente, Point Loma, and Punta Santo Tomás. This water has moderately high phytoplankton pigment concentrations.
3. A mass of warm, low-pigment oceanic water extending from the south between the cold-water plume and the coast.

Variations between and within years can be seen in the intensity and size of the mesoscale features and in the detailed shape of frontal boundaries along the coast and around the large cold-water plume. Sea-surface temperature and phytoplankton pigment patterns are somewhat coherent, with an inverse relationship between the two parameters.

8003 (Figure 4a,b)

The cold-water plume defines a boundary on the distribution of spawning activity north of San Clemente Island. The boundary corresponds to approximately the 14.5°C isotherm. Spawning was confined to a 40-km-wide band near the coast south of San Diego. There was no obvious temperature boundary defining this band, although the water offshore was relatively warm (16-17°C). Spawning has been commonly observed in 17-19°C water off Baja California during spring CalCOFI cruises in 1969-79, and Lasker et al. (1981) attributed the offshore absence of spawning in this case to the slightly higher salinity of this warm-water pool (0.1-0.2°/oo; see Figure 1). The phytoplankton pigment image, however, reveals a much more obvious boundary. Spawning is limited to a coastal band of relatively high-pigment water south of San Diego.

8102 (Figure 5a,b)

The cold-water plume at this time extended more to the south than to the southeast, as it did during cruise 8003. Spawning was excluded from the plume north of Santa Catalina Island, although some spawning did occur in relatively cool water in the Santa Barbara Channel (13.5-14°C). Phytoplankton pigment levels from the CZCS were higher than during 8003, a difference that may be due partly to changes in the atmospheric correction algorithm. Although there is

Figure 4a. CalCOFI 8003 A-day anchovy egg distribution, March 20-April 10, 1980. • = 0, 1 = 1-4, 2 = 5-17, 3 = 18-245 eggs/0.05 m^2. Sea-surface temperature (°C) from NOAA-6 AVHRR, channel 4, April 7, 1980.

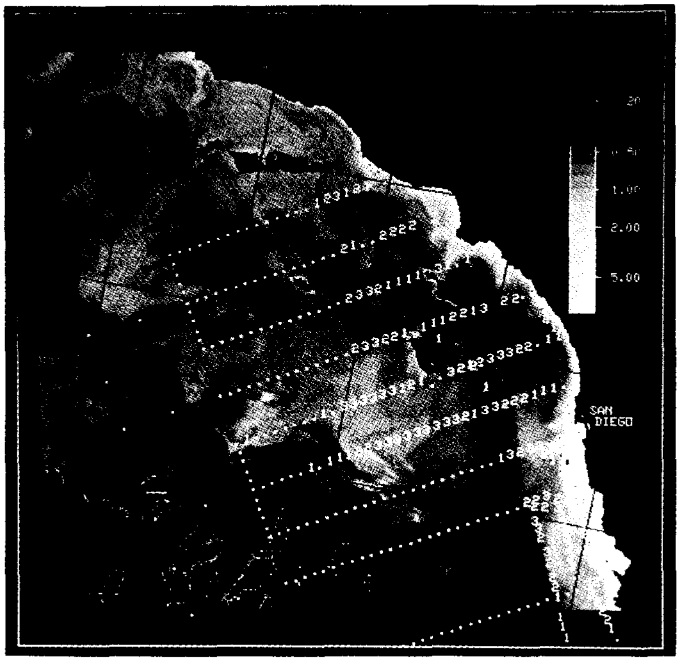

Figure 4b. CalCOFI 8003 A-day anchovy egg distribution, March 20-April 10, 1980. • = 0, 1 = 1-4, 2 = 5-17, 3 = 18-245eggs/0.05m ^{2}. Phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, April 8, 1980.

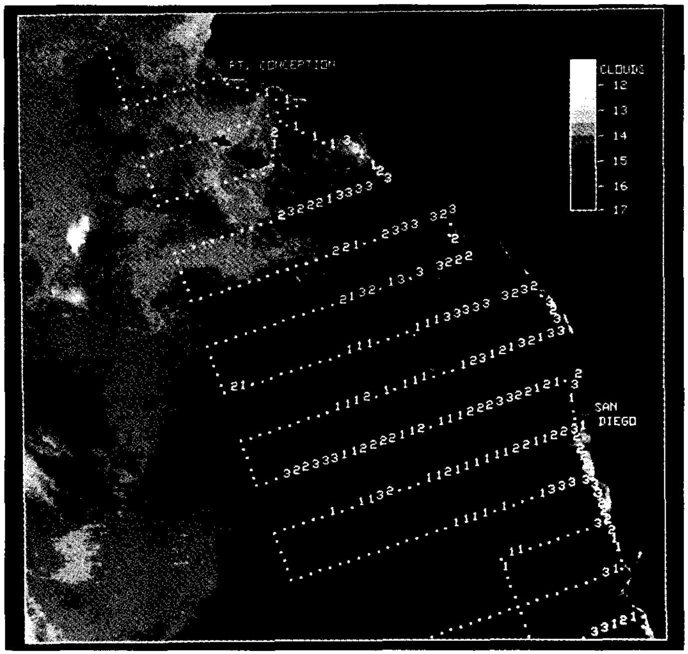

Figure 5a. CalCOFI 8102 A-day anchovy egg distribution, February 12-March 10, 1981. • = 0, 1 = 1-4, 2 = 5-15, 3 = 16-157 eggs/0.05 m^2. Sea-surface temperature (°C) from NOAA-6 AVHRR, channel 4, February 21, 1981.

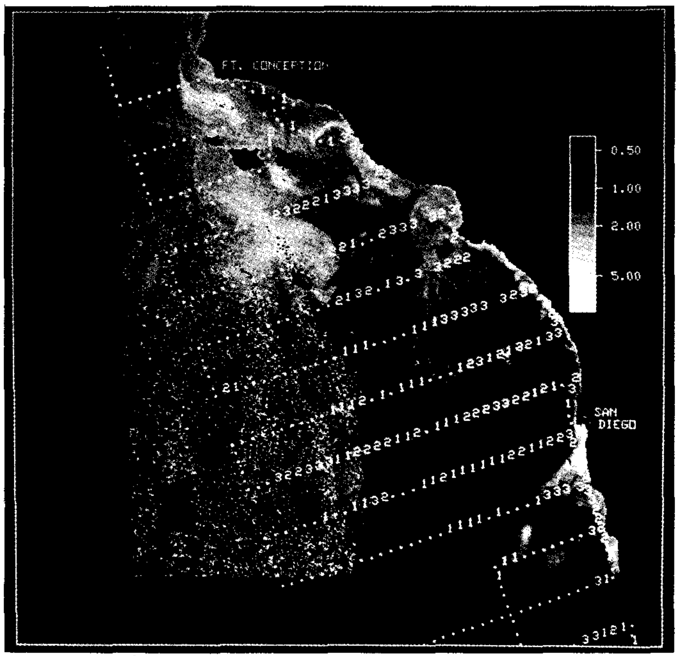

Figure 5b. CalCOFI 8102 A-day anchovy egg distribution, February 12-March 10, 1981. • = 0, 1 = 1-4, 2 = 5-15, 3 = 16-157 eggs/0.05 m^2. Phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, February 23, 1981.

no absolute lower limit on the distribution of spawning apparent in the satellite phytoplankton-pigment image, higher egg abundances south of Santa Catalina Island tended to occur at stations with higher pigment levels ($r = +0.23$, $P = <0.018$, product-moment correlation of log-transformed values).

8104 (Figure 6a,b)

Temperatures were generally colder than during 8102, and the cold-water plume extended farther east among the Channel Islands. Spawning did not extend as far to the northwest, although an isolated pocket of spawners remained in the cool Santa Barbara Channel.

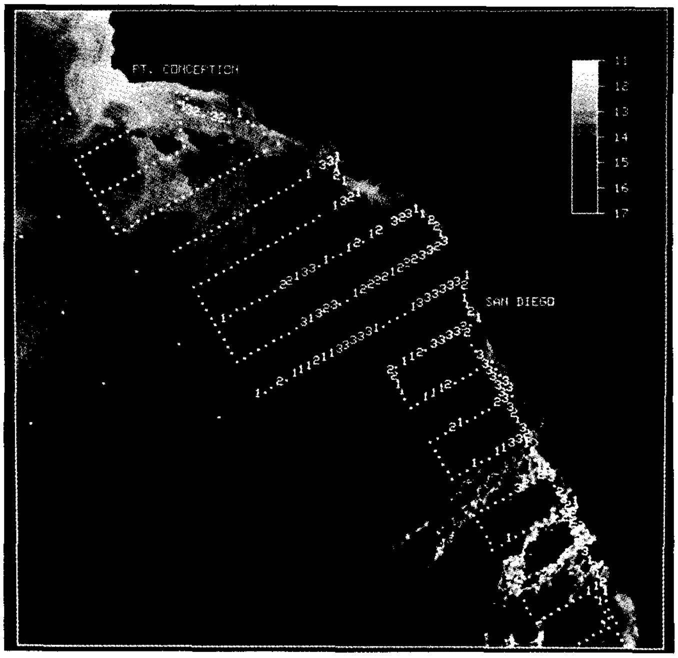

Figure 6a. CalCOFI 8104 A-day anchovy egg distribution, March 31-April 12, 1981. • = 0, 1 = 1-4, 2 = 5-13, 3 = 14-323 eggs/0.05 m^2. Sea-surface temperature (°C) from NOAA-6 AVHRR, channel 4, April 5, 1981.

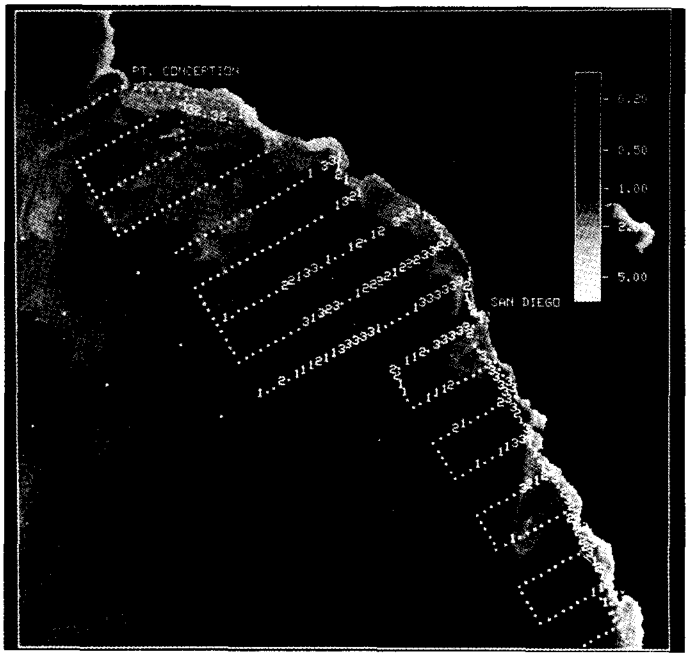

Figure 6b. CalCOFI 8104 A-day anchovy egg distribution, March 31-April 12, 1981. • = 0, 1 = 1-4, 2 = 5-13, 3 = 14-323 eggs/0.05 m^2. Phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, April 4, 1981.

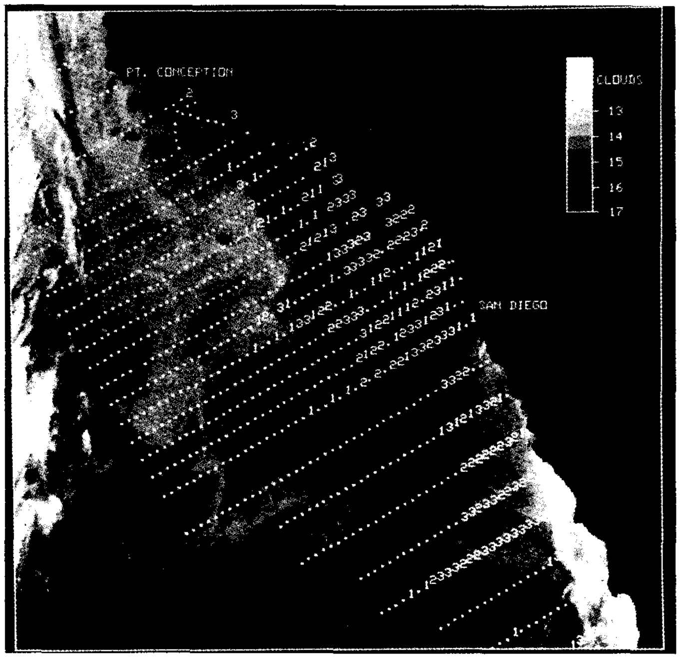

Figure 7a. CalCOFI 8202 A-day anchovy egg distribution, January 27-February 27, 1982. • = 0, 1 = 1-3, 2 = 4-12, 3 = 13-170 eggs/0.05 m^2. Sea-surface temperature (°C) from NOAA-7 AVHRR, channels 4 and 5, February 18, 1982.

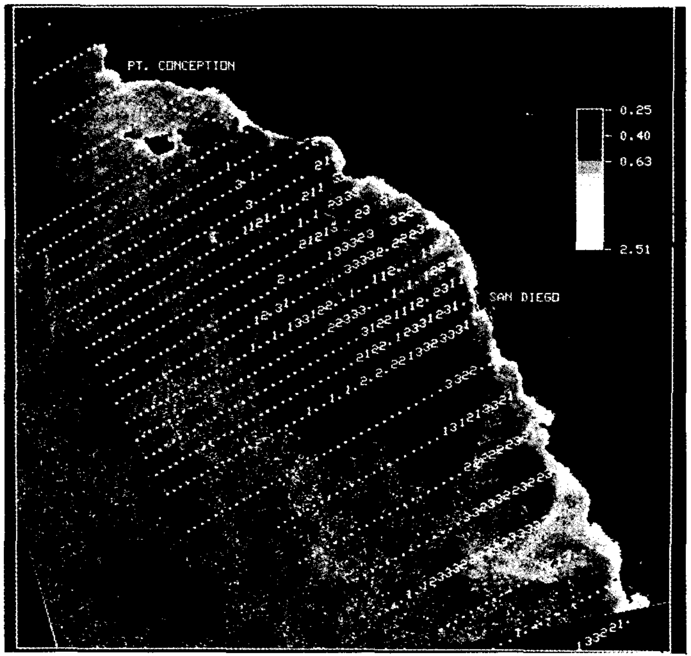

Figure 7b. CalCOFI 8202 A-day anchovy egg distribution, January 27-February 27, 1982. • = 0, 1 = 1-3, 2 = 4-12, 3 = 13-170 eggs/0.05 m^2. Phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, January 29, 1982.

More spawning occurred south of San Diego, especially in high-pigment waters near the coast.

8202 (Figure 7a,b)

Sampling was intensified between lines 83.3 and 95.0 on this survey, with transects separated by 18.5 km. The cold-water plume once again formed a definite boundary on the northwestern extent of spawning activity. To the south, spawning was confined near the coast except off Punta Santo Tomás, south of Ensenada, where a plume of cool water with high phytoplankton pigment levels extended far offshore.

DISCUSSION AND CONCLUSIONS

The satellite images reveal mesoscale and smaller patterns of sea-surface temperature and phytoplankton pigments that define boundaries on northern anchovy spawning in the Southern California Bight. While neither parameter alone is sufficient, both together may define the spatial distributions nearly completely. In general, the northern extent of spawning in the bight, and the offshore extent north of Santa Catalina Island, are limited by cold, upwelled water advected south of Point Conception. Spawning activity to the south is limited by low phytoplankton pigment levels in oceanic water found 20-100km offshore, rather than by temperature.

During cruise 8003, spawning did not occur in water <14°C or <0.2 mg pigments m^{-3} (Figure 8A). At higher temperature and phytoplankton pigment levels, spawning was apparently limited by an interaction, in that the lower temperature limit decreased as pigment concentration increased. A similar relationship holds for cruise 8102 (Figure 8B), although a lower phytoplankton pigment limit was not observed. Note, however, that no eggs were found at many stations with temperature and pigment concentrations within the ranges in which spawning occurred at other stations.

Surface temperature and phytoplankton pigment concentration cannot, therefore, be the only factors determining the distribution of spawning activity. In fact, they may merely indicate more directly important environmental conditions. Spawning in waters favorable for larval survival is an adaptive strategy in the life cycle of many species of fish (Cushing 1975). Lasker (1981) hypothesized that the survival of first-feeding anchovy larvae depends upon the aggregation of nutritionally suitable food organisms in a stratified water column. Large dinoflagellates are preferred food organisms often found in dense near-surface layers in the Southern California Bight.

Satellite observations of relatively warm surface temperatures along with moderately high pigment levels may indicate a stratified water column with a mature phytoplankton community dominated by dinoflagellates. On the other hand, a well-mixed water column would be indicated by colder surface temperatures caused by upwelling or storm mixing; unsuitable food conditions would be indicated either by the low phytoplankton pigment levels of unproductive oceanic water or by very high levels associated with surface diatom blooms in recently upwelled water.

Satellite images of temperature and phytoplankton pigments are "snapshots" of the surface waters of the anchovy environment. Although smaller-scale features change noticeably on time scales of a few days, mesoscale patterns in the Southern California Bight may change little during a 2- to 4-week CalCOFI egg survey (Bernstein et al. 1977). Therefore, satellite data can supplement a survey's environmental data by providing higher-resolution views of sea-surface temperature covering regions larger than the survey grid and by providing estimates of phytoplankton pigment concentrations not normally measured on the surveys. The images presented here demonstrate the utility of satellite data for interpreting spatial distributions from fishery surveys.

Rapid collection and processing of satellite data allow real-time application in planning oceanographic

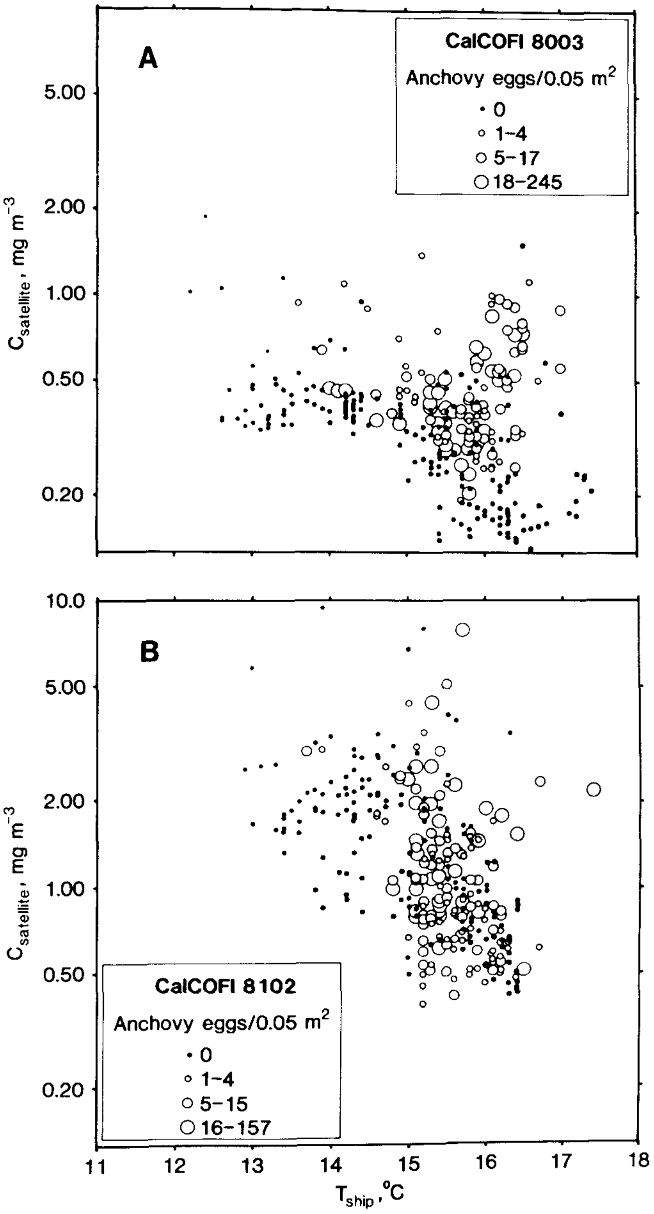

Figure 8. Anchovy A-day egg abundance vs ship-bucket temperature (T ship) and satellite chlorophyll (phytoplankton pigment) concentration. (*A*) Cruise 8003. (*B*) Cruise 8102.

cruises. The primary objective of CalCOFI egg surveys is to estimate anchovy spawning biomass for calculating optimum yield according to the Northern Anchovy Fishery Management Plan. The efficiency of these surveys could improve tremendously if satellite images were used to omit portions of the sampling grid where environmental conditions preclude spawning. This application is currently being explored, but will require a quantitive formulation of the relationships demonstrated here.

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DIEL CHANGES IN THE VERTICAL DISTRIBUTION OF BIOMASS AND SPECIES IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Displacement volumes were measured, and selected species of zooplankton were counted from sets of vertically stratified samples taken in the Southern California Bight in April 1965 to provide information on vertical distribution and changes in distribution caused by diel migration and bottom topography. Day/night differences were found in total biomass in the upper 225 m, and there was a diel redistribution of selected species and biomass within the water column. Depending on the size fraction sampled, from ⅓ to ⅔ of the nighttime biomass in the upper 56 m of water was redistributed below this depth during the day. For most copepods considered, this change was caused by diel vertical migration, but larger zooplankters could either have been descending below 225 m or avoiding capture in the surface layers more successfully during the day than at night.

RESUMEN

Se han obtenido muestras de plancton a varios niveles de profundidad en el seno del Sur de California, durante Abril de 1965, con objeto de obtener información sobre la distribución batimétrica y variaciones en la distribución en relación con la luz y la topografía del fondo. Se midieron los volúmenes de plancton por el método de desplazamiento, y se contaron las especies seleccionadas de estas muestras. Diferencias nocturnas y diurnas han sido observadas en la biomasa, para los estratos de 225 m. a 0 m. de profundidad, y las especies seleccionadas así como la biomasa, presentaron una redistribución diaria en esa columna de agua. De acuerdo con la magnitud de la fracción de la muestra utilizada (⅓ hasta ⅔ del total), la biomasa nocturna en el estrato de 0–56 m. de profundidad, aparecía distribuida durante el dia por debajo de aquel nivel. En la mayor parte de los copépodos analizados, este cambio era debido a la migración vertical; pero los zoopláncteres de mayor talla podían descender por debajo de los 225 m. de profundidad o evitar ser capturados por la red en dichos estratos, efecto que conseguirían con mayor éxito durante el día que de noche.

INTRODUCTION

Very little information is available on the vertical distribution of zooplankton within the Southern California Bight. In April 1965 a set of vertically stratified samples was taken with two different mesh sizes at locations within the bight. We analyzed samples from 28 of these stations where a vertical series was complete for differences in the vertical distribution of biomass and species with time of day, and in the areal distribution of biomass with respect to bottom topography. The basins may provide refuge for a significant biomass of mesopelagic animals that migrate into the upper 200 m at night.

MATERIAL AND METHODS

Samples from Expedition X were obtained from the Scripps Institution of Oceanography Invertebrate Collection. The cruise was conducted off the southern California coast in April 1965 (Figure 1). Series of vertically stratified samples were collected using the Brown-McGowan opening-closing nets (bongo nets) (McGowan and Brown 1966). The two nets on each

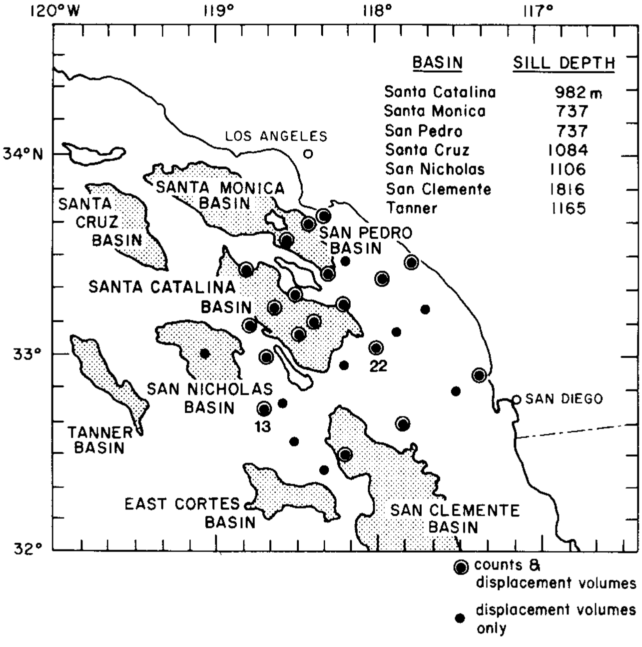

Figure 1. Station locations of samples from Expedition X showing basin topography at sill depth.

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frame were of different mesh sizes, 333 μm and 505 μm.

Four bongo frames were placed equidistant on the wire, and a depth recorder on the bottom frame was used to trace the course of the tow. The maximum wire paid out during a tow was 400 m. According to the expedition leader, Edward Brinton, (pers. comm.) a messenger was sent to open the nets when 300 meters of wire was out. Another 100 m of wire was lowered, and then raised. The nets were set to close after a predetermined volume of water was filtered (440.5 m^3 per net). The winch speed was adjusted so that the nets made an oblique tow within a stratum before they closed. It is not certain that the nets fished each depth uniformly within the desired stratum only, but every effort was made to achieve this. Adding together the catches of the four frames is thus an integration to 225 m.

The maximum depth of each tow was determined from depth recorder traces, and a mean maximum depth for all tows was calculated. We calculated the depths of the shallower frames on the assumption that the frames were equidistant on the wire and the wire angle was kept constant. The mean strata fished were 0–56 m, 56–113 m, 113–169 m, and 169–225 m. At several stations this vertical series was complete for one of the sizes of nets but not the other.

Displacement volumes were measured on all samples from stations shown in Figure 1. Because the mesh size on the two nets on each frame differed, two size fractions of samples were represented, and are considered separately. Displacement volumes were measured by pouring the sample into a graduated cylinder, noting the volumes, removing the animals by pouring the sample through 333-μm mesh netting into a second graduated cylinder, waiting up to 5 minutes until the dripping ceased, and then noting the volume of liquid in the second cylinder. The difference between the first measurement and the second is the displacement volume of the organisms (Ahlstrom and Thrailkill 1963). We removed larger gelatinous organisms and small fish before measuring.

The following organisms were enumerated in the 333-μm samples at stations shown in Figure 1: female *Calanus pacificus*, male *C. pacificus*, *C. pacificus* copepodite stages III–V (counted separately), female *Eucalanus bungii*, male *E. bungii*, *E. bungii* copepodites (lumped), female *Pleuromamma borealis*, male *P. borealis* and copepodites (lumped), and sexually mature (greater than 11 mm) *Euphausia pacifica* males and females. These animals were selected because of their abundance in all samples. *E. pacifica* is the only one that could migrate below 500 meters into the basins during the day. Samples were split with a Folsom plankton splitter. From 1/32 to 1/4 of each sample was counted for the above organisms.

RESULTS

The ratio of the displacement volumes from samples taken with nets of two different meshes (333 μm and 505 μm) was calculated for each depth and—because a balanced set of data existed—a one-way analysis of variance was performed to see if that ratio differed with depth. The mean ratio varied from 2.2 at the surface to 1.3 in the deepest strata. The ANOVA was weakly significant ($.05 < P < .10$). Figure 2 shows the mean displacement volumes of the different size fractions in separate strata. There is an enhancement of smaller organisms near the surface day and night in the 333-μm fraction.

A variation of the Rank Sum test was used to test for differences in the biomass, integrated to 225 m from each kind of net, between samples taken over the basins and those taken away from basins. (Basins and stations are shown in Figure 1.) The test gives equal weight to day and night, combining them to increase sample numbers and look for overall effects of the basins. The test was not significant for either the 333-μm or the 505-μm samples, thus suggesting no effect of seabottom topography on biomass in the overlying water column above 225 m at these deepwater locations. However, considering only night samples, for which the effect of the basins is hypothesized, there was significantly more material caught over the basins in the 505-μm samples when compared with nonbasin locations (Rank Sum $p = .05$). The 333-μm samples showed no difference in location. These results may

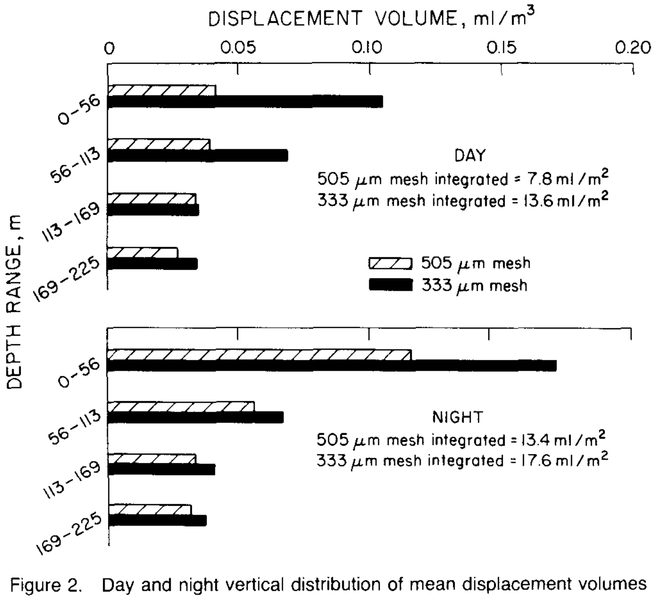

Figure 2. Day and night vertical distribution of mean displacement volumes from nets of two different mesh sizes.

TABLE 1
Radio (Night:Day) of Displacement Volumes

	505 µm	333 µm	
0-56	2.9	1.6	333 µm n = 8 day
56-113	1.4	1.0	n = 11 night
113-169	1.0	1.2	505 µm n = 9 day
169-225	1.2	1.1	n = 10 night
Integrated	1.7	1.3	

Volumes are for those stations at which all strata were sampled by one (but not necessarily both) of the meshes of net.

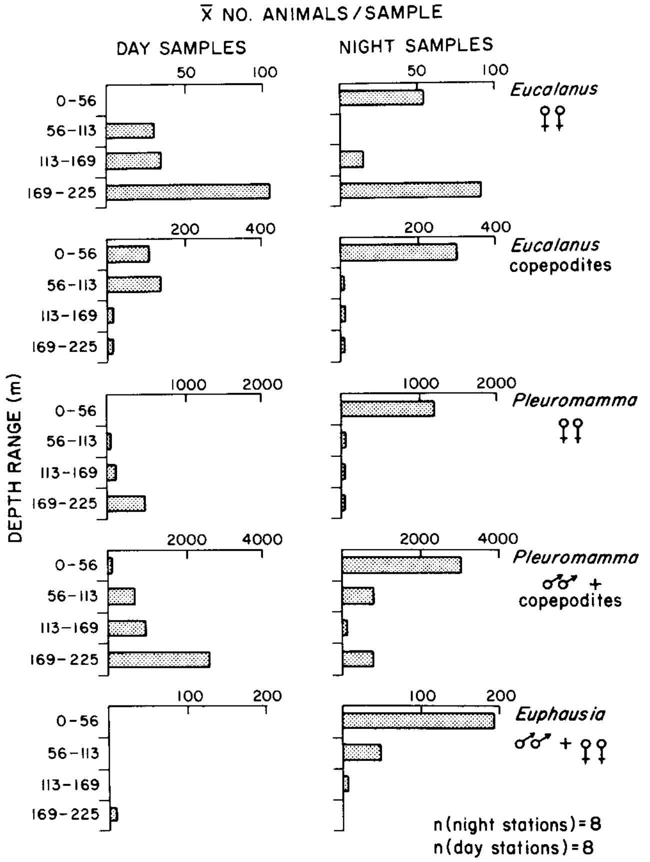

Figure 3. Day and night vertical distribution of selected species.

be complicated by onshore/offshore differences in abundance independent of "enrichment" by basins. Further tests of this hypothesis should be based on stations equidistant from shore over and away from basins.

Rank Sum tests comparing day samples to night samples showed a significant difference in the integrated catch for the 505-µm samples ($P < .01$), with more material being caught at night (Figure 2, Table 1). This difference in the 505-µm samples suggests either that there are large animals migrating from below 225 m into the upper water column at night, or that avoidance of the nets by large animals is reduced at night. We roughly estimated the fraction of that increase in biomass at night caused by *E. pacifica,* since the migration of this species was determined by microscopic analysis of the samples (see below). Although the lengths of euphausids were not recorded, a minimum and maximum estimate is possible. The weight of individual euphausids was obtained from Miller (1966). Weibe et al. (1975) estimated that wet weight is 0.73 g/ml of displacement volume. We used that estimate to determine that 11-mm and 20-mm *E. pacifica* were from 14–67% of the mean displacement volume in the night 0–56-m stratum, and none during the day (Figure 3). Other kinds of euphausids were present in the samples, so it seems that a major portion of the night enhancement of total biomass comes from euphausids.

Because the 333-µm samples include, of course, the 505-µm fraction, it might be expected that the 333-µm samples also should show a significant difference between day and night, but the test was not significant. A comparison of the 333–550-µm fraction of animals in the upper 56 m of water, obtained by subtracting the displacement volume of the 505-µm-mesh catch from that of the paired 333-µm-mesh catch, showed no change in this biomass associated with time of day. Thus we detected little or no movement of organisms of this size into the upper 225 m at night. This 333–505-µm fraction constituted from 32–61% of the total biomass caught with the 333-µm net in the 0–56-m stratum, but was less in deeper water (from 1–25%). The nocturnal enhancement in the 505-µm fraction apparently is obscured by nondiel variation in the larger biomass of the more conservative 333-µm fraction, and so the integrated 333-µm catches show no day/night differences. However, when the upper stratum is considered alone (Table 1), there is significantly more material caught by the 333-µm net at night than by day (Rank Sum $P < .01$). Figure 2 and Table 1 indicate that most of the difference in integrated 505-µm night catch also occurs in the upper strata.

A comparison of total counts of all animals identified (Figure 4), integrated to 225 m, shows no difference between day and night (Rank Sum Test). Tests of individual kinds of animals day vs night showed no difference in numbers in the water column except for *Euphausia pacifica.* Either euphausids migrated at night from below 225 m into the sampled water column, or they were less able to avoid the nets at night; there is no way to distinguish which. Brinton (1967) presents inconclusive evidence for the diel changes in avoidance capability of *E. pacifica,* but also shows it to be a strong migrator. Pieper (1979), using acoustics, showed an upper daytime depth of *E. pacifica* to be between 130 and 280 m in the San Pedro and Santa Catalina basins off southern California. Thus the low

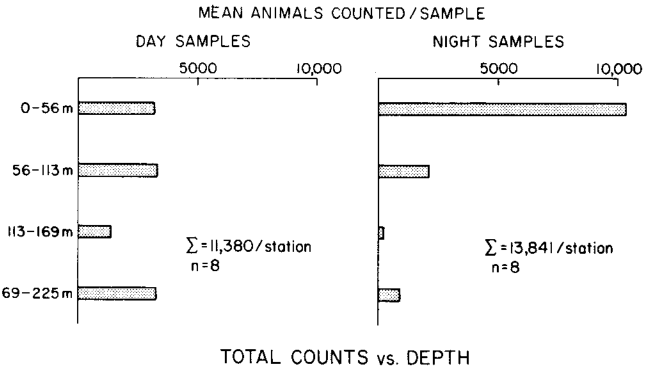

Figure 4. Day and night vertical distribution of total animals counted.

number of this species caught in the surface during the day may not be the result of avoidance.

Within the water column sampled, however, there was a change in the distribution of animals day and night. Most groups counted were concentrated nearer the surface at night (Figures 3–5). Only for *Calanus* CIII and IV were there no differences in the day vs night distribution. If these stages make diel migrations, they might be doing so within the 56-m surface stratum, and the migration could not be detected by the sampling regime. *Calanus* adults and CV, however, performed a detectable migration within the upper 169 m (Figure 5), as did all other groups of animals counted (Figure 3). *Pleuromamma, Eucalanus,* and *Euphausia* migrated to the upper 56 m at night from at or below 169 m. There appeared to be a group of *Eucalanus* females that remained below 169 m and did not come to the surface at night.

Figure 6 shows the density (σt) distribution at two stations on the sampling grid, and the horizontal lines indicate the strata sampled by the bongo nets. These stations are shown in Figure 1. There was a gradient extending from about 30 m to 100 m, above and below which the density is fairly uniform. Animals migrating into the surface strata thus swam through a pronounced density gradient into the mixed layer.

DISCUSSION

Banse (1964), in a review of the literature on vertical distribution, finds that at least half of the night population of animals fished by 0.3-mm nets in the surface layers remains in the upper layers during the day. Our results also show that a large fraction of the biomass remains in the surface during the day, since the night:day ratio of the 333-μm catches in the upper 56 m is only 1.6 (Table 1). Comparison of the biomasses of the 333–505-μm fraction showed no difference in day vs night, suggesting populations of smaller animals always resident in the surface. Although it is impossible to detect the effect of reduced avoidance of

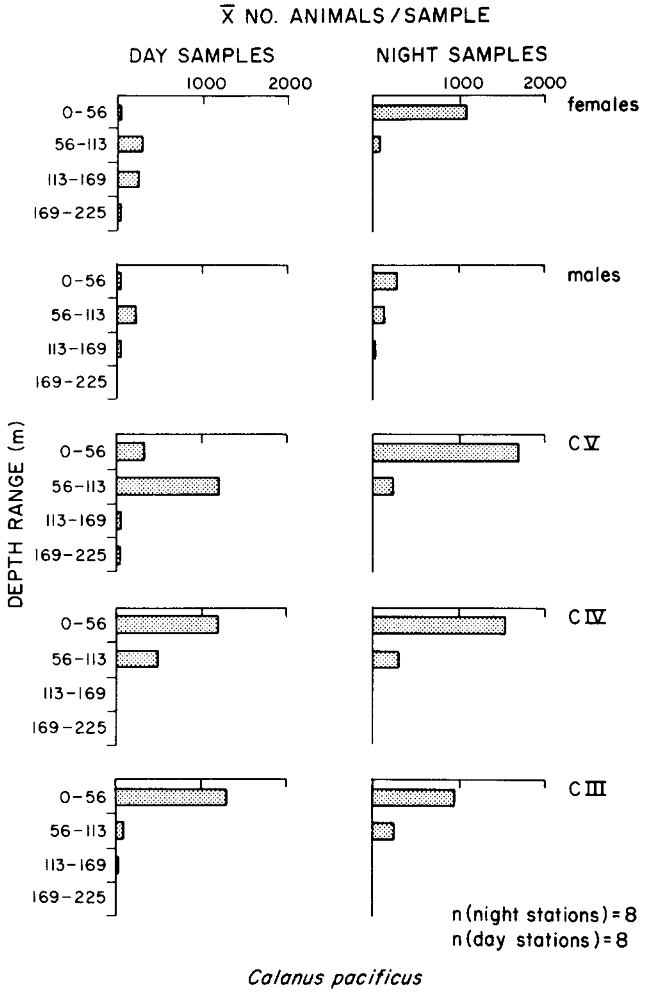

Figure 5. Day and night vertical distribution of developmental stages of *Calanus pacificus*.

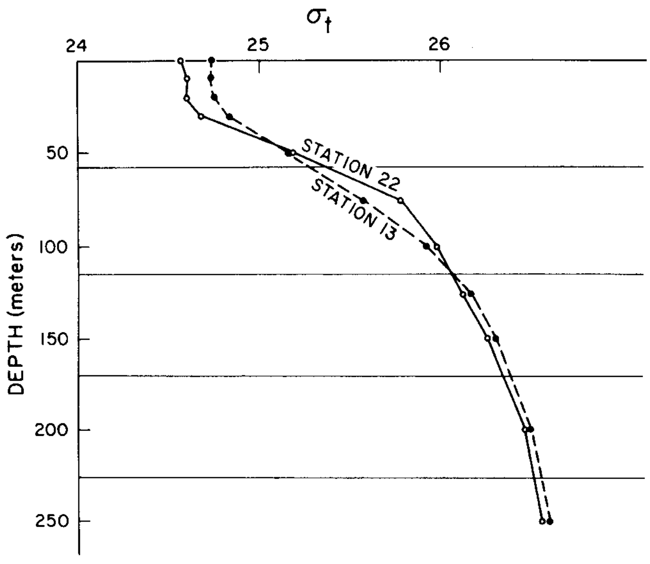

Figure 6. Vertical distribution of σt at two selected stations.

nets by rare, larger animals at night, the fact that there was no significant difference in the biomass of this 333-μm fraction day vs night, and that the integrated counts of all species (except *Euphausia*) showed no diel difference, indicates that most animals were being sampled uniformly day and night, and that changes in their apparent distribution according to time of day were not artifacts of differential efficiency of capture.

To assess the transport of material into deeper water, it is necessary to know the diel changes of animals within the water column. Animals remaining in the surface contribute to the organic matter in deeper water only through a rain of fecal material, exoskeletons, and corpses falling from the surface. Actively migrating animals, however, represent a behavioral transport of materials to depth, and estimates of that transport from this study indicate that about ⅓ of the nighttime 333-μm catch at the surface, and ⅔ of the nightime 505-μm catch at the surface are redistributed deeper during the day, mainly in the form of euphausids. Vinogradov (1968) concludes that this behavioral transport is the more important route of material from surface to deep water. Kuenzler (1967) calculates that transport of a heavy metal downward by migrating zooplankton may be equal to or greater than transport by vertical eddy diffusion. Animals eating at the surface and migrating deep during the day can hasten the transport of organic matter through excreting, defecating, and moulting at depth. However, Fowler (1982), in a review of biological transport processes, suggests that the more important route for vertical flux of pollutants downward is from biogenic debris in the form of fecal pellets.

The results also suggest that the fraction of the biomass in the form of smaller organisms is greater at the surface than at depth. This is likely because herbivores, which tend to be smaller, remain near the surface within the euphotic zone where the phytoplankton is.

Huntley and Brooks (1982) demonstrated an ontogenetic development of vertical migration in *Calanus pacificus* reared in a large tank. The present data shows further evidence of this phenomenon. There was no detectable diel vertical migration of *Calanus* CIII and CIV in the data, but CV and adults showed clearly different day and night depths (Figure 5). *Eucalanus* females also migrate from deeper depths than do *Eucalanus* copepodites (Figure 3). It is likely that the ontogenetic development of diel vertical migration is fairly widespread among many kinds of organisms, with the smaller juvenile stages undergoing smaller migrations within the surface waters, and the amplitude increasing as they get older (Gardiner 1933). Thus the smaller plankton of the surface contains juvenile forms of many organisms that will later be part of the migrating plankton.

In this study the population of migrating *Calanus* seemed to be contained within the upper 169 m. Esterly (1911) found *Calanus* off San Diego migrating from depths of 365–457 m. Since the sampling on Expedition X did not go any deeper than 225 m, we cannot say for certain that there were no deeper *Calanus,* but there may be seasonal effects on diel vertical migration (Koslow and Ota 1981). Esterly's study was done in June and July, whereas Expedition X was undertaken in April. All of the other organisms counted were contained in the deepest strata sampled in this study, indicating that the deepest part of their range may be below 225 m. But except for *Euphausia* the total numbers contained in the 225-m water column did not change from day to night, indicating that animals deeper than 225 m were not migrating to the surface at night. Longhurst et al. (1966), from a vertical profile in May, showed that *Eucalanus* and *Pleuromamma* occur deeper than 225 m in the Southern California Bight, while the bulk of the *Calanus* population is contained in the upper 250 m. *Euphausia pacifica* occurs to 600 m (Brinton 1967). Thus our samples may not bracket the entire population of *Pleuromamma, Eucalanus,* and *Euphausia* in the water column.

It was unlikely that there would be any demonstrable effect of bottom topography on biomass in the overlying 225 m, yet the night 505-μm tows caught a greater biomass over the basins than away from the basins. This may be a statistical artifact, or it may mean that the basins concentrate larger organisms. More intensive sampling throughout the water column, and identification of the specific organisms responsible for the increase in biomass are necessary to investigate this effect. Clearly, the biggest differences were in the changes in the day/night distributions of biomass and species, changes showing a crowding of larger organisms toward the surface at night, and a diel redistribution of species within the water column.

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GROWTH OF THE BLUE ROCKFISH *(SEBASTES MYSTINUS)*

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ABSTRACT

Weight-length and age-length data were obtained for samples of blue rockfish (*Sebastes mystinus*) taken off southern California.

For weight-length, $W = aL^b$, the value of a was found to be 2.043×10^{-5}; the value of b, 3.059.

The Von Bertalanffy curve was used for age length. It was determined that $L_\infty = 327.6$ mm, $k = 0.1428$, and $t_0 = -1.553$.

RESUMEN

Colecciones de *Sebastes mystinus* obtenidas en la región meridional de California, han proporcionado los datos básicos para establecer las relaciones entre peso y longitud, así como entre edad y longitud.

Para la relación peso y longitud, $W = aL^b$, se obtuvo el valor resultante 2.043×10^{-5}; siendo $b = 3.059$.

La curva de von Bertalanffy se utilizó para la relación edad y longitud. Así se ha determinado que $L_\infty = 327.6$mm, $k = 0.1428$, y $t_0 = -1.553$.

INTRODUCTION

The blue rockfish, *Sebastes mystinus,* is an important sport fish along the California coast, especially in central and northern California, where it was the most abundant species taken by hook-and-line fishermen in a 1957-61 survey (Miller and Geibel 1973). In the central California partyboat fishery, blue rockfish accounted for 27% of the total catch of all species and 31% of the rockfish catch.

The blue rockfish is less important in the southern California sport catch. In this area the sport fishery relies more on migratory surface species in summer and on rockfish during the winter when the other species are less available. In central California, although the blue rockfish are nonmigratory, the catch tends to be very low in the winter and high in the summer; Miller and Geibel (1973) attribute this to a seasonal change in feeding habits.

The purpose of this paper is to present growth data on blue rockfish off southern California. Such data are necessary to an understanding of the life history and population dynamics of the species. A secondary purpose is to compare and contrast these data with other published data on the blue rockfish.

MATERIALS AND METHODS

Blue rockfish were caught on hook and line off southern California (Table 1). Standard length, fork length, total length, and weight were obtained for each fish. Otolith and scale samples were taken.

Scales were used for aging the blue rockfish because they appeared to be easier to read than otoliths and also because it is much more convenient to back-calculate lengths from scales. In addition, *Sebastes* species tend to exhibit nonisometric growth of otoliths. For a 130-mm fish the otolith equals 5.4% of standard length, whereas for a 330-mm fish it equals only 4.1% of standard length. This further complicates back-calculating lengths from otoliths.

There is no good way to verify isometric growth of rockfish scales relative to length. We assume that growth is isometric primarily because the scales and scale pockets are integral parts of the covering of the fish's body. One objection raised to back calculations of length from scale annuli is that the scales do not begin to form until the rockfish are about 15 mm long. However, when the scale does form, it forms as a plate and not as a point.

In many fishes, especially temperate freshwater species, the scale annuli are formed by a change in spacing of circuli. The circuli are more widely spaced when water temperatures, feeding, and metabolism are high, and more closely spaced when these factors are low.

In many species of saltwater fishes, annuli consist

TABLE 1
Blue rockfish Caught Off Southern California

			Standard length (mm)	
Locality	Date	Number	Mean	Range
Bird Rock (La Jolla)	1-25-78	4	165	156-179
San Nicolas Island	5-31-79	35	252	193-301
San Nicolas Island	9-07-79	20	231	190-290
Santa Barbara Island	5-31-79	11	220	172-283
San Clemente Island	9-06-78	9	221	147-308
San Clemente Island	5-29-79	1	235	
San Clemente Island	8-09-79	3	195	180-223
Osborne Bank	8-04-71	2	256	252-259
Tanner Bank	3-1-77	10	271	260-286
Tanner Bank	9-07-78	12	275	233-325
Cortes Bank	5-30-79	12	221	162-266
Cortes Bank	9-05-79	5	200	172-248
		124		147-325

[Manuscript received February 2, 1983.]

of bands of broken circuli. These are especially noticeable in species with a marked fat cycle, such as the California sardine, *Sardinops sagax (S. caeruleus).* The sardine gains weight during the summer and loses weight during the winter. A sardine taken in September might be 20% heavier than one of similar length taken in March.

The circuli on the scales of sardines are about equally spaced throughout the year. However, when the fish loses subcutaneous fat deposits during the winter, apparently the elastic skin tightens enough to exert pressure on the scale pockets. This causes an erosion and breaking of circuli around the edge of the scales. When the fish begins to gain weight and grow more rapidly in the spring, normal circuli are again laid down at the edge of the scale. All of the blue rockfish scales had checks caused by broken circuli.

Loss of scales can cause a change in scale-pocket tension on adjacent scales and result in false annuli being formed in the scales near the area of scale loss. These false annuli are often noticeably more or less prominent than the true annuli and also may be markedly asymmetrical, depending on their distance and direction from the area of scale loss. Sampling scales from several locations on both sides of the fish decreases the chance of obtaining scales with false annuli in similar positions relative to the scale center.

Rockfish scales tend to be deciduous. In some species it is almost impossible to find scales that are not regenerated, whereas in others only a small percentage of the scales are regenerated. Blue rockfish fall somewhere between the two extremes.

In sampling rockfish scales it is often useful to include lateral-line scales in the sample in case no other unregenerated scales can be found. These scales are seldom deciduous, but there is a tubelike structure in the center of each scale that generally obscures the first annulus and makes the center of the scale difficult to locate. Fortunately, the blue rockfish generally had enough unregenerated regular scales so that it was not necessary to rely on lateral-line scales for most of the fish sampled.

The scales were mounted dry between two microscope slides and projected on a sheet of white paper at about 30× to 50× magnification. The scale center, annuli, and scale margin were marked for the six best scales for each fish. I obtained back-calculated lengths for each of the six scales and compared the readings to determine the age and average back-calculated lengths.

Annuli were considered valid if they appeared in the approximate same location in at least four of the six scales. The average value was obtained for each of the sets of readings to arrive at length at age for each fish.

LENGTH-WEIGHT RELATIONSHIP

Length and weight data were obtained from 98 blue rockfish ranging from 147 to 325 mm in standard length.

The usual formula describing a length-weight curve for fishes is $W = aL^b$. This may be obtained by transforming the straight line, $\log W = \log a + b \log L$, or directly by nonlinear methods (Marquardt's least squares) (Figure 1). The former should give the best least-squares fit to the logs of length and weight; the latter should give the best fit to the arithmetic curve. If the values of b are close to 3, the formula $W = aL^3$ may be used in which $a = K$; ($K = W/L^3$).

The values of a and b for the three curves are:

nonlinear $a = 2.04262 \times 10^{-5}$ $b = 3.05934$
log log $a = 2.12486 \times 10^{-5}$ $b = 3.05240$
cubic $a = 2.82587 \times 10^{-5}$ $b = 3.00000$

The calculated values of weight are the same between lengths 20 and 340 mm for the nonlinear and log log curves. The weights calculated from the cubic curve are slightly higher than those for the other two curves for lengths up to 240 mm, and slightly lower above 240 mm (Table 2).

The residuals from the nonlinear fit (Figure 2) increase with increasing length. An arithmetic standard error of estimate is useless for determining limits of weight divisions. There is no increase in residuals of log weight with log length. For the curve, $\log W = -4.67267 + 3.05240 \log L$, $Sy = 0.038498$. This value of S_y may be applied to the arithmetic curve as a

TABLE 2
Calculated Weights (grams) for Blue Rockfish

	Southern California		Monterey[(a)]		
Standard length (mm)	Male & female	Male & female	Female	Male	Male & female
20	0.20	0.23	0.37	0.22	0.73
40	1.65	1.81	2.60	1.72	4.27
60	5.69	6.10	8.11	5.77	12.0
80	13.7	14.5	18.2	13.6	24.8
100	27.1	28.3	34.1	26.6	43.7
120	47.2	48.8	56.8	45.8	69.3
140	75.5	77.5	87.6	72.6	103
160	111	116	127	108	144
180	163	165	177	154	194
200	224	226	238	211	253
220	300	301	311	280	322
240	391	391	397	363	402
260	500	497	498	462	492
280	627	620	613	576	594
300	774	763	744	708	708
320	942	926	892	858	834
340	1133	1111	1058	1029	972
Number of fish	98	98	147	58	278
Log a	−4.67267	−4.54885	−4.8346	−4.55299	−3.43180
b	3.05240	3.00000	2.80779	2.98849	2.53589

(a) Miller and Geibel 1973.

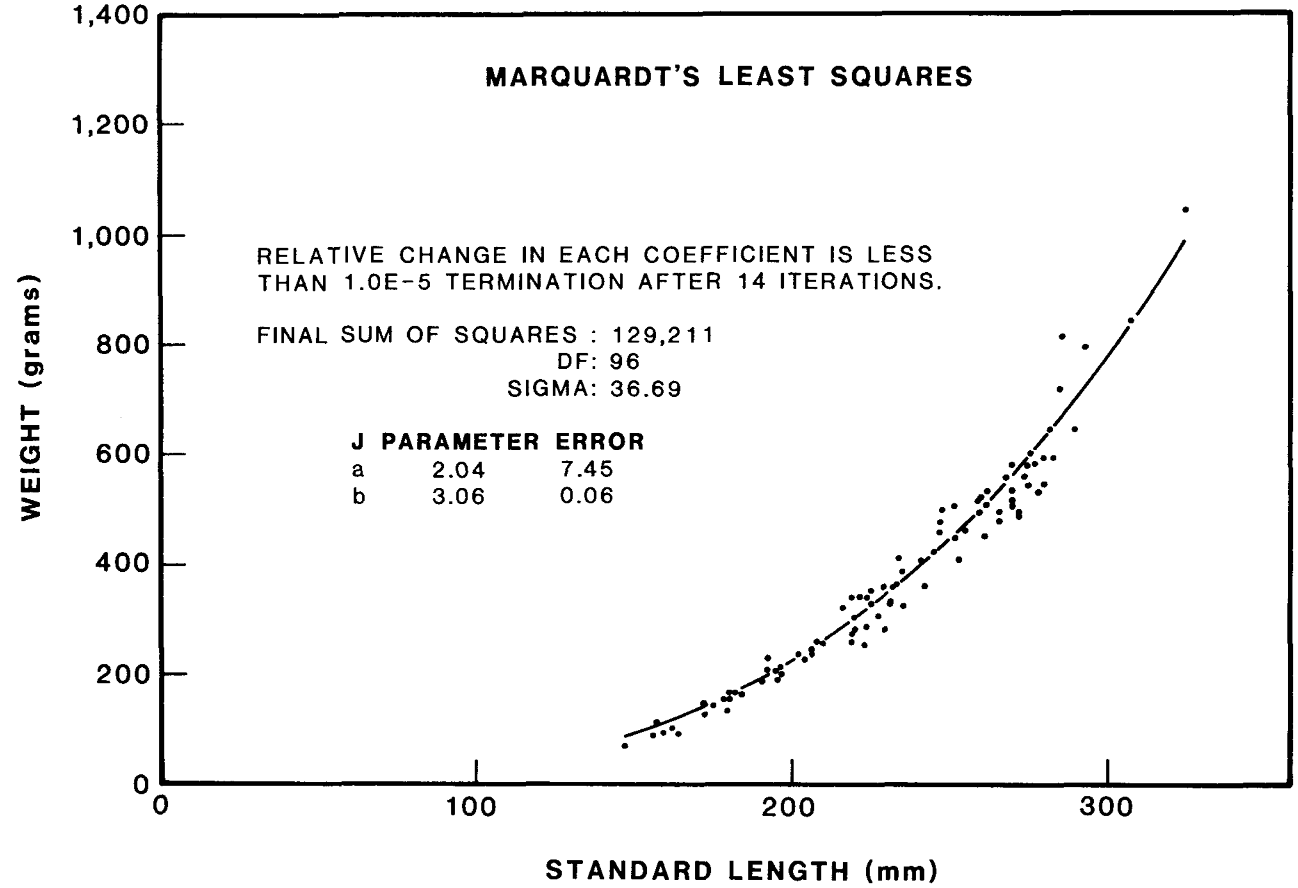


Figure 1. Length-weight curve ($L = 2.045W^{3.059}$) for blue rockfish taken off southern California.

percentage: $S_Y = +9.27\%, -8.48\%$; $2S_Y = +19.39\%, -16.24\%$.

Miller and Geibel (1973) give length-weight formulas that they obtained for blue rockfish from the Monterey area. Their data were collected in total length in mm and weight in pounds. We have converted these formulas to standard length and grams for comparison ($SL = 0.8127\ TL$) (Table 2).

They also give length-weight curves for male fish, females, and sexes combined. The females do give a slightly higher curve, but this is probably fortuitous. When they added 73 apparently unsexed fish to get a combined curve, they obtained values higher than either the male- or female-only curves. However, the curves all agree well with that based on the data from this study (Figure 3).

AGE-LENGTH RELATIONSHIP

We were unable to get samples of young fish to obtain length-frequency data that could establish the ages of these fish. Wales (1952) and Miller and Geibel (1973) obtained samples of juvenile blue rockfish from the Monterey area; we have compared these with average observed lengths back-calculated from scales for younger blue rockfish from southern California (Table 3).

The data of Wales (who used fork length) and Miller and Geibel (who used total length) were converted to standard length by the formulas $SL = 0.8506\ FL$ ($\sigma = 0.0069$) and $SL = 0.8127\ TL$ ($\sigma = 0.0091$). These formulas were based on measurements from fish 147 mm SL and larger and may not be entirely applicable to the smaller fish. The agreement with Wales's data seems to be very good. Miller and Geibel's samples show little growth in the second year, but this may be because larger fish migrate out of the nursery area to deeper waters.

The Von Bertalanffy growth curve is widely used to describe fish growth. The equation takes the form:

$$L_t = L_\infty (1 - e^{-k(t - t_0)})$$

There are several methods of solving the equation. The values of L_∞, k and t_0 may be obtained from two simple equations of the $Y = a + bX$ type.

In the first equation X equals length at age t (L_t), and Y equals length at age $t + 1$ ($L_t + 1$) (Figure 4.)

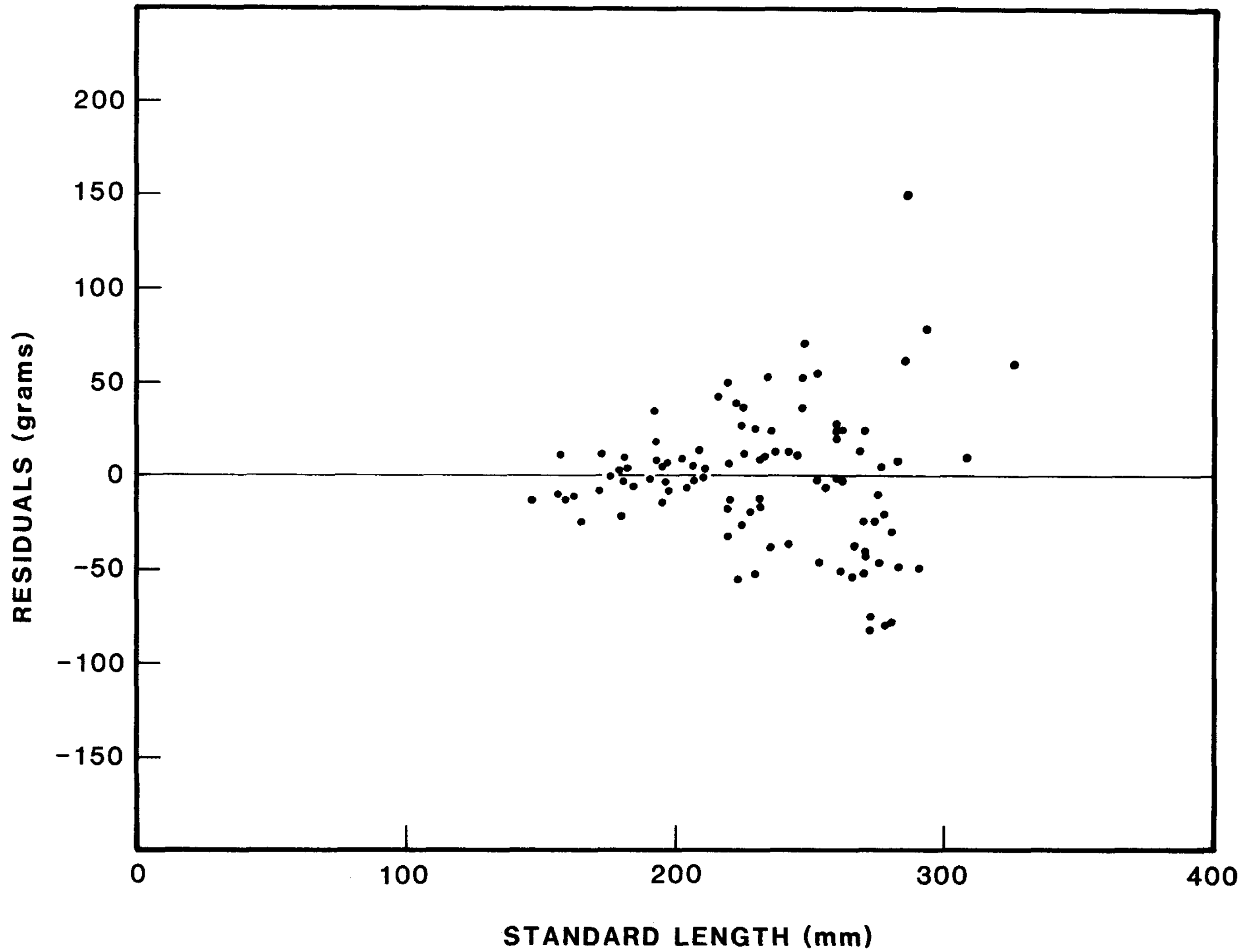


Figure 2. Residuals (L_o-L_c) of length-weight curve for southern California rockfish.

Length at infinity (L_∞) is assumed to be the point at which the computed line intersects the 45° diagonal from the origin. The value of k is obtained from $k = \log_e{}^{1/b}$. It is obvious from the angle at which the computed line intersects the diagonal that little variation around the line would take in a considerable range of lengths at age at infinity.

In the second equation X equals age, and Y equals $\log_e (L_\infty - L_t)$ (Figure 5). The value of t_0 (age at length zero) is obtained from $t_0 = a - \mathrm{Log}_e L_\infty / K$.

The second equation, when plotted, gives a good visual representation of the final age-length fit. Ricker (1958) suggests adjusting this equation to obtain a better fit by using trial values of L_∞, that is, iterating to get a better value of L_∞ for the Von Bertalanffy equation.

We have arbitrarily obtained two additional estimates of L_∞ by recalculating the first equation omitting the first pair of values (L_1 and L_2) from one equation and the second pair (L_2 and L_3) from the other. Both of these increase the value of L_∞. Length at infinity equals 313, 336, and 362 for the 12, 11, and 10 pairs of values, respectively.

Calculated values of length are closer to observed values for the second (336 mm) and third (362 mm) values of L_∞ than for the first (313) (Table 4). The sum of the squares of deviations of calculated length from observed length for the 12 pairs of values for the first value of L_∞ is 320; for the second, 128; and for the third, 284.

These equations can be used instead of the Von Bertalanffy equation to get the same calculated lengths and without the necessity of obtaining k and t_0. The equation $\log_e (L_\infty - L_t) = a + bt$ (in which t equals age) can be changed to $L_t = L_\infty - e^{(a + bt)}$, which also is easier to use than the Von Bertalanffy equation.

TABLE 3
Length-Frequency Data Used to Estimate Length at Age for Juvenile Blue Rockfish

			Monterey	
Month	Age	Southern California	Wales	Miller and Geibel
April				41 (one fish)
June				57 mean
July			58-65 = Range	56 mean
Aug.				58 mean
Sept.				62 mean
Oct.				65 mean
Nov.				69 mean
Dec.				70 mean
Jan.				73 mean
Mar.	1	95		80 mean
Apr.				83 mean
May				88 mean
June				
July			96-126 = Range	87 mean
Aug.			(115 = mean)	99 mean
Sept.				
March	2	133		
June			mean = 149	
March	3	163		
June			mean = 170	
March	4	181		

Monterey in 1929-30 (Wales 1952) and the 1964 year class in 1964-65 (Miller and Geibel 1973) compared with observed lengths back calculated from scales for southern California. All lengths are standard lengths in mm.

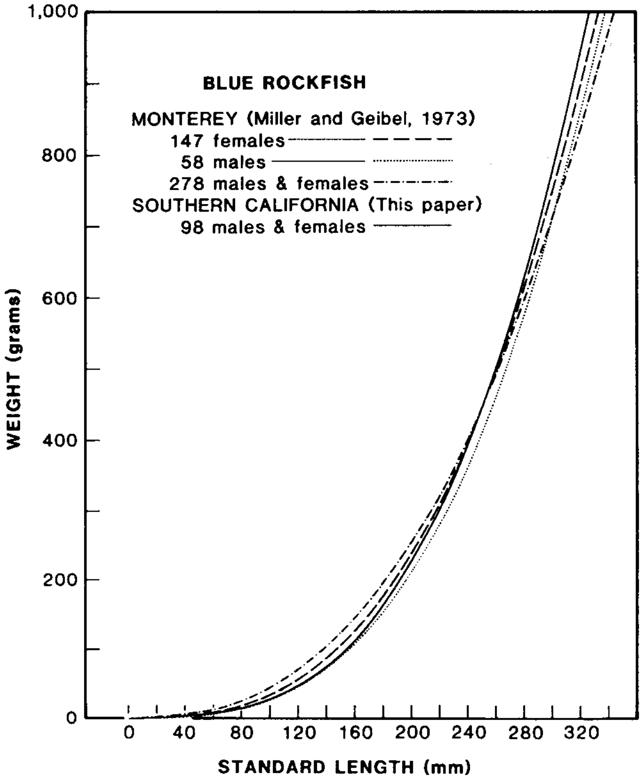


Figure 3. Comparison of blue rockfish length-weight curves, southern California and Monterey (Miller and Geibel 1973).

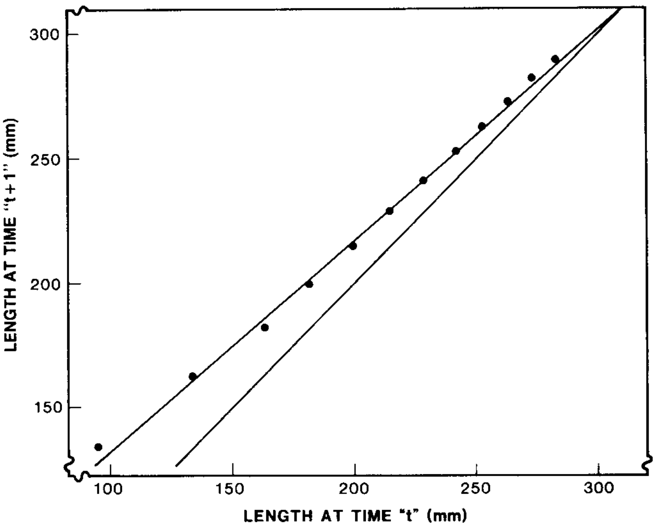


Figure 4. Plot of length at age plus one against length at age with the calculated regression line for blue rockfish.

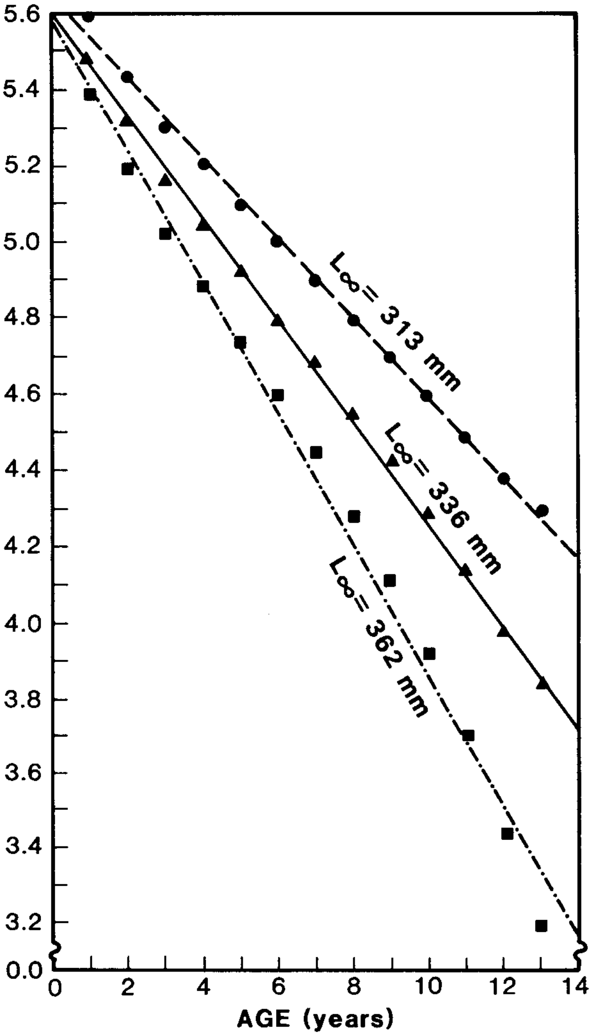


Figure 5. Plots of $\log_e (L_\infty - L_t)$ against age for blue rockfish.

In the Von Bertalanffy equation for the blue rockfish $k = 0.1316$ and $t_0 = -1.738$ for $L_\infty = 336$.

Tomlinson and Abramson (1961) give a method of fitting a Von Bertalanffy curve by least squares. Using this method, a value of 327.3 mm is obtained for L_∞; 0.1430 for k; and $-$ 1.5487 for t_0. The sum of d^2 is 118.

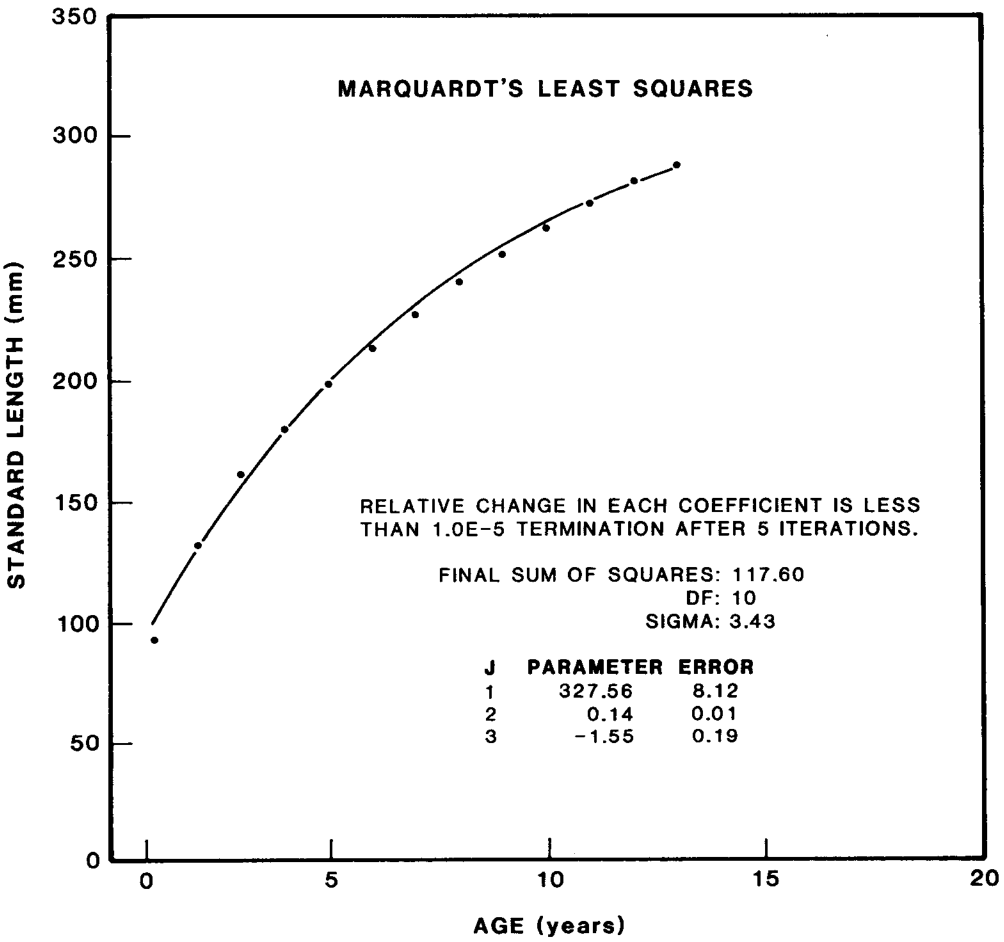
TABLE 4
Computed Values of Length at Age for Blue Rockfish: $L_t = L_\infty - e^{(a+bt)}$.

Age	Observed length	Calculated length		
		$L_\infty = 313$	$L_\infty = 336$	$L_\infty = 362$
1	94.5	87.1	101.8	109.3
2	113.4	123.3	130.8	134.4
3	162.5	153.7	156.2	157.1
4	181.4	179.3	178.4	177.5
5	199.5	201.3	197.9	195.9
6	214.4	218.8	215.0	212.5
7	228.1	233.9	230.0	227.4
8	241.3	246.6	243.1	240.8
9	252.5	257.3	254.6	252.9
10	263.1	266.3	264.7	263.8
11	273.2	273.8	273.5	273.6
12	282.5	280.2	281.2	282.4
13	289.1	285.5	288.0	290.4
	$a =$	5.59644	5.58816	5.63799
	$b =$	-0.17437	-0.13225	-0.10488
	$\Sigma d^2 =$	374.84	128.47	284.20

Using a Marquardt nonlinear least squares computer program to minimize the sum of d^2 by iteration from estimated values, 327.6 mm is obtained for the value of L_∞; 0.1428 for k; and $-$ 1.5535 for t_0 (Figure 6).

All of the above curves are based on average lengths at each age. A nonlinear least squares curve based on all length measurements at each age was also calculated (Figure 7). This weights the curve to those lengths for which there is most data. When back-calculated lengths are used, this means that the curve is weighted more heavily to the lengths at younger ages. It would appear that fewer older fish are more representative of their true size at age than lengths influenced by extrapolations of the more heavily weighted younger fish (Table 5). The value of L_∞ for the weighted curve is 313.0 mm; of k, 0.1600; and t_0, $-$ 1.3696.

The standard error of estimate for the weighted curve is 18.6 mm. However, the residuals (Figure 8)



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RELATIVE CHANGE IN EACH COEFFICIENT IS LESS
THAN 1.0E-5 TERMINATION AFTER 5 ITERATIONS.

FINAL SUM OF SQUARES: 117.60
                  DF: 10
               SIGMA: 3.43

J  PARAMETER  ERROR
1    327.56    8.12
2      0.14    0.01
3     -1.55    0.19
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Figure 6. Von Bertalanffy length-age curve using mean lengths at age for blue rockfish.

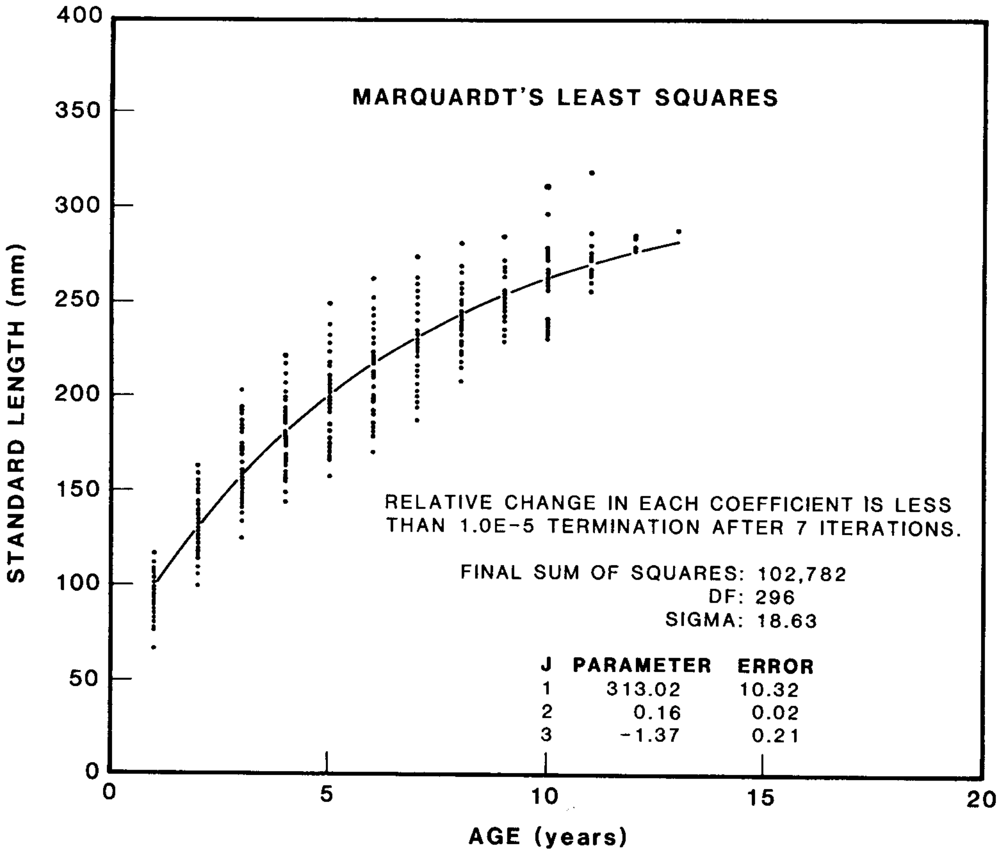

Figure 7. Von Bertalanffy length-age curve using sample of 299 age readings for blue rockfish (28 readings, age 1 through 10; 14 readings, age 11; 4 readings, age 12; 1 reading, age 13).

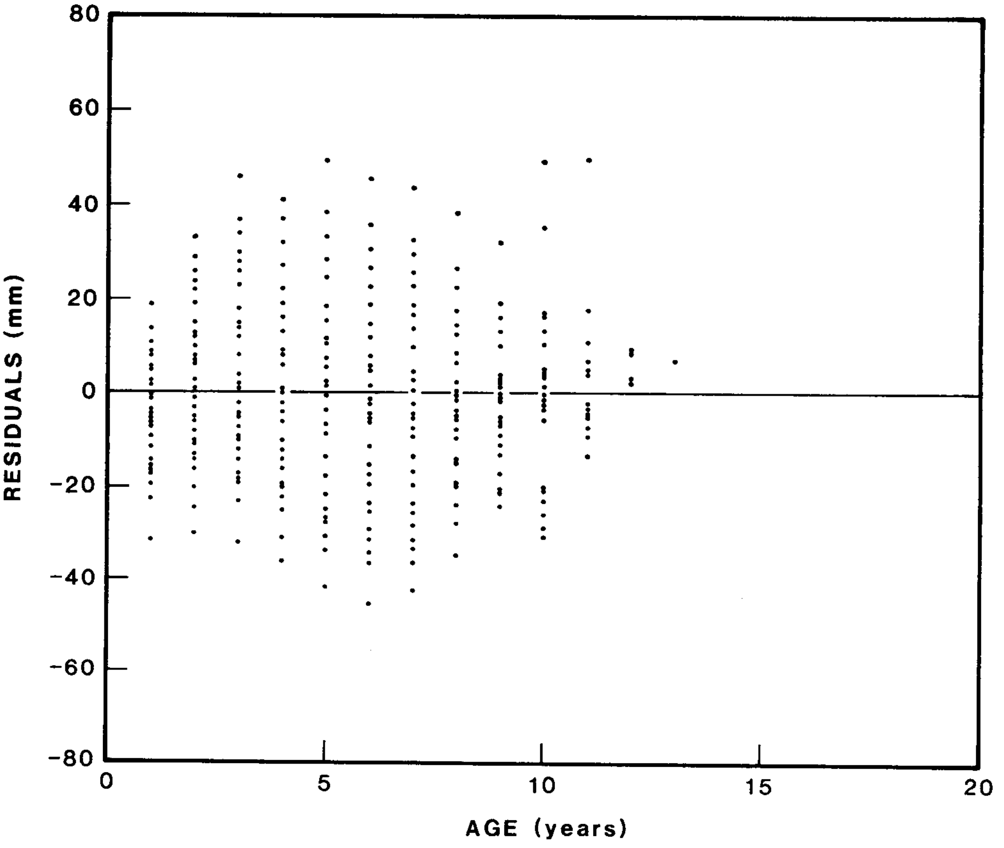

Figure 8. Residuals ($L_o - L_c$) of length-age curve for blue rockfish.

TABLE 5

Standard Lengths (mm) at Age for Various Calculations of the Von Bertalanffy Growth Curve Compared to Back-calculated Observed Length for Blue Rockfish

Age (years)	Observed length (mm)	Standard length (mm)					
		Trial values of L_∞ Ricker (1958)			Least squares Tomlinson and Abramson (1961)	Marquardt	
						Unweighted	Weighted
1	95	87	102	109	100	100	99
2	133	123	131	134	130	130	130
3	163	154	156	157	157	157	157
4	181	179	178	178	179	179	180
5	200	201	198	196	199	199	200
6	214	219	215	213	216	216	216
7	228	234	230	227	231	231	231
8	241	247	243	241	244	244	243
9	253	257	255	253	255	255	253
10	263	266	265	264	265	265	262
11	273	274	274	274	273	273	270
12	283	280	281	282	280	280	276
13	289	286	288	290	286	286	282
	Length at Infinity =	313	336	362	327.3	327.6	313.0
	k =		−0.132		−0.1430	0.1428	0.1600
	t_0 =		−1.738		−1.549	−1.553	−1.370

increase in error to age six, followed by a decrease. If we calculate standard deviations for each age using the nonlinear curve value as a "mean" we obtain:

Age	σ	*Age*	σ
1	12.6	7	23.0
2	17.0	8	16.8
3	20.9	9	12.3
4	20.3	10	17.9
5	23.2	11	16.3
6	23.5	12	8.1

I have used the unweighted nonlinear curve values for further comparison with the data of Miller and Geibel (1973). They computed a Von Bertalanffy curve for their age-length data based on scale readings, but they do not give values for either the parameters of the curve or their age-length data. We have picked approximate values from their figured curve for combined sexes and have recomputed the age-length curve to compare with our data (Table 5, Figure 9). Their values are lower than ours for the first few years but eventually catch up.

The biggest difference is in the first year's growth in which the average back-calculated length attained by southern California fish is 95 mm, and by Miller and Geibel's Monterey fish only 75 mm. For the next 5 years the growth increments of the Monterey specimens are slightly greater until, at age seven, fish from both areas are approximately the same length.

We did not take any samples of mature blue rockfish during the winter and, therefore, could not delimit

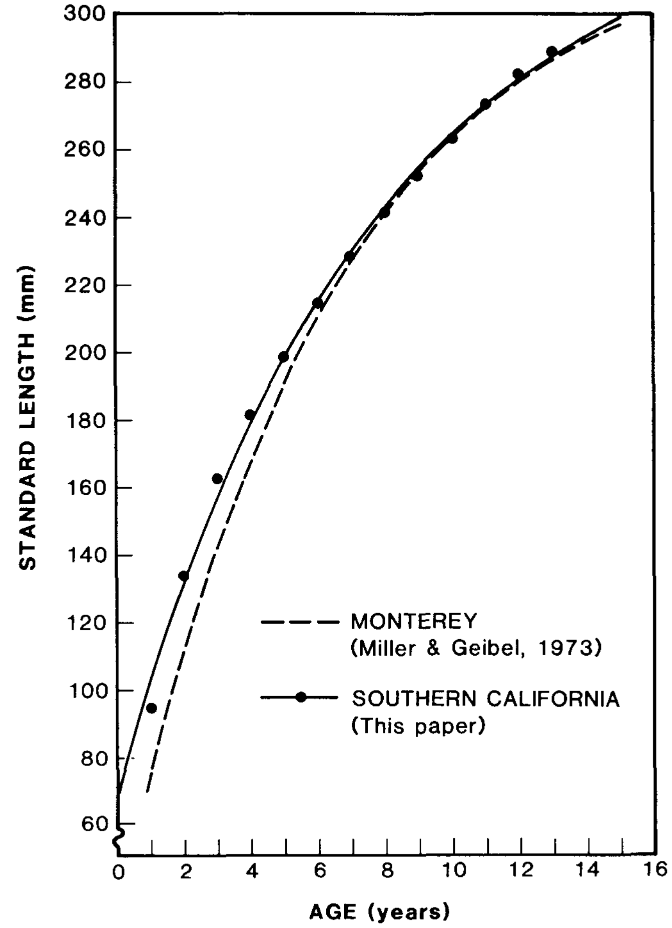

Figure 9. Comparison of length-age curves, blue rockfish, southern California and Monterey (Miller and Geibel 1973).

the spawning season off southern California. Wales (1952) states that spawning took place in the Monterey area in November, December, and January. Miller and Geibel (1973) found that annuli are formed in March and April. Because annuli do not form on the scales when the fish are only a few months old, the first annulus may be formed when the fish is one year and three months old and the second approximately a year later at age two years and three months. Thus the first "year" may be longer or shorter than a year for different species of fishes, depending on when annulus formation occurs in relation to the spawning season.

This phenomenon is more marked in some species. Sardines in the northern part of their range tended to spawn later than those off southern California and northern Mexico, and showed apparent slow growth (i.e., a shorter first year) in length at age one back-calculated from scales. However, they grew much faster than the more southerly populations of sardines in subsequent years and soon outgrew them.

Actually, although the blue rockfish probably have a long first "year", their first year's growth appears to be less than a year's growth compared with the best-fitting curves that we computed. However, 9 of 10 species of rockfish show negative deviations of observed values from Von Bertalanffy curves for the first year in Phillips's (1964) data (Table 6).

Considering the possible variation that one might expect, the pattern of deviations in Phillips's data is noteworthy. From the second to fifth year the observed values tend to be higher than computed values; from the sixth to eleventh year they tend to be lower; and from the twelfth on, higher (Table 6). For the blue rockfish the pattern is remarkably similar.

One possible explanation of this is that male rockfish of many if not all species tend to be slower growing and shorter lived than females. For the first few years the fish grow more rapidly, and there is less difference in growth rates between the two sexes (plus deviations) until sexual maturity is reached. Then, for several years, the slower growth of the males causes the curve to dip (minus deviations). The increasing higher mortality of the slower-growing males in the later years gradually increases the proportion of faster-growing females in the population causing a final rise in the curve (plus deviations).

CONCLUSIONS

The length-weight data for blue rockfish from southern California show nearly isometric growth. Therefore the formula $W = KL^3$ may be used instead of $W = aL^b$.

The length-weight curve for southern California blue rockfish was close to the curves obtained by Miller and Geibel (1973) for samples from Monterey.

Several modifications of the Von Bertalanffy growth curve were used to describe the age-length relationship. Growth of southern California blue rockfish appeared to be more rapid than for Monterey samples for the first few years. This was caused by the smaller length at age one calculated for Monterey fish. Growth increments were actually greater for the following 5 years until they caught up with southern California fish.

There was a tendency toward a slight "S" shape to the curve of observed values of age length, which caused it to not quite fit the Von Bertalanffy curve. This tendency appears to hold true for other species of rockfishes also, and may be caused by differences in growth rates and mortality between male and female rockfish.

Conversions to standard length from fork length and total length (in millimeters) are: $SL = .8506FL$ and $SL = .8127TL$.

TABLE 6

Deviations of Observed Total Length from Von Bertalanffy Curve for Ten Species of Rockfish (Phillips 1964) Compared to Deviations (Standard Length) of Blue Rockfish from Southern California

Species of rockfish	Deviation at age													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Bocaccio	-4.4	+4.0	+4.4	+1.2	-3.0	-6.5	-2.4	+0.5	+2.4	+0.5	+2.4	+4.4	+3.2	+6.3
Chilipepper	-4.7	+2.7	+6.4	+5.3	-0.3	-5.8	-8.4	-7.1	-1.7	+2.2	+3.9	+6.0	+11.1	+16.8
Yellowtail	-1.0	-1.2	+1.0	+3.2	+3.7	+0.5	-3.5	-4.0	-5.8	-6.4	-4.5	+0.8	+5.8	+11.5
Dark blotched	+1.4	-1.6	-1.8	-0.4	+0.5	+2.8	+4.9	+0.1	-3.3	-4.8	-4.7	-2.4	-0.3	+9.3
Splitnose	-1.0	+1.4	+1.5	-0.3	-1.4	-0.3	+0.7	+0.3	-1.0	-1.2	+1.3	+0.4	+0.8	+1.5
Canary	-0.3	-1.8	0.0	+2.2	+2.2	+1.3	+0.8	-1.7	-4.7	-3.5	-1.7	-1.4	+7.1	+9.5
Vermilion	-4.5	+1.0	+4.5	+2.6	+3.0	-0.8	-3.2	-1.5	-0.9	-2.7	-5.2	-2.7	+2.8	+0.1
Widow	-0.1	-1.2	+0.2	+6.0	-0.1	-7.0	-6.4	-4.5	-1.4	+0.3	+2.6	+6.3	+8.7	+17.6
Stripetail	-2.9	+2.7	+2.2	+1.9	-0.9	-0.5	-0.4	-3.1	-4.7	-2.5	-0.9	0.0	+1.0	+2.9
Shortbelly	-0.1	+0.5	+0.8	0.0	-1.4	-2.2	-0.8	+3.0	+3.2	+3.3	—	—	—	—
Mean deviation	-1.8	+0.7	+1.9	+2.2	+0.2	-1.9	-1.9	-1.8	-1.8	-1.5	-0.8	+1.3	+4.5	+8.4
Blue rockfish	-7.3	+2.6	+6.3	+3.0	+1.6	-0.6	-1.9	-1.8	-2.1	-1.6	-0.3	+1.3	+1.1	—

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DESCRIPTION OF THE LARVAE OF THE CUSK EELS *OPHIDION SCRIPPSAE* AND *CHILARA TAYLORI* (FAMILY OPHIDIIDAE)

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ABSTRACT

Larvae of the two species of cusk eels (Ophidiidae) found in the CalCOFI region, *Ophidion scrippsae* and *Chilara taylori*, are described from specimens reared in the laboratory and from specimens collected in the field. Larvae are distinguished by morphological, meristic, and pigment-pattern differences. *C. taylori* larvae are proportionately longer and more slender, have more vertebrae, and have more dorsal and anal fin rays than do *O. scrippsae*. The gut loop forms at a longer body length in *C. taylori* (ca. 14.1 mm) than in *O. scrippsae* (ca. 7.5 mm). *O. scrippsae* larvae have no pigment in the caudal fin, and the anal fin usually has numerous melanophores, whereas *C. taylori* larvae have caudal fin pigment and little, if any, pigment in the dorsal and anal fins. Analysis of ophidiid larvae collected in CalCOFI survey cruises from 1972 to 1978 revealed a relatively low abundance and a distribution centered around points and capes from San Diego to the vicinity of Magdalena Bay, reflecting the nearshore nature of these fish.

RESUMEN

Se describen las larvas de dos especies de Ophidiidae, *Ophidion scrippsae* y *Chilara taylori*, obtenidas en la región explorada por el programa CalCOFI. Los ejemplares estudiados proceden de cultivos en el laboratorio y material recolectado en el mar. Las larvas de estas dos especies se distinguen por las características morfológicas, merísticas y la distribución del pigmento. Las larvas de *C. taylori* son más largas y delgadas, tienen más vertebras y más radios en las aletas dorsal y anal, que las larvas de *O. scrippsae*. En *C. taylori*, el asa del tubo digestivo se forma cuando los ejemplares alcanzan unos 14.1 mm, mientras que en *O. scrippsae* ya aparece en larvas de 7.5 mm de longitud. Las larvas de *O. scrippsae* carecen de pigmento en la aleta caudal, pero en la aleta anal aparecen generalmente muchos melanoforos. En *C. taylori* las larvas presentan la aleta caudal pigmentada y escaso o ningún pigmento en las aletas dorsal y anal. Los Ophidos recolectados desde San Diego hasta las cercanías de Bahía Magdalena, durante los cruceros CalCOFI, en el periodo 1972-1978, no han sido abundantes, y aparecen concentrados en las zonas de cabos y salientes de la costa, lo que indica que estos peces son de régimen nerítico.

INTRODUCTION

Two species of cusk eels (Ophidiidae) are found in the CalCOFI region, *Ophidion scrippsae* and *Chilara taylori* (Robins et al. 1980). *O. scrippsae* ranges from the Gulf of California north of Guaymas, Mexico, to Point Arguello, California, (ca. 34°N) in depths of 3 m to 76 m. *C. taylori* has been taken from San Cristobal Bay, Baja California, (ca. 27°N) to northern Oregon from depths of 1 m to over 260 m (Miller and Lea 1972).

Neither species is fished commercially, but both are often taken with bottom trawling gear, purse seines, and bait nets. Cusk eels are preyed upon by numerous commercially important fishes, diving sea birds, and California sea lions (Fitch and Lavenberg 1968). Primarily nocturnal, adult cusk eels are burrowing tail-standers inhabiting a variety of substrates including silty sand and green mud (Mearns 1979), eel grass (Herald 1953), rubble, crevices, and holes (Fitch and Lavenberg 1968). The pelagic larvae are collected in coastal CalCOFI plankton tows primarily in the fall.

The purpose of this paper is to describe the development of the early larval stages of *O. scrippsae* and *C. taylori* and to summarize the distribution of larvae in CalCOFI samples made from 1972-78.

METHODS AND MATERIALS

Life-history series for *O. scrippsae* were assembled from larvae reared at the Southwest Fisheries Center from eggs collected in plankton tows at La Jolla Cove. Some early larval stages of *C. taylori* were obtained by rearing batches of mixed, unidentified eggs collected in nearshore plankton tows; however, most of the specimens were obtained from CalCOFI plankton tows. Reared fish were kept at 17.6°-20.6°C in black 100-liter pots and fed *Brachyonis* (a rotifer), harpacti-

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[Manuscript received November 23, 1982.]

coid copepods, and *Artemia* (a brine shrimp). We attempted to maintain the prey concentrations at approximately 50 *Brachyonis*/ml, and the copepods and *Artemia* both at 1/ml.

A series was established for the study of morphological development, morphometry, and pigment formation using the techniques and terminology of Ahlstrom et al. (1976). Another series was stained in Alizarin Red-S and X-rayed to obtain meristic data.

DESCRIPTION

Literature

Larvae of two Atlantic species of *Ophidion* have been described: *O. vassali* (Padoa 1956) and *O. barbatum* (Padoa 1956; Aboussouan 1972).

Distinguishing Features

O. scrippsae eggs are slightly off-round, and have homogenous yolk, no oil globule, and a mean size of 1.00 × 1.06 mm. Larvae are 2.5 mm long at hatching, are slender, and have a gut that ends just short of mid-body. The eggs of *C. taylori* are unknown.

Larvae of *O. scrippsae* and *C. taylori* may be distinguished from those of the bythidid *Brosmophysis marginata* on the basis of myomere count and pigmentation. *B. marginata* have 63-65 vertebrae compared with 67-69 for *O. scrippsae* and 86-91 for *C. taylori*. *B. marginata* larvae lack pigment at the finfold margin and have five large blotches along the dorsum, four postanal and ventral blotches, and a diffuse band near the tip of the notochord.

The larval morphology, meristics, and pigmentation patterns of *O. scrippsae* and *C. taylori* are unique to these species. *C. taylori* larvae are proportionately longer and more slender than *O. scrippsae*. Notochord flexion occurs at a much larger size in *C. taylori* larvae (21.1-29.6 mm) than in *O. scrippsae* (9.6-11.5 mm). The gut loop forms at a longer body length in *C. taylori* (ca. 14.1 mm) than in *O. scrippsae* (ca. 7.5 mm). *O. scrippsae* has fewer dorsal fin rays (136-153) and anal fin rays (112-119) than does *C. taylori* (198-216 dorsal and 156-170 anal fin rays). *O. scrippsae* larvae have no pigment in the caudal fin, and the anal fin usually has numerous melanophores, whereas *C. taylori* larvae have caudal fin pigment and little, if any, pigment in the dorsal or anal fins.

Ophidion scrippsae

Morphology. Ophidion scrippsae eggs are slightly off-round with a mean size of 1.00 × 1.06 mm. They possess a homogenous yolk, a wide perivitelline space, and no oil globule. The elongate slender larvae (body depth only 10% of body length) hatch at about 2.5 mm in a relatively undifferentiated state, with eyes incompletely formed and unpigmented. The larvae have a straight tubular gut, a large yolk-sac, and no mouth, branchial apparatus, or pectoral fins. By 3.8 mm (3 days after hatching) the yolk-sac has been absorbed, the eyes are pigmented, and the mouth and pectoral fins have formed (Figure 1). Notochord flexion occurs between 9.6-11.5 mm body length (Table 1). Morphological proportions are summarized in Table 2. Ontogenetic trends show a relative shortening of the gut length, a decrease in the relative eye size, an increase in body depth, and the anterior migration of the pelvic fins.

Timing, positioning, and size at torsion of the gut in ophidiid larvae are useful taxonomic characters (D. J. Gordon, Univ. of Miami, pers. comm.). The gut of *O. scrippsae* coils at a size range of 7.5-8.5 mm on about the 18th day after hatching (Figure 2). Coiling is always in the same direction, with the posterior portion of the gut displaced away from the observer when the left side of the larva is viewed. The single coil occupies a large middle portion of the visceral cavity.

Fin formation and meristics. Dorsal and anal fin pterigiophores begin to ossify by the onset of notochord flexion at about 9.6 mm (Table 3). The full complement of anal fin rays (112-119) and dorsal fin rays (136-153) are ossified near the end of notochord flexion. Pelvic fin buds are visible at the start of notochord flexion, and as growth proceeds one ray of each pair becomes longer. Pectoral fin and principal caudal fin rays begin ossification near the end of the notochord flexion period at ca. 11.5 mm body length. Ossification of the vertebral column begins after notochord flexion. By ca. 15.8 mm, the pectoral and caudal fins attain their full complement of rays (22-24 and 4 + 5, respectively), and the full complement of 67-69 vertebrae is ossifying.

Pigmentation. O. scrippsae larvae are unpigmented at hatching. By the second day (2.8-3.0 mm) small melanophores are forming over the entire body, giving the larvae a speckled appearance. At day 4 (3.6-3.9 mm) serial melanophores are present near the margins of the dorsal and anal fin folds, and along the dorsal and ventral margins of the body (Figure 1). Melanophores are sparse or lacking laterally on the body, and the eyes are becoming pigmented. After gut torsion on about the 18th day (ca. 7.5 mm), little pigment remains in the dorsal fin fold. Melanophores on the anal fin fold and developing anal fin increase in density, and pigment begins to appear over the branchiostegal rays. Body pigment is still primarily at the dorsal and ventral margins, but is becoming more diffuse. By the 45th day (ca. 20.3 mm, Figure 3) a few scattered melanophores appear on top of the brain, and

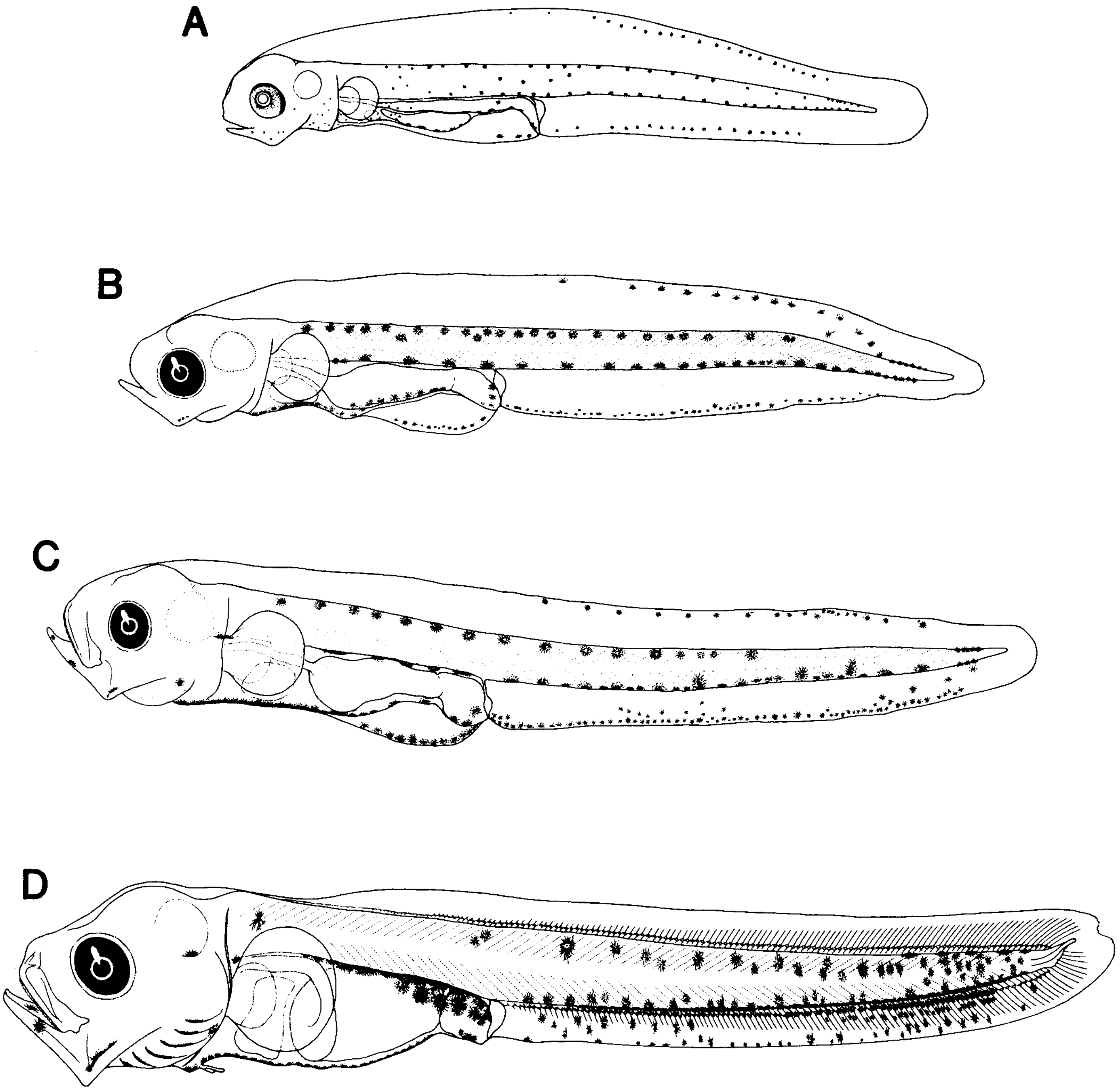

Figure 1. Larvae of *Ophidion scrippsae*: (*A*) 3.8 mm with yolk remnant, day 4; (*B*) 4.8 mm, day 8; (*C*) 7.1 mm, day 14; (*D*) 10.6 mm, day 42.

the ventral surface of the gut becomes less pigmented. The caudal fin remains unpigmented throughout the larval development of *O. scrippsae*.

Xanthophores are conspicuous along the dorsal and ventral body margins and in the dorsal fin fold in living *O. scrippsae* larvae. This pigment fades rapidly after fixation, leaving only the melanophores. By 14.7 mm, the xanthophores highlight the dorsal body surface, and melanophores dominate the anal fin and ventral body, producing a complementary effect similar to that discussed by Moser (1981).

Behavior. O. scrippsae larvae were active water-column feeders, especially around the edges of the tank, until about 36 days after hatching, when they settled to the bottom and lay in wait for their prey. By day 41, many of the larvae had burrowed into the sand at the bottom of the tank, in a manner similar to adult behavior.

TABLE 1
Measurements in mm of Reared Developmental Series of *Ophidion scrippsae*

Age days	Body length	Snout to anus	Head length	Snout length	Eye diameter	Body depth at pectoral fin base	Snout to dorsal fin origin	Snout to anal fin origin	Snout to pelvic fin origin	Pectoral fin length	Pelvic fin length long	Pelvic fin length short	
2	3.2	1.7	.64	.16	.06	.16	—	—	—	—	—	—	yolk-sac
4	3.8	1.8	.60	.12	.22	.36	—	—	—	.12	—	—	yolk-sac
5	4.0	1.8	.62	.16	.22	.42	—	—	—	.16	—	—	
8	4.8	2.1	.76	.18	.26	.44	—	—	—	.24	—	—	
8	5.4	2.5	.86	.26	.26	.54	—	—	—	.20	—	—	
10	6.1	2.8	1.1	.23	.32	.70	—	—	—	.20	—	—	
12	6.7	3.0	1.1	.30	.34	.68	—	—	—	.40	—	—	
14	7.1	3.2	1.2	.40	.32	.86	—	—	—	.40	—	—	
19	7.2	3.2	1.2	.34	.38	.90	—	—	—	.46	—	—	
21	7.5	3.3	1.3	.36	.40	1.0	—	—	—	.60	—	—	
21	7.8	3.3	1.4	.36	.40	1.0	—	—	—	.56	—	—	
16	8.2	3.7	1.3	.44	.38	1.0	—	—	.72	.50	—	—	
24	9.6	4.6	2.2	.72	.48	1.6	3.3	4.6	1.8	.60	—	—	
24	10.0	4.6	1.9	.56	.48	1.7	3.3	4.6	1.9	.60	—	—	
42	10.6	4.9	2.2	.67	.58	1.7	3.3	5.1	1.8	.80	.24	.14	
31	11.0	4.9	2.2	.58	.67	1.8	3.1	5.1	1.9	.80	.26	.14	
36	11.5	5.4	2.4	.76	.67	1.8	3.8	5.4	2.0	1.0	.20	.16	
36	13.2	5.6	2.6	.67	.68	2.2	3.6	5.7	2.3	1.2	.34	.28	
44	15.0	6.2	2.7	.83	.67	2.5	3.8	6.3	2.0	1.1	—	—	
55	15.8	6.3	2.9	.75	.80	2.5	3.9	6.6	2.1	1.0	.72	.56	
55	17.2	6.8	3.2	.90	.83	2.4	4.8	6.8	2.3	1.0	.70	.50	
50	19.6	8.3	3.7	.92	.92	3.2	5.2	7.8	2.1	1.2	1.1	.60	
38	20.3	8.0	3.3	.75	.92	3.3	4.7	7.9	2.1	1.6	.90	.60	
55	21.3	7.8	4.0	1.0	.92	3.1	5.2	8.0	2.1	1.8	1.1	.70	
45	21.7	8.5	4.3	.92	.92	2.8	5.5	8.5	1.8	1.4	1.2	.80	
50	21.9	8.4	4.1	1.0	.93	3.2	5.5	8.5	2.0	1.8	1.2	.80	
43	22.3	8.1	4.1	1.0	.92	2.8	5.0	8.1	2.2	2.0	1.3	.82	
49	22.7	8.7	4.4	1.1	1.0	3.2	6.0	8.7	2.5	2.0	1.6	1.0	
43	23.2	8.7	4.1	1.0	.92	3.2	5.8	9.0	2.6	1.6	1.4	.84	
50	23.2	9.6	4.2	1.0	1.1	3.8	6.5	9.7	1.5	2.0	1.2	.70	
55	24.7	9.3	4.6	1.2	1.0	3.5	6.0	9.2	2.2	2.4	1.6	.80	
50	25.2	9.6	4.6	1.1	1.1	3.8	6.3	9.5	2.1	1.9	1.9	1.0	
50	27.4	11.0	5.4	1.3	1.3	4.3	7.2	11.2	2.0	2.8	2.2	1.2	

Specimens between dashed lines are undergoing notochord flexion.

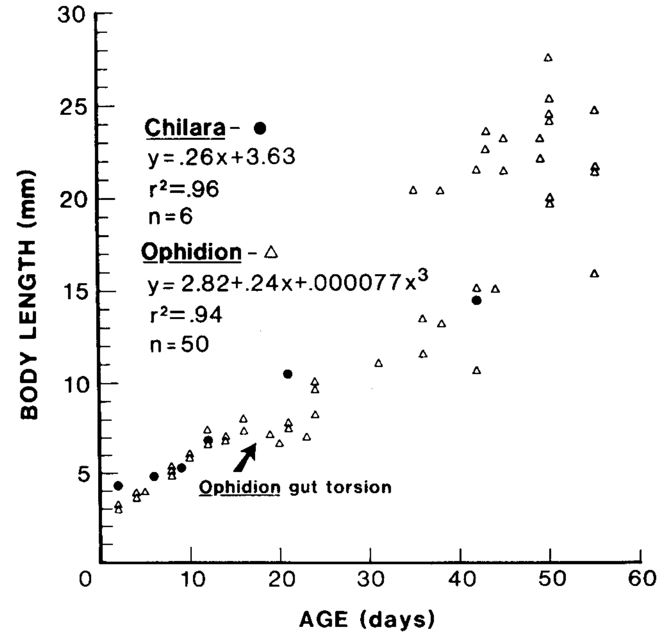

Figure 2. Growth rates of reared *Ophidion scrippsae* and *Chilara taylori*.

Chilara taylori

Morphology. *C taylori* larvae are relatively larger at hatching and at subsequent developmental stages compared with *O. scrippsae* larvae, but follow similar developmental trends such as the anterior migration of the pelvic fins and the relative shortening of the gut length. The gut of *C. taylori* begins to loop at ca. 13.3 mm. Looping is in the same direction as in *O. scrippsae*, but the coil is relatively smaller and is usually located slightly more posteriad in the visceral cavity. Notochord flexion occurs at ca. 20-30 mm body length (Table 4). Morphologial proportions are summarized in Table 2.

Fin formation and meristics. Dorsal and anal fin pterigiophores begin to ossify before notochord flexion at ca. 15.1 mm. Full anal fin (156-170) and dorsal fin (198-216) ray complements are ossifying near the end of notochord flexion at 29.6 mm (Table 3). Pelvic fin buds become visible at the start of flexion, and one ray is longer than the other in each pair by ca. 29.0 mm. Pectoral fin and principal caudal fin rays

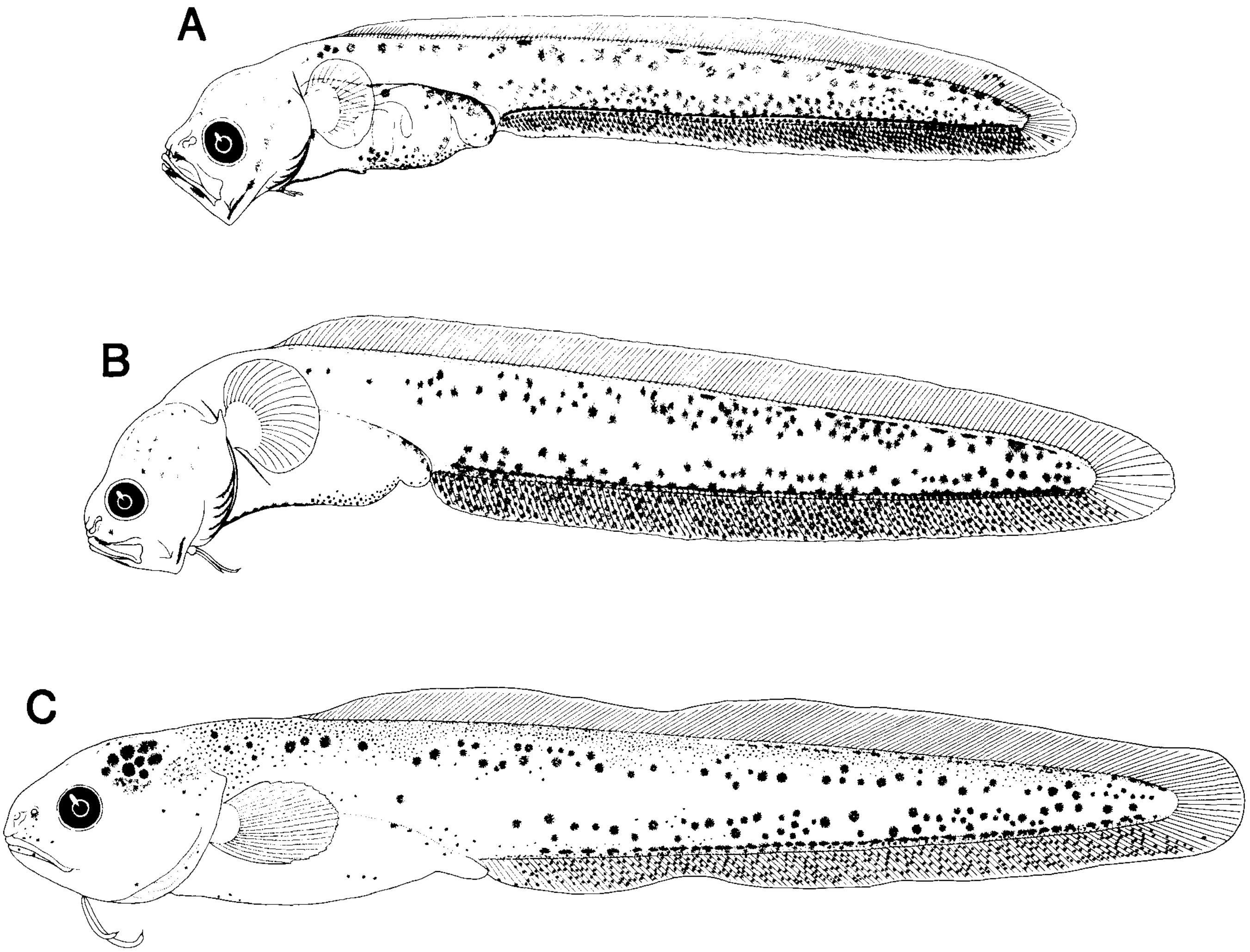

Figure 3. Developmental stages of *Ophidion scrippsae:* (*A*) 15.0-mm larva, day 44; (*B*) 20.3-mm larva, day 35; (*C*) 27.4-mm juvenile, day 50.

TABLE 2

Body Proportions of Larvae of *Ophidion scrippsae* and *Chilara taylori*

Body proportion	N	Snout to anus / body length	Head length / body length	Snout length / head length	Eye diameter / head length	Body depth at pectoral fin base / body length	Snout to dorsal fin / body length	Snout to anal fin / body length	Snout to pelvic fin / body length	Pectoral fin height / body length
Ophidion scrippsae										
Preflexion	12	45.5 ± 2.68 (42-53)	16.9 ± 1.24 (16-20)	26.8 ± 4.22 (20-34)	29.4 ± 7.04 (9-37)	10.7 ± 2.31 (5-13)	—	—	8.9 N = 1	5.3 ± 1.62 N = 11 (3-8)
Flexion	5	46.4 ± 1.14 (45-48)	20.8 ± 1.48 (19-23)	30.0 ± 2.74 (26-33)	26.2 ± 3.03 (22-30)	16.4 ± 0.55 (16-17)	31.8 ± 2.39 (28-34)	47.0 ± 1.00 (46-48)	17.8 ± 1.10 (17-19)	7.2 ± 1.30 (6-9)
Postflexion	16	39.2 ± 1.76 (36-42)	18.6 ± 1.02 (16-20)	24.9 ± 2.21 (21-31)	24.3 ± 2.14 (21-28)	15.1 ± 1.29 (13-17)	25.3 ± 1.66 (22-28)	39.6 ± 2.00 (36-43)	10.4 ± 2.73 (6-17)	7.9 ± 1.41 (6-10)
Chilara taylori										
Preflexion	24	38.7 ± 3.25 (31-44)	12.5 ± 1.69 (8-15)	25.1 ± 4.48 (14-31)	31.5 ± 5.58 (23-41)	8.2 ± .97 (7-9) N = 22	26.5 N = 1	35.9 N = 1	12.9 N = 1	3.4 ± .91 (2-5) N = 22
Flexion	3	30.7 ± 1.53 (29-32)	11.7 ± 1.15 (11-13)	28.7 ± 2.52 (26-31)	23.7 ± 2.08 (22-26)	7.3 ± .58 (7-8)	18.0 ± 3.61 (15-22)	31.0 ± 3.00 (28-34)	10.0 ± 2.00 (8-12)	2.7 ± .58 (2-3)
Postflexion	3	27.3 ± 2.08 (25-29)	12.3 ± 1.53 (11-14)	24.7 ± 3.21 (21-27)	23.3 ± 2.89 (20-25)	7.3 ± .58 (7-8)	17.0 ± 0 (17)	27.7 ± 1.53 (26-29)	7.3 ± .58 (7-8)	2.7 ± .58 (2-3)

Values are expressed as percentage of body or head length (mean, standard deviation, and range).

TABLE 3
Meristics of Larvae of *Ophidion scrippsae* and *Chilara taylori*

Size (mm)	Dorsal fin	Anal fin	Pectoral fin	Caudal fin	Vertebrae	Branchiostegal rays	Gill rakers
Ophidion scrippsae							
4.0	—	—	—	—	—	—	—
6.1	—	—	—	—	—	—	—
7.8	—	—	—	—	—	4	—
9.6	104	96	—	—	—	7	—
11.5	138	118	5	2 + 5	—	7	0 + 5
15.8	139	113	24	4 + 5	67	7	0 + 5
19.6	146	116	22	4 + 5	67	7	3 + 5
21.9	148	117	22	4 + 5	67	7	2 + 6
24.7	141	112	22	4 + 5	67	7	3 + 7
Adult complement	136-153	112-119	22-25	4 + 5	67-69	7	—
Chilara taylori							
4.6	—	—	—	—	—	—	—
7.6	—	—	—	—	—	—	—
10.4	—	—	—	—	—	—	—
14.1	—	—	—	—	—	6	—
21.1	180	163	6	3 + 5	—	7	0 + 7
29.6	203	168	22	4 + 5	—	7	0 + 8
32.6	203	162	22	4 + 5	—	7	0 + 8
36.1	210	168	22	4 + 5	91	7	0 + 7
47.0	204	163	25	4 + 5	90	7	3 + 8
Adult complement	198-216	156-170	22-25	4 + 5	86-91	7	1-4 + 5-9

Specimens between dashed lines are undergoing notochord flexion.

TABLE 4
Measurements in mm of Developmental Series of *Chilara taylori*

Station or age (day)	Body length	Snout to anus	Head length	Snout length	Eye diameter	Body depth at pectoral fin base	Snout to dorsal fin origin	Snout to anal fin origin	Snout to pelvic fin origin	Pectoral fin length	Pelvic fin length	
											long	short
5910- 80.52	3.6	1.1	.28	.04	.08	.32	—	—	—	—	—	—
7510- 97.50	3.9	1.6	.44	.12	.18	.24	—	—	—	—	—	—
6310- 80.51	4.3	1.7	.60	.12	.22	.38	—	—	—	.14	—	—
2	4.3	1.9	.63	.12	.24	.38	—	—	—	.12	—	—
6706-120.35	4.6	1.8	.60	.10	.20	.44	—	—	—	.12	—	—
6	4.8	2.0	.72	.16	.24	.41	—	—	—	.20	—	—
4	5.0	2.2	.68	.13	.24	.38	—	—	—	.20	—	—
9	5.2	2.2	.68	.16	.28	.40	—	—	—	.24	—	—
6706-120.35	5.6	2.3	.64	.16	.24	.60	—	—	—	.24	—	—
Bathtub Rock	6.7	2.7	.72	.17	.26	.52	—	—	—	.26	—	—
12	7.3	2.8	.90	.28	.30	.48	—	—	—	.40	—	—
6706-120.35	7.6	3.1	.76	.20	.28	.60	—	—	—	.28	—	—
6310- 80.51	8.2	3.3	.96	.24	.28	.64	—	—	—	.20	—	—
6310- 80.51	9.7	3.6	1.00	.28	.32	.68	—	—	—	.28	—	—
21	10.4	3.9	1.30	.37	.40	.76	—	—	—	.48	—	—
5711- 87.36	10.5	4.2	1.40	.40	.36	.80	—	—	—	.32	—	—
7207-117.40	10.6	3.7	1.28	.40	.37	1.00	—	—	—	.40	—	—
5910- 80.52	12.1	4.8	1.72	.68	.40	.96	—	—	—	.34	—	—
6107-93.55	12.6	4.6	1.48	.40	.36	.88	—	—	—	.34	—	—
6310- 80.51	13.3	5.0	1.80	.44	.42	1.00	—	—	—	.34	—	—
6609-113.65	14.1	5.0	2.00	.58	.50	1.17	—	—	—	.36	—	—
42	14.4	5.5	2.00	.58	.60	1.20	—	—	—	.48	—	—
6210- 77.55	15.0	5.0	2.00	.56	.48	1.16	—	—	—	.36	—	—
6110- 83.55	15.1	5.3	2.00	.56	.52	1.24	4.00	5.42	1.96	.28	—	—
6706-113.35	21.1	6.7	2.67	.83	.58	1.50	4.60	7.08	2.48	.53	.20	—
6210- 80.60	22.5	7.0	2.58	.76	.60	1.56	3.80	7.08	2.20	.52	—	—
6110- 83.70	29.6	8.6	3.25	.83	.83	2.25	4.50	8.33	2.50	.88	.28	.14
5206-107.55	32.6	9.3	3.75	1.00	.92	2.50	5.67	9.42	2.33	1.00	.44	.24
6908- 73.60	36.1	10.0	4.00	.83	1.00	2.67	6.17	10.00	3.00	.88	.68	.52
6110- 63.60	47.0	11.8	6.50	1.69	1.33	3.33	8.00	12.17	3.08	1.24	1.48	1.04

Specimens between dashed lines are undergoing notochord flexion.

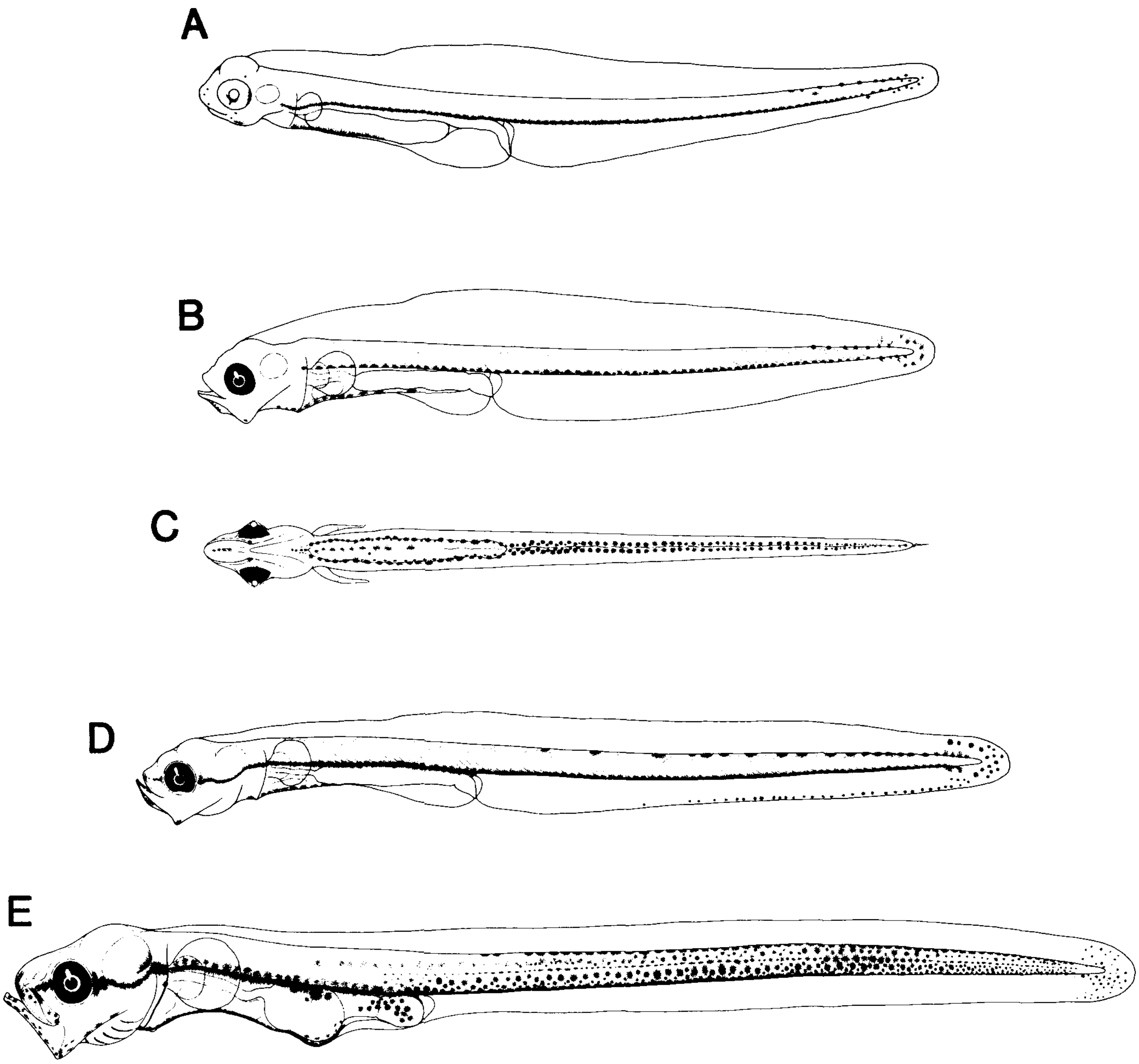

Figure 4. Larvae of *Chilara taylori*: (*A*) 5.0 mm with yolk remnant, day 4; (*B*) 4.8 mm, day 6; (*C*) 4.8 mm, day 6; (*D*) 7.3 mm, day 12; (*E*) 14.4 mm, day 42.

begin to ossify early during the notochord flexion period at ca. 21.1 mm. The adult complement of 4 + 5 principal caudal rays is formed near the end of notochord flexion at ca. 29.6 mm. Ossification of the vertebral column begins after the completion of notochord flexion, and the full complement of 86-91 vertebrae is ossified by 36.1 mm.

Pigmentation. Yolk-sac *C. taylori* larvae have unpigmented eyes and melanophores along the ventral region of the body (Figure 4). By the 6th day after hatching the eyes are pigmented; the yolk-sac has been absorbed; stellate melanophores are frequently present in the caudal fin fold; and two serial rows of ventral melanophores become quite conspicuous. Pigment appears in the angular region of the jaw at about this time and persists throughout larval development. By ca. 6.0 mm, the ventral body pigment line extends anteriorly along the base of the brain and onto the snout. This head pigment persists until at least 15.0 mm but is usually lost by 21.0 mm. By 10.6 mm, the lateral midline becomes pigmented in the caudal region, and the ventral body melanophores increase in number. By 14.4 mm, the caudal region is highly pigmented, and the characteristic lateral midline stripe is heavier. Ventral body pigment decreases and becomes more scattered by 36.1 mm. The dorsal fin fold remains unpigmented throughout larval development, whereas the characteristic caudal fin pigment persists from as early as 4.8 mm. Xanthophores highlight the dorsal and ventral body surfaces of living *C. taylori* larvae.

DISTRIBUTION

Ophidiid larvae occur in comparatively low numbers in CalCOFI samples; however, this probably reflects the relatively low sampling effort in the nearshore region inhabited by these fish. *O. scrippsae* occurred in only 24 (1%) and *C. taylori* in 16 (0.7%) of the 2,361 tows made seaward to station 50 on all CalCOFI lines occupied during 1972-78 (Figure 5). Forty-five *O. scrippsae* larvae were collected in these tows: 4% were captured in June, 7% in August, and 89% in October. Distribution centered around points and capes from San Diego to the vicinity of Magdalena Bay, and around the inshore areas of Viscaino Bay and San Cristobal Bay.

During the same period, 22 *C. taylori* larvae were collected: 4% were taken in February, 4% in July, 28% in August, and 60% in October. Distribution centered around Punta Eugenia at Viscaino Bay, but larvae were collected as far north as Cape Flattery, Washington, and south to San Cristobal Bay. *C. taylori* larvae were collected farther offshore than the majority of the *O. scrippsae* larvae; however, the larval size of both species appeared to be independent of the distance offshore.

The CalCOFI stations at which larval cusk eels were captured tended to be in areas where the adult habitat extended farther offshore either at points of land or in the vicinity of bays where the shelves are broader.

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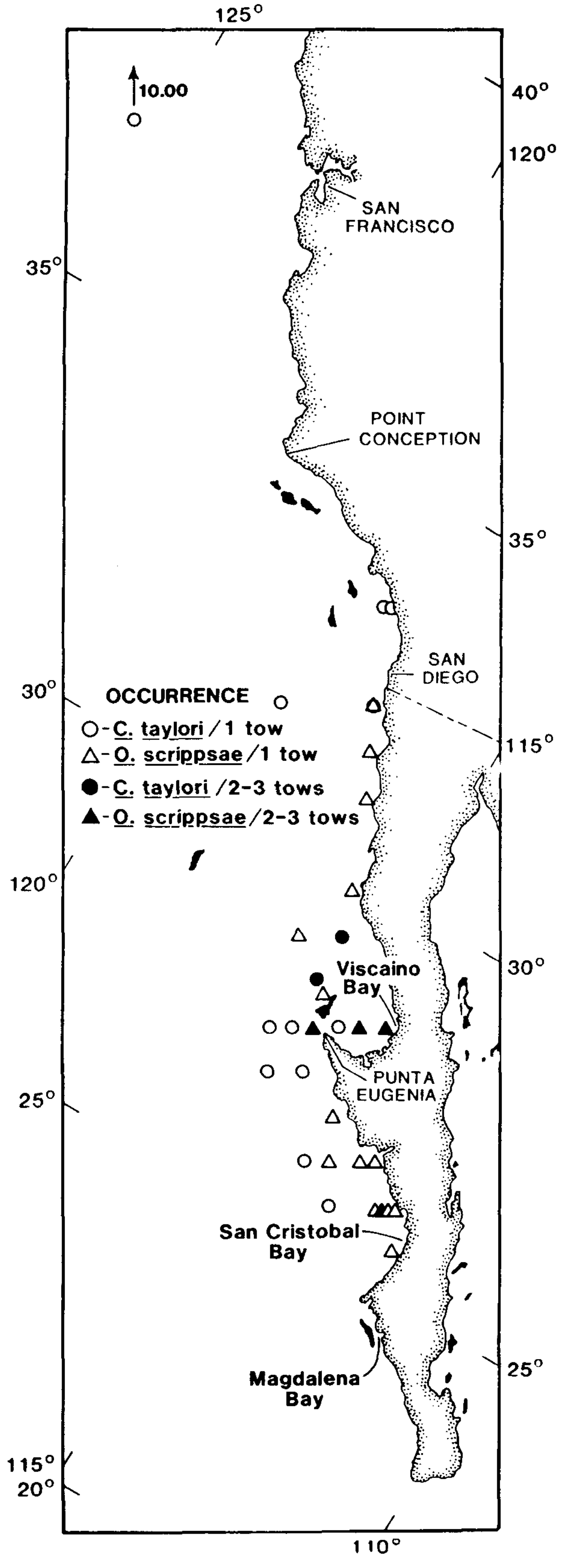

Figure 5. Distribution of *Chilara taylori* and *Ophidion scrippsae* larvae in CalCOFI tows made during 1972-78.

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NEARSHORE PRODUCTION OF YOUNG ANCHOVY

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ABSTRACT

The daily production of northern anchovy eggs and larvae is determined for the nearshore region (within ca. 3 mi of the coast) of the Southern California Bight. Stage-specific catches were obtained from monthly Ichthyoplankton Coastal and Harbor Studies (ICHS) cruises during 1979-80. Age-specific production estimates are derived by pooling and adjusting the catches for growth and sampler bias. Hazard functions are introduced, and a production curve is fit to the data. Production of young anchovy was compared with that for the greater Southern California Bight; there was no evidence for greater production inshore. The spawning cycle and survival of young in the nearshore region reflected that occurring throughout the Southern California Bight.

RESUMEN

Se determina la producción diaria de huevos y larvas de anchoa (*Engraulis mordax*) en la zona costera (a menos de tres millas de la costa) en la región del seno de la California Meridional. Los datos utilizados se basan en la serie de fases de desarrollo, que aparecían en las colecciones del programa de Ictioplancton costero y estudios de estuarios y bahías (ICHS), cruceros 1979-80.

Las estimaciones de edades en esta producción se han determinado agrupando las capturas y ajustándolas en relación al crecimiento y a las variaciones ocasionadas por el muestreo. Funciones del azar se incluyen en los cálculos, ajustando así los datos en la curva resultante. Esta producción de anchoa se compara con la obtenida para todo el seno de la California Meridional, y no hay evidencia de que las aguas costeras presenten una mayor producción. El ciclo de puesta y la supervivencia de los jóvenes en la región costera, reflejan lo que acontece en todo el seno de la California Meridional.

INTRODUCTION

The abundance and distribution of several fish populations off the Pacific coast of North America have been monitored using ichthyopolankton surveys conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) since 1949. These surveys extended from Baja California to Washington state and several hundred km offshore, and were directed at the detection of gross changes in abundance and distribution patterns (Smith 1972). These data have also been used to estimate production and survival of early life stages, with the ultimate goal of explaining and predicting variations in population growth (Smith 1973; Lasker and Smith 1977; Zweifel and Smith 1981; Hewitt 1981; Hewitt and Methot 1982; Hewitt 1982). The principal species of interest has been the northern anchovy (*Engraulis mordax*), partly because of its importance in the natural economy of the California Current and partly because it is typical of clupeoid populations, which are highly productive and support some of the largest fisheries in the world.

Another source of ichthyoplankton data is the Ichthyoplankton Coastal and Harbor Studies (ICHS) (Brewer et al. 1980; Brewer and Smith 1982). During this project the nearshore zone of the Southern California Bight was sampled monthly from June 1978 through July 1980. This zone, within ca. 3 miles of the coast, often harbors high densities of phytoplankton and microzooplankton (Eppley et al. 1978; Beers and Stewart 1967; Lasker 1981) and may also be a region of enhanced larval survival and elevated anchovy productivity.

Brewer and Smith (1982) described the ICHS collections of anchovy and sardine (*Sardinops caerulea*) eggs and larvae. They reported that the seasonal cycle and standing stock of anchovy eggs and larvae in the nearshore zone were comparable to those estimated for the greater Southern California Bight from CalCOFI surveys. The nearshore region accounted for 3.8% of the area and 3% of the larvae contained by the greater Southern California Bight. Brewer and Smith concluded that the nearshore zone was not a preferred spawning habitat; however, they withheld judgment on the importance of the region as a nursery ground.

In this paper we compare the production of larval anchovy in the nearshore zone with that throughout the Southern California Bight. We pooled stage-specific catches through the 1980 spawning season

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[Manuscript received February 4, 1983.]

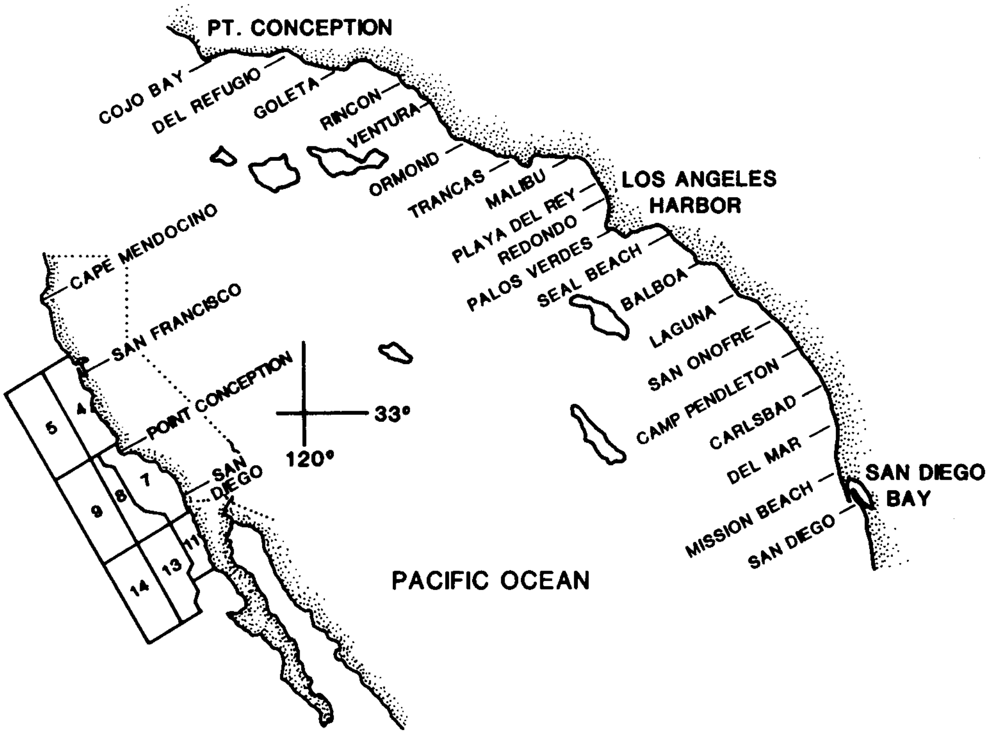

Figure 1. The Ichthyoplankton Coastal and Harbor Studies (ICHS) sampled 20 transects in the nearshore zone (within 3 miles of the coast) of the Southern California Bight between Point Conception and San Diego. Region 7 of the CalCOFI sampling grid is defined here as the greater Southern California Bight (inset).

and derived age-specific production estimates by adjusting the catches for growth and sampler bias. We briefly discuss three hazard functions and fit production curves to the data. Finally, we contrast the curves from the two regions and discuss their interpretation.

MATERIALS AND METHODS

We define the greater Southern California Bight as CalCOFI region 7, encompassing the area between Point Conception and the international border at San Diego, and seaward approximately 200 km (Figure 1). The nearshore zone is defined as that portion of the bight within the 43-m isobath and the mainland coast, and contains 2,652 km^2 (3.8%) of the total 69,055 km^2 area of CalCOFI region 7. The data reported here were obtained from August 1979 through July 1980 (ICHS Phase II; Brewer and Smith 1982), and the production comparisons were made for the 1980 spawning season (January through June 1980).

The ICHS sampling regime consisted of 46 stations, along 20 transects, that were occupied each month. Stations were positioned over the 8-m and 22-m isobaths on each transect and additionally over the 15-m and 36-m isobaths on the Ormond, Redondo, and San Onofre transects (Figure 1). The sampling gear was a 70-cm diameter bongo frame, fitted with 333-micrometer mesh Nitex nets and an opening-closing device. The gear was deployed to the bottom; the net apertures were opened; and the gear was retrieved obliquely to the surface, filtering an average of 8.1 m^3 of water per m of depth fished. Additional details regarding sampling techniques and laboratory procedures are described by Brewer and Smith (1982).

CalCOFI region 7 was sampled during four cruises conducted in March, April, and May 1980. Two gear types and respective station grids were employed. The first was a 70-cm oblique bongo tow deployed on standard CalCOFI stations; the net was 505-micrometer Nitex with no opening-closing device, fished to 210-m depth and filtering an average of 3.7 m^3 per m of depth (see Stauffer and Picquelle 1981, for a description of these cruises, and Kramer et al. 1972, Smith and Richardson 1977, for sampling techniques and laboratory procedures). The second gear was a 25-cm diameter frame, with a 333-micron Nitex net, deployed to 70-m depth and retrieved vertically (see Hewitt, in press, for a brief description of the CalCOFI vertical egg tow-CalVET sampler). The CalVET sampler was deployed over a dense grid of stations with the purpose of intensively sampling anchovy egg production.[1]

Plankton samples were preserved and returned to the laboratory, where they were sorted, and the anchovy eggs and larvae were identified and enumer-

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[1] Stauffer, G. D., and S. J. Picquelle. MS. Egg production estimates of spawning biomass of the northern anchovy for 1980 and 1981.

TABLE 1
Survey Cruises Contributing to the ICHS Sample of the Nearshore Zone and the CalCOFI Sample of the Greater Southern California Bight (Region 7)*

Cruise designation	Dates	Number of stations	Percent positive	Egg density (#/m^2)	Larval density (#/m^2)
ICHS	1979				
15	13-24 Aug	46	98	38	20
16	10-21 Sept	46	100	3	15
17	8-18 Oct	46	85	22	4
18	5-16 Nov	46	54	15	3
19	3-13 Dec	46	78	69	9
	1980				
20	7-19 Jan	46	91	70	81
21	11-28 Feb	46	100	191	91
22	10-22 Mar	46	98	295	195
23	7-17 Apr	46	100	124	50
24	12-25 May	46	93	34	22
25	16-26 June	46	87	6	7
26	14-25 July	46	65	4	2
CalCOFI bongo					
8003TK	24 Feb-2 Mar	24	100	——	106
8003JD	27 Mar-6 Apr	20	95	——	204
8005JD	11 Apr-29 Apr	29	90	——	94
8005JD	24 May-30 May	24	71	——	57
CalCOFI CalVET					
8003/04JD	27 Mar-29 Apr	458	64	326	——

*The sample obtained with the CalVET net includes tows made in regions 8 and 11 as well.

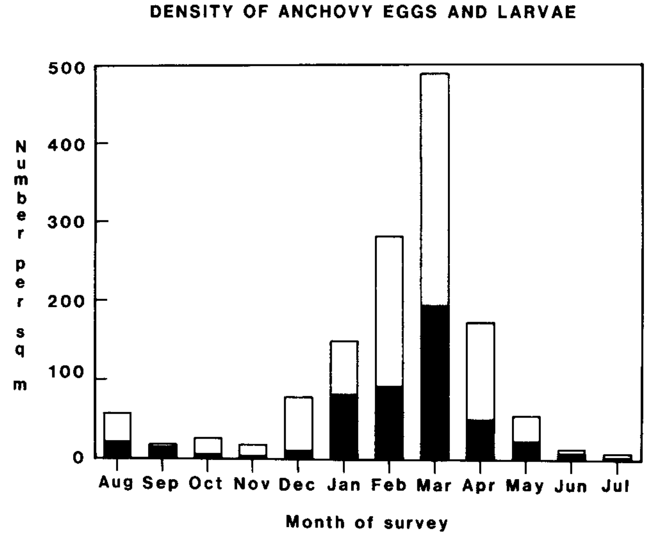

Figure 2. Densities (number under 1 m^2 of sea-surface area) of anchovy eggs (clear) and larvae (shaded) in the nearshore zone by survey month. The bell-shaped spawning curve is similar to that observed throughout the spawning habitat.

ated by developmental stage. Results were expressed in numbers of eggs or larvae under 1 m^2 of sea-surface area.

RESULTS

Standing Stock

Anchovy eggs and larvae were caught at most stations during every ICHS survey (Table 1). On the other hand, the density of eggs and larvae varied two orders of magnitude as the spawning season progressed. Low spawning activity in the fall is followed by an increase in spawning in December, achieving a maximum in March and declining through July. The bell-shaped seasonal spawning curve (Figure 2) is similar to that found throughout the spawning habitat (Brewer and Smith 1982; Hewitt 1980; Hewitt and Methot 1982).

Seasonal catches by stage are described in Figure 3. Nine percent of the year's catch was taken between August and November. The early fall spawning peak, apparent in the August survey, was limited to the western portion of the Santa Barbara Channel. Very little spawning occurred in September and October, and larger larvae (10-mm mode in September, 15-mm mode in October) were encountered in Santa Monica Bay. Some spawning and small larvae were detected in the Santa Barbara Channel in November. By December, spawning increased in intensity and spread south and east to Santa Monica Bay. In January spawning extended from the Santa Barbara Channel to the Los Angeles harbor, and larger larvae were evident from the December spawning. By February, spawning was evident from the Santa Barbara Channel to San Diego and peaked in March with extensive spawning all along the coast. In April, May, and June spawning was progressively reduced and displaced southward. By July very little reproduction was evident; catches of large larvae from the previous months' spawning were made along the coast between Los Angeles and San Diego.

Data from the January through June cruises were pooled to draw the composite catch curve (Figure 4). These data constitute 85% of all the eggs and larvae retained, and describe the rise, peak, and decline of the spawning cycle.

Production

To appreciate trophic dynamics, and more specifically to assess the biological importance of a region, one must consider the flux of organic material (or production) rather than the simple standing stock. To do so we assumed that the average standing stock by stage was representative of a single cohort as it progressed through the larval period. This is the critical assumption and implies steady-state production of eggs and a stable age distribution. That eggs are continually produced in the population is supported by estimates that the average female spawns every 7 to 10 days during the spawning season (Hunter and Gold-

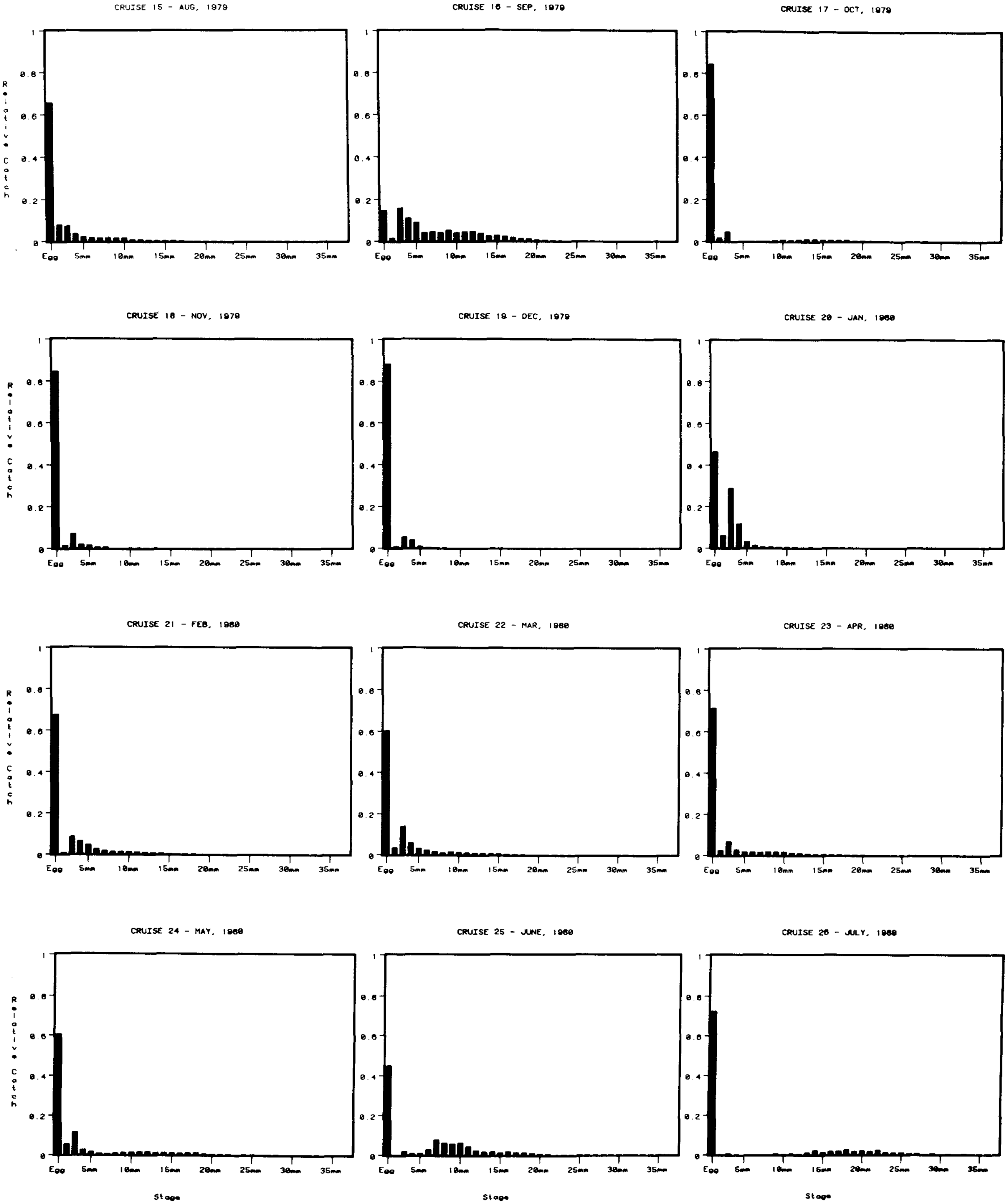

Figure 3. Relative catches by stage for each ICHS survey month reflect the seasonal spawning curve. Egg production in August resulted in catches of large larvae in September and October; large larvae again became a substantial portion of the catch in May, June, and July when egg production rapidly declined.

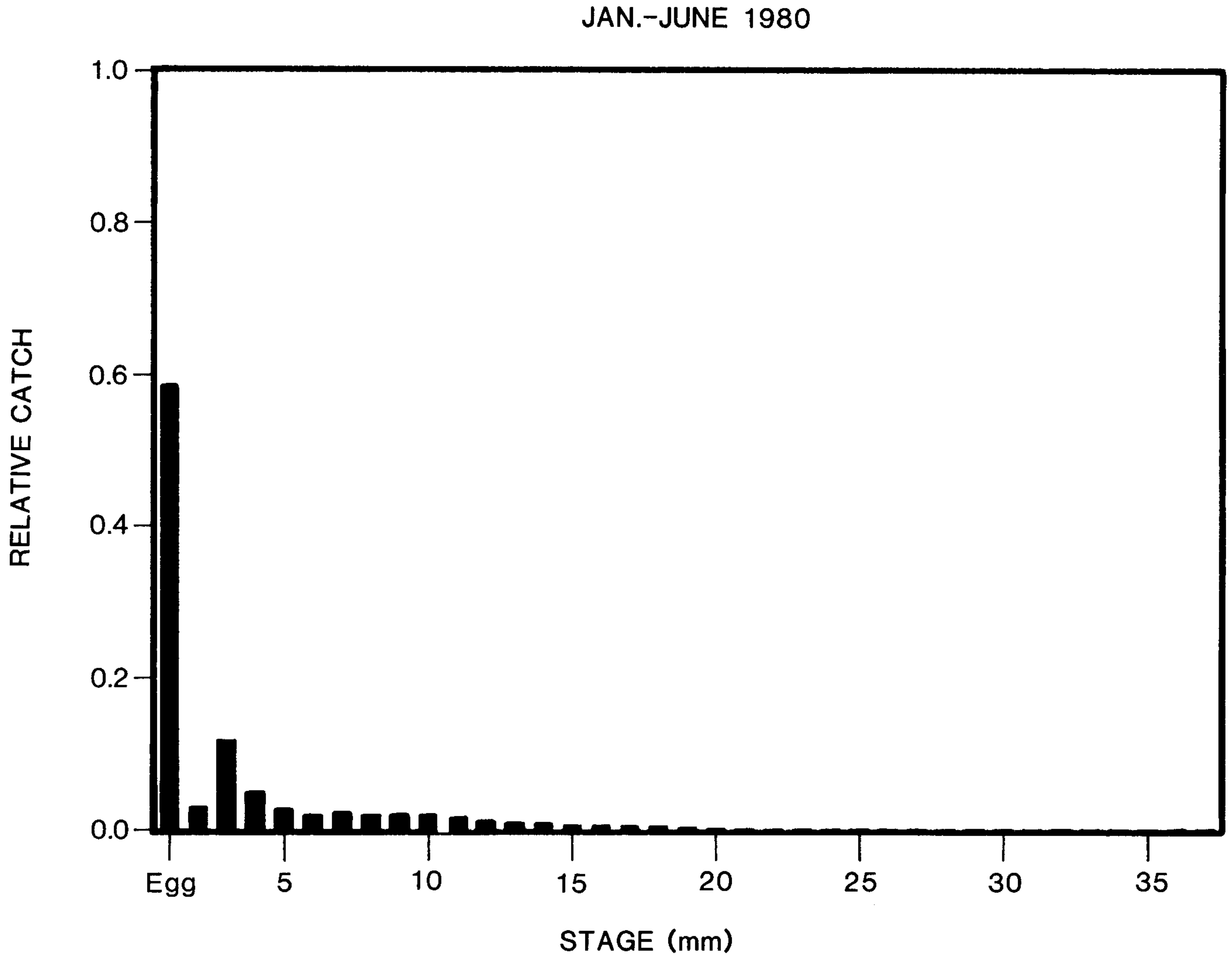

Figure 4. The average catch curve for the ICHS surveys conducted during the period January through June accounts for 85% of all eggs and larvae retained. These data were collected through the rise, peak, and decline of the spawning season. We assumed that the average standing stock by stage was representative of a single cohort as it passed through the larval period.

berg 1980; Hunter and Macewicz 1980; Picquelle and Hewitt 1983). Hewitt and Methot (1982) showed that an unbiased age distribution may be obtained by pooling data collected through the spawning season.[2]

The pooled catch curve (Figure 4) was then adjusted for sampling bias and variability: individual observations were adjusted for variations in the volume of water filtered per m of depth; bias corrections were applied for extrusion of small larvae through the meshes of the net; and the adjusted catches were divided by the duration of growth, through each stage, to estimate the age-specific production rate (P_t). The adjustments were accomplished by fitting a weighted negative binomial model to the sample frequency distributions of each size class. Each observation was weighted by a factor that is the product of the various adjustments, and the means of the final distributions are unbiased estimates of production (P_t). The procedure was developed in a series of papers: Bissel 1972; Zweifel and Smith 1981; Hewitt 1981, 1982; Hewitt and Methot 1982. The calculations are summarized in Table 2, and the results are described in Figure 5.

Estimates of production declined with age as the larvae starved or were preyed upon (Figure 5); initial mortality was severe and abated somewhat as the larvae developed. Our intention was to describe these data with a functional form; this curve is sometimes referred to as the mortality curve or, conversely, the survival curve; here we label it the production curve.

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[2] Alternately one may plot the seasonal curves of daily production for each stage and estimate total seasonal production as the area under the curves (Bannister et al. 1974). This method and the one described in the text yield essentially the same results; i.e., total seasonal production estimated from the seasonal curves of daily production is not different from the average daily production summed over the averaging period. Furthermore, the rate of decline in production with age is also the same.

TABLE 2
Size-Specific Catches of Anchovy Larvae and Age-Specific Estimates of Daily Production

Preserved size (mm)	Fraction retained in net[1]	Average adjustment for sampling and sorting variability[2]	Average duration of growth[3]	Average catch $\left(\frac{\text{number}}{\text{tow}}\right)$	P_t $\left(\frac{\text{number}}{\text{m}^2\text{-day}}\right)$[4]	Age since fertilization (days)
Egg	0.917	15.848	2.43	1978.61	56.03	1.22
1.75	0.630	1.087	0.38	5.98	22.99	2.63
2.75	0.630	0.998	2.93	25.12	13.64	4.28
3.75	0.630	1.214	3.34	12.36	4.84	7.44
4.75	0.950	1.244	2.48	6.36	2.17	10.34
5.75	1.000	1.457	2.28	4.55	1.37	12.74
6.75	1.000	1.699	2.13	4.09	1.13	14.76
7.75	1.000	1.957	2.05	3.65	0.91	16.91
8.75	1.000	1.862	2.01	3.93	1.05	18.85
9.75	1.000	1.954	1.99	3.85	0.99	20.88
10.75	1.000	2.084	1.99	3.11	0.75	22.78
11.75	1.000	2.040	2.00	2.53	0.62	24.80
12.75	1.000	2.199	2.06	2.31	0.51	26.73
13.75	1.000	2.246	2.12	2.00	0.42	28.80

1. Extrusion corrections are based on relative retention rates between 75-micrometer and 333-micrometer mesh nets (Lo, in press).
2. Accounts for partial sorting of samples, and standardizes sampling volume to 1m^3 per m of depth. An average of 17% of the larvae were sized.
3. Temperature-dependent embryonic growth is determined from laboratory experiment (Lo, in press), and post-yolk-sac growth follows Methot's (1981) description.
4. Production rates (P_t) may be estimated by dividing the average catch by the product of columns 2, 3, and 4. In practice however, P_t is the mean of a weighted negative binomial model fit to the distribution of individual observations (i.e., plankton tows).

To begin, we model the mortality as a portion of those living:

$$\frac{dp}{dt} = P\,Z(t)$$

where *P* is the production rate, *t* is age, and *Z(t)* is the hazard function (Watson and Leadbetter 1964), also referred to as the conditional failure rate, age-specific death rate, or instantaneous mortality rate. By integrating the expression from O to *t* we can express the probability of an animal's living to time *t* as:

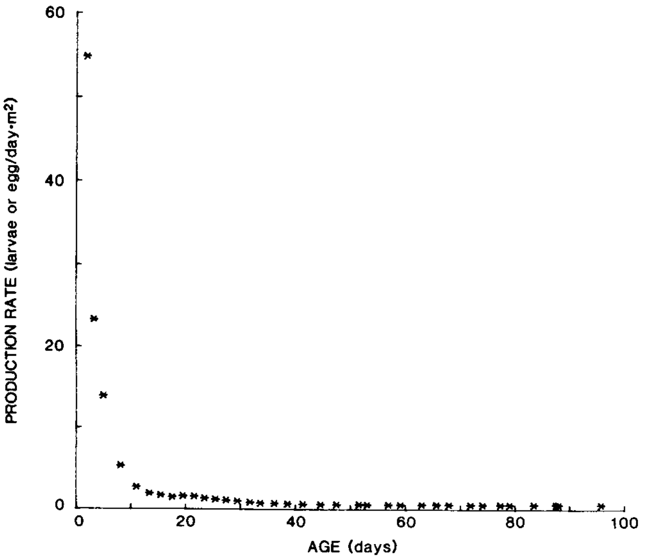

Figure 5. Estimates of age-specific production rates were derived from the pooled catch curve by adjusting the catches for growth and sampler bias. A production curve fit to these data must describe initially severe mortality, which abates somewhat as the larvae develop.

$$\frac{P_t}{P_o} = \exp\left(\int_o^t z(t)dt\right) \quad .$$

By rearrangement the production curve is:

$$P_t = P_o \exp\left(\int_o^t z(t)dt\right) \quad .$$

Several forms may be used for *Z(t);* here we describe the consequences of three. Because animals are dying, the hazard function is always negative.

$$\text{Case 1: } Z(t) = -Z \text{ (a constant)}$$

This is the well-known constant mortality or exponential decay model. The production curve becomes:

$$P_t = P_o\, e^{-Zt} \quad .$$

If the population followed this model, the logarithm of the production rate would be a linear function of age, and the slope would be equal to $-Z$. With no increase in the number of parameters, the hazard function can be modeled to decrease with age[3]:

$$\text{Case 2:} \qquad Z(t) = \frac{-\beta}{t} \quad .$$

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[3] Lo, N. MS. Egg production of central stock of northern anchovy: 1951-82.

As t increases, $Z(t)$ decreases, describing improving survival with age. The production curve becomes:

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

Although this form is attractive because only two parameters are required (P_h and β), it cannot be extrapolated to time zero. Picquelle and Hewitt (1983) applied this model to larval production data where t_h is the age of hatching, and time zero is the moment of fertilization. If the population followed this model, the logarithm of the production rate would be a linear function of the logarithm of age. The production curve may be extended to the origin by adding a third parameter (α):

$$\text{Case 3:} \qquad Z(t) = \frac{-\beta}{\alpha + t} \quad .$$

This form also describes improving survival with age; in addition, as t approaches zero, $Z(t)$ remains finite. The production curve becomes:

$$P_t = P_o \left(\frac{\alpha}{\alpha + t}\right)^{\beta} \quad .$$

As with Case 2, a linear plot of the logarithm of the production rate on the logarithm of age would be consistent with this model.

A semilog plot of production on age (Figure 6A) is nonlinear, particularly at ages less than 20 days, suggesting that a constant mortality model (Case 1) would not be appropriate. During this period aggregated eggs are disbursing and hatching; yolk-sac larvae are developing locomotor abilities; and post-yolk-sac larvae are rapidly acquiring sensory capabilities. Given the rapid ontogeny compressed into this phase of the life history, it may be biologically unreasonable to expect constant mortality. A log-log plot of the data (Figure 6B) is linear with a break at approximately 30 days of age; either of the decreasing mortality models described as Case 2 and Case 3 would be appropriate to describe the first 30 days. We fit the Case 3 model to the age-specific production rates for animals less than 30 days old using a nonlinear least squares method. The resulting production curve is described in Figure 7; parameter values are listed in Table 3. Average egg production over the spawning season (January to June) in the nearshore zone was approximately 190 eggs per day per m^2 (standard error = 25).

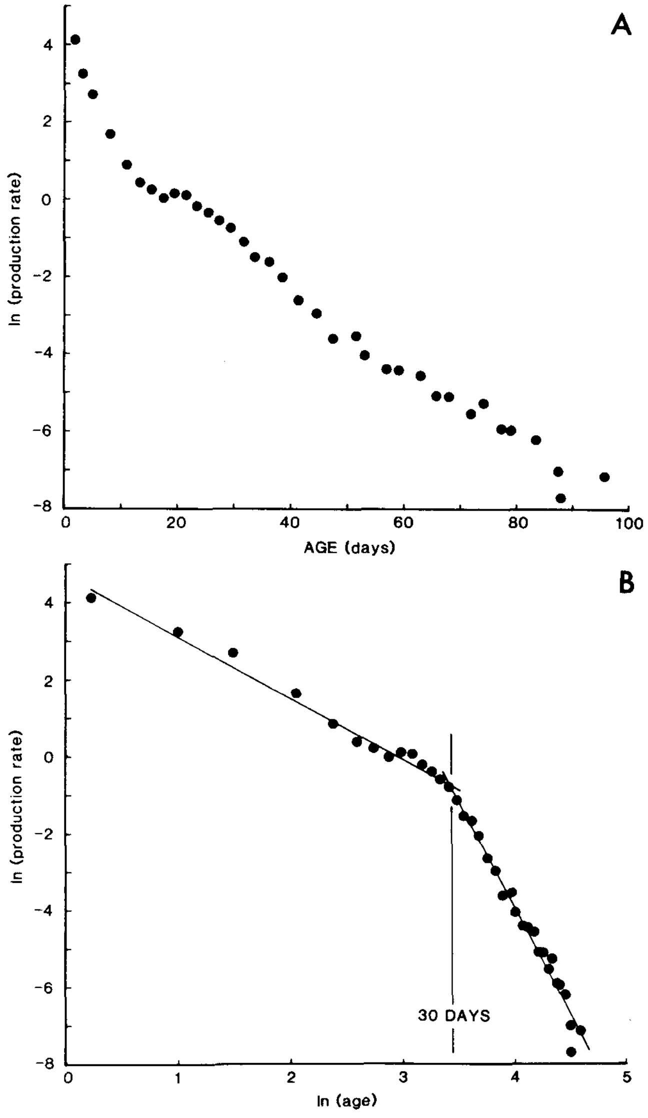

Figure 6 *A*. The semilog plot of production rate on age is nonlinear for the youngest stages, suggesting that the constant mortality model described as Case 1 would be inappropriate.

B. The log-log plot of production rate is linear with an abrupt change in slope at 30 days post fertilization. The lines are drawn by eye for the purpose of emphasizing the linearity and the break point.

TABLE 3
Parameter Values and Production Rate Estimates for Production Curves Fit to the ICHS and CalCOFI Samples

	ICHS		CalCOFI	
Parameter	Parameter value	(Std. error)	Parameter value	(Std. error)
α	1.5	0.42	16.4	9.01
β	2.0	0.22	6.3	2.85
P_o	187.6	24.6	230.2	11.3
$\hat{P}_{10}$	3.0	—	11.4	—
$\hat{P}_{20}$	0.8	—	1.5	—
$\hat{P}_{30}$	0.4	—	0.4	—

Data representing the greater Southern California Bight are drawn from two sources: CalVET and bongo samples (Figure 8). The CalVET sample is a collection of observations made with a small vertical tow designed to sample pelagic fish eggs. These

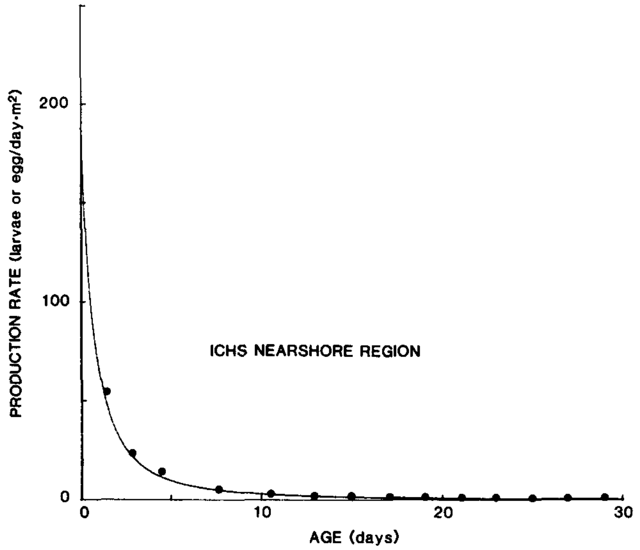

Figure 7. The production curve for the ICHS nearshore zone is of the form described as Case 3, and is fit to the production rate estimates for larvae less than 30 days old.

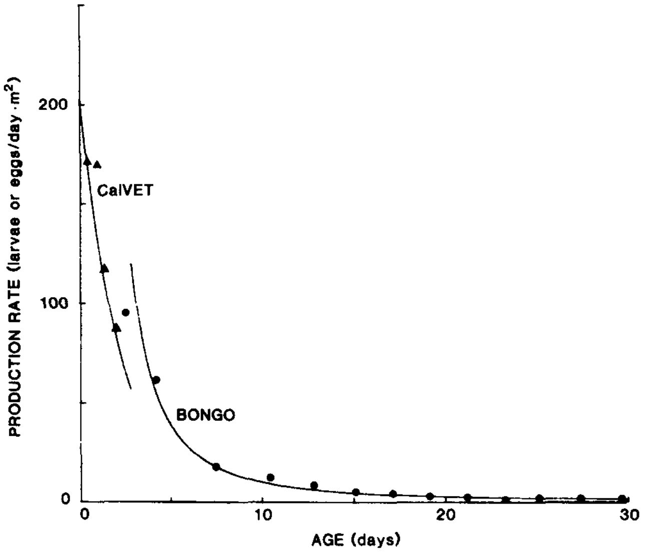

Figure 8. Anchovy egg and larvae production rates for the greater Southern California Bight are estimated from CalVET and bongo net samples obtained in CalCOFI region 7 during March, April, and May. The production curve fit to the CalVET data is of the form described as Case 1; the production curve fit to the bongo data is of the form described as Case 2.

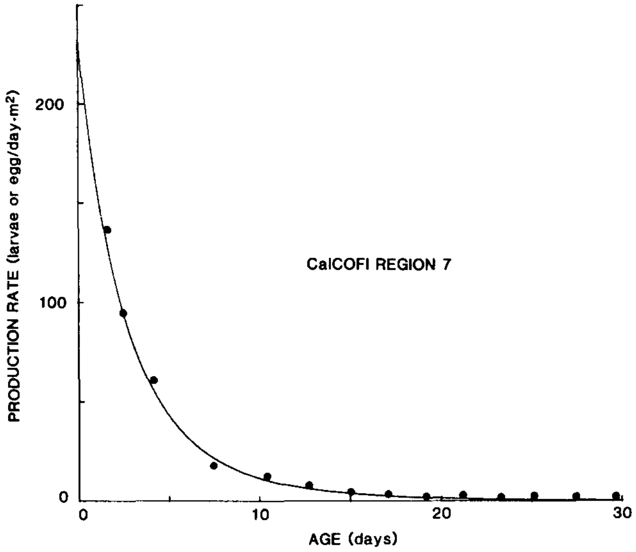

Figure 9. The production curve for the greater Southern California Bight (CalCOFI region 7) is of the form described as Case 3, and is fit to production rate estimates derived from both the CalVET and bongo samples.

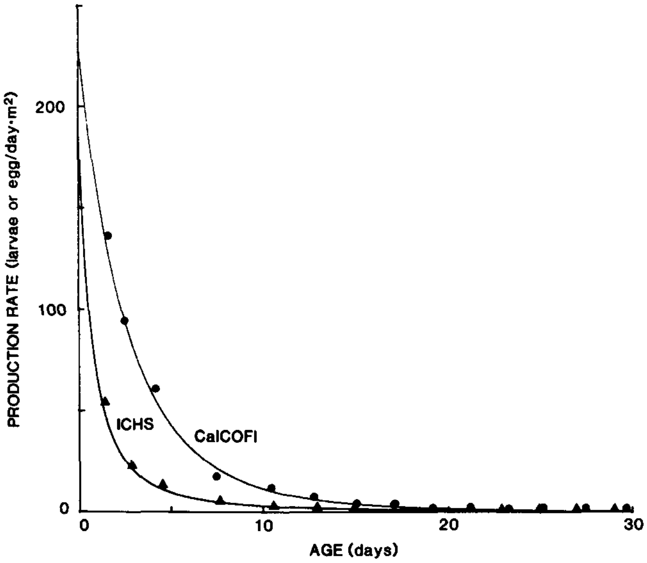

Figure 10. Initial egg production rates in the nearshore zone (ICHS sample) and the greater Southern California Bight (CalCOFI sample) are comparable. Mortality on eggs and yolk-sac larvae appears to be more severe in the nearshore zone; however, the production of 30-day-old larvae is again comparable between the two regions.

data are presented as estimates of egg production in half-day increments over the incubation period (2.8 days at an average temperature of 15.15°C). Stauffer and Picquelle[4] fit the egg-production curve using the constant mortality model described as Case 1. The bongo sample is a collection of observations made with a larger, oblique tow designed to sample larvae. The production curve is the functional form described as Case 2 proposed by Lo[5] and is analogous to analyses reported by Picquelle and Hewitt (1983). Although the sampling gears are quite different in design, they generate complementary and consistent data (Figure 8). The data were merged, and a single production curve (Case 3 functional form) was fit (Figure 9 and Table 3). Although a constant mortality for eggs and variable mortality for larvae may be

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[4] See footnote 1 on page 236.

[5] See footnote 3 on page 240.

biologically reasonable, a two-phase production curve is indistinguishable from the single curve for this data set. Average egg production over March, April, and May in the greater Southern California Bight was approximately 230 eggs per day per m^2 (standard error = 11).

The production curves for the nearshore zone (ICHS) and for the greater Southern California Bight (CalCOFI region 7) are superimposed in Figure 10. Initial production of eggs is comparable in both areas, although early mortality appears to be more severe in the nearshore zone. Later mortality in the nearshore zone is less severe, and the production of 30-day-old larvae is comparable between the two areas.

DISCUSSION

The primary conclusion that may be drawn from these data is that there is no evidence for enhanced production of young anchovy larvae in the nearshore zone. In addition, differences between the shapes of the production curves (Figure 10) are provocative. Anchovy eggs and yolk-sac larvae appear to suffer a more severe mortality in the nearshore zone than in the Southern California Bight. These are also the stages that are most contagious (patchy) in their distribution patterns (Hewitt 1981, 1982), and the most proximate to the adult schools that spawned them. Cannibalism on anchovy eggs is a significant source of mortality (Hunter and Kimbrell 1980), and it may be that the restricted depth range of the nearshore zone acts to increase the incidence of cannibalism. Higher densities of juvenile anchovy and general planktivores in the nearshore zone may cause heavier predation on these stages, which are very aggregated and not yet fully mobile.

Nearshore survival of feeding larvae appears to improve so that the production of 30-day-old larvae in the nearshore zone is comparable to that in the greater Southern California Bight at 0.4 larvae per day per m^2. The improved survival in the nearshore zone may be due to better feeding conditions, although Methot (1981) reported that most young anchovy were growing at the maximum rate, suggesting that food may not be limiting their survival. Increased turbidity of nearshore water may enhance protection from visually oriented predators, but this advantage must be offset partially by the increased density of predators. Regardless of the cause, if the difference in survival rates continued into the juvenile stage, then the nearshore zone would be an area of enhanced anchovy productivity. This question cannot be addressed until methods are developed to effectively sample late larvae and juvenile fish.

Large larvae were caught during the ICHS cruises, although the downward bend in the production curve at 30 days (Figure 6B) suggests that larvae either entered a region of higher mortality or they were increasingly able to avoid the sampling gear. The CalCOFI data also displayed a change in the slope of the production curve at 30 days, and because of the causal ambiguity we eliminated older larvae from the analyses. After comparing the day and night catches of successively larger larvae, Hewitt and Methot (1982) suggested that anchovy larvae, 30 days and older, are increasingly able to avoid capture at night as well as during the day. The ICHS sample contained a greater fraction of large larvae than the CalCOFI sample, although less than would be expected from an extension of the production curve beyond 30 days. Larger larvae become increasingly aggregated as they adopt the schooling habit (Hewitt 1981), and it may be that the difference between the data sets is because the ICHS gear samples a much larger volume of water per tow and thus increases the probability of encountering an aggregation of large larvae. With this interpretation, the difference in catch rates of large larvae may not represent a density difference so much as an example of a problem with sampler threshold. Alternately, the density of large larvae may indeed be higher in the nearshore zone; again this question cannot be addressed until more appropriate samplers are developed.

The critical assumption involved in deriving a production curve from catch data is that a stable age distribution prevails. The errors introduced by seasonal variation in egg production can be minimized by pooling data collected throughout the spawning season (Hewitt and Methot 1982), as we have done with the ICHS surveys.

Immigration and emigration of eggs and larvae to and from the nearshore zone may also upset the assumption of a stable age distribution. Because we are comparing production between regions, we cannot pool spatially as we did temporally and must therefore examine the monthly distribution maps and catch curves for evidence of larvae moving in or out of the nearshore zone. There was nothing to suggest significant immigration or emigration: larvae were more dispersed but encountered in the same general area as eggs; egg production in August resulted in catches of large larvae in September and October; large larvae again became a substantial portion of the catch in May, June, and July, when egg production rapidly decreased. If there was constant transport into the nearshore zone, the apparent mortality would tend toward that of the bight;

whereas constant transport out of the nearshore zone would tend to exaggerate the apparent mortality relative to that of the bight. In fact, neither transport nor spawning are steady through the season and may interact to produce a complex pattern of effects. However, the continuity of geographic patterns between stages and from survey to survey suggests that these effects are not great.

The survey data presented here suggest that production of young anchovy (less than 30 days old) in the nearshore zone is representative of production throughout the greater Southern California Bight. The seasonal production cycle, the density, and the survival of spawn are comparable between the regions. We emphasize, however, our lack of knowledge regarding the late larval and juvenile stages; until this can be improved, the significance of the nearshore zone to anchovy production cannot be fully appreciated.

ACKNOWLEDGMENTS

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THE VISUAL FEEDING THRESHOLD AND ACTION SPECTRUM OF NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) LARVAE

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ABSTRACT

The visual feeding threshold and action spectrum of 10-15-mm northern anchovy larvae were determined, using as criterion the incidence of two or more rotifers in the guts of 50% of larvae tested under different spectral irradiances. The threshold sensitivity to broadband blue-green light is at 0.15 μWcm^{-2} = 0.61 lux. The action spectrum shows a maximum in the green wavelengths around 530 nm: the weighted threshold irradiances at various wavelength bands converge at a mean value of 0.14 $\mu\text{Wcm}^{-2}{}_{\text{anch eff}}$.

The visual abilities of the anchovy allow them to feed at a depth of 74 m at noon on clear days, and at the surface during twilight and bright nights, and appear to be well adapted to the anchovy's habitat in turbid, greenish coastal waters. Comparisons with younger anchovy larvae show that changes in visual function accompany changes in eye and retinal morphology, specifically the recruitment of rods. Moreover, 10-15-mm anchovy larvae can feed to a limited extent (10%) in the dark when food densities are high (20-40 rotifers/ml). In March, which is the peak spawning season of the anchovy in southern California and Baja California, the 10-15-mm larvae have 13 hours each day to feed.

RESUMEN

Se determina en larvas de *Engraulis mordax* (anchoa) de 10-15 mm. de longitud, el umbral de visibilidad para capturar alimento y la acción del espectro, usando como criterio la incidencia de dos o más rotíferos en el tubo digestivo del 50% de las larvas sometidas a estudio bajo diversas condiciones espectrales de radiación. La sensibilidad del umbral en la amplia banda de la luz verde y azulada se encuentra a los 0.15 μWcm^{-2} = 0.61 bujías. La acción del espectro señala un máximo en las longitudes de onda de la banda verde, alrededor de los 530nm: la estimación del umbral de la anchoa en bandas de distinta longitud de onda, converge en un valor medio de 0.14 μWcm^{-2}.

La anchoa tiene una habilidad visual que le permite capturar alimento a una profundidad de 74 m. al mediodia en dias despejados, y en la superficie del mar al atardecer y en noches claras. Al parecer las anchoas se adaptan bien a su habitat de aguas costeras verdosas y turbias. Comparaciones efectuadas con larvas de anchoa más jovenes, indican que los cambios en la función visual corresponden con las variaciones en la morfología del ojo y de la retina, especialmente con la incorporación de los bastones. Las larvas de anchoa de 10-15 mm. de longitud, pueden alimentarse, con ciertas limitaciones (10%) en la oscuridad, cuando la densidad del alimento en el habitat es elevado (20-40 rotíferos por ml.). En el Sur de California y Baja California, el máximo de puesta de la anchoa se produce en Marzo, y entonces las larvas de 10-15 mm. de longitud disponen de 13 horas diarias de luz, que es suficiente para capturar el alimento.

INTRODUCTION

In this paper we determine the visual threshold and action spectrum of 10-15-mm northern anchovy (*Engraulis mordax*) larvae, and consider some implications of their feeding ecology. Studies on morphology and behavior have shown the importance of vision to anchovy (O'Connell 1963; Loukashkin and Grant 1965; Schwassmann 1965; Hunter 1972). At hatching, anchovy larvae are nearly transparent and have neither functional eyes nor jaws. O'Connell (1981) found that the oculomotor muscles differentiate at 3.5 mm SL; the photopic system is functional when feeding starts at 4 mm; and an area temporalis is present at 5 mm. The lens retractor muscle appears at 7 mm, and the rods at 10 mm. These developments indicate that an early feeding anchovy larva has a well-defined visual axis, good eye mobility, and binocular vision. The ability to accommodate to greater distances increases the perceptive field for feeding, and the recruitment of rods with commensurate increase in visual sensitivity increases the time that perception of food (and predators) is possible. Thus 10-mm anchovy can be expected to be more visually adept than 6-mm larvae. The ontogeny and maturation of sensory and locomotor systems and behavior patterns are important elements in larval survival (Hunter 1976a, 1977, 1981).

The visual threshold and action spectrum were de-

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termined to find out whether the morphological changes described above resulted in changes in visual function, and to obtain a basis for estimating the daily feeding period of larvae at sea.

MATERIALS AND METHODS

Anchovy larvae were reared at 16.5°-17.5°C from eggs spawned in the laboratory (Hunter 1976b; Leong 1971). Larvae grew to 10 mm in 3 weeks and then were transferred from the 300-liter rearing tank to 10-liter black plastic pots (30 cm dia, 10 cm deep), with 20-40 larvae in each pot. They were covered and kept in complete darkness for at least 12 hr to allow the guts to clear and the larvae to acclimate. Rotifers (*Brachionus plicatilis*) were used as prey because they are similar in size (180 μm) and optical density to most zooplankton and are easily cultured. Initially, we assumed that anchovy larvae could not feed in the dark, and the rotifers were added 12 hr before the tests at densities of 20-30/ml. When it became clear that some larvae could feed in the dark, the rotifers were added to the pots and dispersed just before the tests.

The apparatus, set in a darkroom, consisted of a completely sealed black box with three compartments, and three slide projectors (Kodak 600H with 127-mm f/2.8 lens with multimirror lamps GE ELH 300W, 120V) as light sources mounted 3 m away on the opposite wall (Figure 1). The three projectors were used simultaneously, their light beams isolated from each other by means of black cloth tubes. Slots in front of the lens held the various filters. In tests to determine the visual feeding threshold under broad-band blue-green light, we used a green glass filter (Schott BG-18) in combination with a 1-cm-thick glass cell filled with 5% copper chloride ($CuCl_2$) solution to approximate the spectrum at 20-m depth in waters with 0.8 mg Chl *a* m^{-3}. The color filters used for the action spectrum treatments were glass-mounted Kodak Wratten gelatin filters that selectively transmitted wavelength bands 60 to 112 nm wide with varying peaks (Table 1; Figure 2). Kodak neutral density absorption filters, calibrated with the spectroradiometer, were used to reduce intensities in logarithmic steps, nominally −0.5, −1.0, and −2.0.

A spectroradiometer (Optronic Laboratories 741V) interfaced with a Hewlett-Packard calculator-plotter was used to measure the spectral irradiance from 362 nm to 800 nm of each color filter at the level of the water surface of the test pots. This instrument was not sensitive to irradiance levels lower than the maximum projector output through each color filter; consequently, lower test irradiances were computed from the energy integral of the color filter multiplied by the transmission ratios of the neutral-density filters used.

TABLE 1
Filter Characteristics

Filters	Peak wavelength (nm)	Bandwidth[a] (0.01; in nm)	Irradiance[b] (μWcm^{-2})
Kodak Wratten			
18A + $CuCl_2$[c]	370	334 to 402; 68	0.80
47B	440	386 to 498; 112	15.22
75	485	458 to 540; 82	8.81
74	530	502 to 582; 80	11.53
73	570	552 to 612; 60	3.46
72B	600	582 to 650; 68	5.20
Schott			
BG-18 + $CuCl_2$	540	380 to 632; 252	153.0

[a] The wavelength range of the 1% bandwidth is identified as that portion of the spectrum spanned and as its width (in nm).

[b] Means (without neutral density filters) of 9 measurements for each color filter and 20 for BG-18.

[c] $CuCl_2$ (copper chloride cell) was used to reduce the transmission of red wavelengths from the projector lamp.

In this paper the feeding response is expressed as a function of irradiance (in μWcm^{-2}), the amount of energy that a unit surface of water intercepts from the light source directly above it, integrated over the wavelength band. To compare our results with those in the literature, we converted these into photometric units (lux) by weighting the spectral irradiances of the filters (Figure 2) against the standard luminosity curve for the human eye.

Eight treatments with eight filter combinations were made in one day, together with a bright control and a dark control. A bright control was exposure of larvae to unattenuated blue-green light from the projector (average irradiance at the water surface 153 μWcm^{-2}); whereas a dark control was completely sealed from light. Treatments consisted of exposure of 10-20 healthy 10-15-mm larvae and about 20-30 rotifers/ml to various spectral irradiances for 1.5 hr. After this interval and with the use of a small flashlight, we poured the larvae onto 300-μm plankton net filters; this almost instantly removed the larvae from water and minimized if not totally prevented defecation. The larvae were then spread on a glass slide. The gut contents were counted under a dissection microscope, a relatively easy operation given the larvae's transparent bodies and straight guts. The larvae were scored positive for incidence of two or more rotifers in the gut. The feeding incidence was used as measure of the larvae's response to differences in prey visibility.

Early in the experiment, we noted that the guts of 10-15-mm anchovy larvae in dark controls were not always empty but that 14.5% of them contained one or more rotifers. This observation ran counter to results under similar conditions for younger (6 mm) larvae (Hunter, unpublished data) and needed to be verified. Groups of 20-40 larvae were transferred into pots,

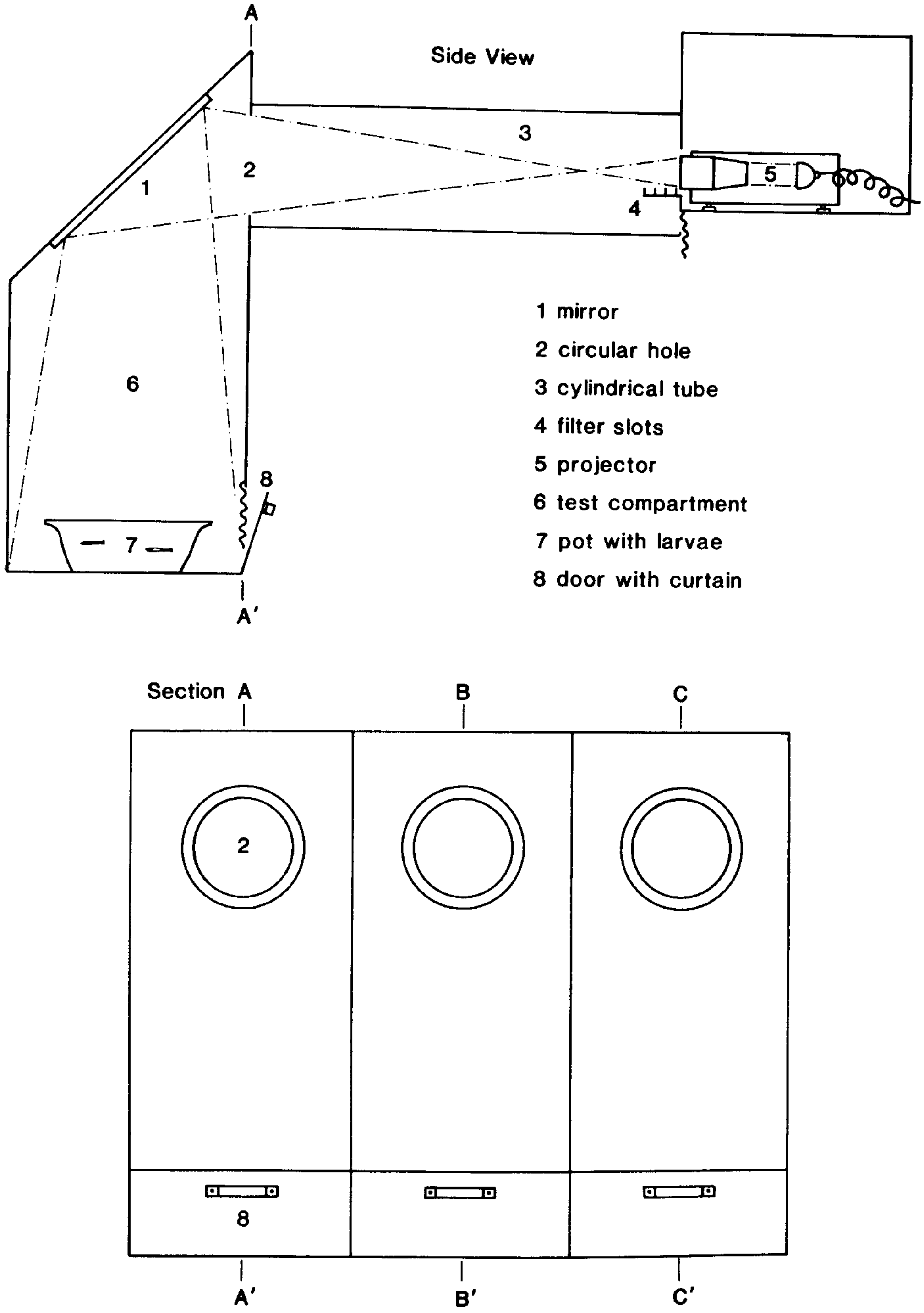

Figure 1. Apparatus for determining the visual thresholds for feeding of 10-15-mm anchovy larvae.

given or not given rotifers, then kept in darkness for different time intervals (from 30 min to 27 hr) and subsequently examined for incidence of food in the guts.

In the analysis of the light experiments, we adjusted the feeding incidence percentages for what turned out to be 10% feeding incidence in the dark (using the criterion of two or more rotifers/gut). Data were submitted to probit analysis (Finney 1971) to determine the irradiance for the 50% feeding thresholds (FT_{50}), under various spectral compositions of light. These FT_{50}'s were used to draw the action spectrum.

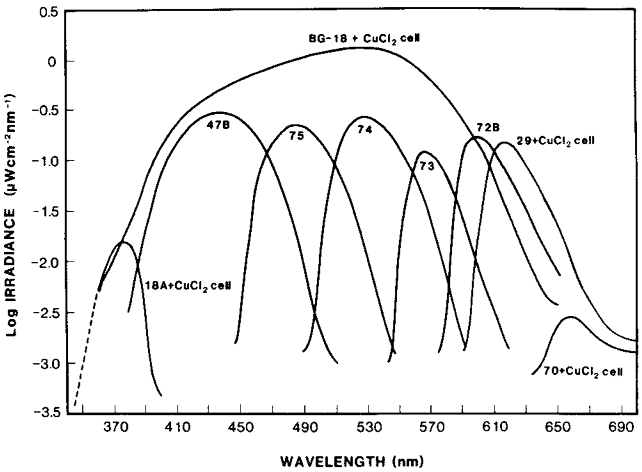

Figure 2. The spectral irradiance of the color filters used in the experiment. Filters used are given at top of each curve. All are Kodak with the exception of the Schott BG-18. BG-18 + CuC1_2 is the filter used for the broadband blue-green light treatments. The other filters are color filters, with maxima (from left to right) of 370 nm, 440 nm, 485 nm, 530 nm, 570 nm, 600 nm, 620 nm, and 660 nm. The irradiance below 362 nm in 18A is estimated from the curve drawn by eye (dashed).

RESULTS AND DISCUSSION

Visual Feeding Threshold under Blue-Green Light

Under bright control conditions, average irradiance 153 μWcm^{-2}, nearly all larvae fed (97.4 ± 1.7%, 36 tests, 475 larvae). This irradiance was equal to that in the rearing tank (150 μWcm^{-2}), where all larvae fed optimally. In most tests, the larvae were gorged with rotifers. The intestines must be very distensible because we once counted 240 rotifers in one gut, many still alive. Usual counts of full guts ranged from 20 to 100 rotifers per larva.

Figure 3 shows plots of the feeding incidence under blue-green light at eight log irradiance levels. The two graphs illustrate how the probit transformation linearizes the sigmoid relation. The probit regression line indicates that the 50% feeding threshold (FT_{50}) under blue-green light is 0.15 μWcm^{-2}, which is equal to 0.61 lux. This value is about one-tenth the threshold irradiance required by 6-mm larvae (FT_{50} = 1.6 μWcm^{-2} = 6.5 lux; Hunter unpubl.). Thus 10-15-mm larvae with both rods and cones are ten times more sensitive to prey than the 6-mm-larvae with cones only. This difference is probably even greater, because the criterion used for positive response was one or more rotifers per gut in the latter, whereas we used a criterion of two or more per gut.

This ten-fold increase in visual sensitivity, based on the feeding response, of 10-15-mm anchovy relative to 6-mm larvae is very probably related to the recruitment of rods and not to improvements in feeding efficiency. The feeding success of anchovy larvae does not change much as they grow from 6 mm to 10-15 mm (Hunter 1972). The proportion of time spent searching for food and the maximum ingestion rates of 6-mm larvae differ little from those of 10-15-mm larvae. The improvement in visual sensitivity may also be due to other developmental changes in the retina, including increase in the number of visual cells and neural connections, the differentiation of the retractor lentis, and greater production of visual pigments.

The visual feeding threshold of anchovy larvae is similar to the thresholds of other fish larvae (Table 2). Some variability in the thresholds exists, depending on the species; the criteria used; the age of the fish (length, presence of rods, degree of motor development); and the type, visibility, and size of prey. Prey density affects feeding thresholds, but few of the studies enumerated gave the densities used.

A more direct comparison between the thresholds for anchovy and herring can be made. Blaxter (1966) detected 10% feeding incidence for 12-14-mm herring at 0.13-0.19 lux. The probit regression line (Figure 3) can be used to estimate the irradiance level at 10% feeding incidence in 10-15-mm anchovy larvae, and this is 10^{-4} μWcm^{-2} or 0.0004 lux. It thus seems that anchovy larvae are at least 100 times more sensitive than herring larvae of similar size. More accurately perhaps, anchovy larvae at 10-15 mm are more advanced developmentally than are herring larvae at 12-14 mm. The adult northern anchovy may have even greater sensitivity than the larvae, considering the special characteristics of its retina and eye (O'Connell 1963). At zero feeding incidence (Figure 3), the irradiance is equivalent to about 10^{-7} lux, which may be close to the absolute threshold of anchovy rods. Protasov (1964) found that the threshold light sensitivity of the adult Mediterranean anchovy (*Engraulis encrasicholus*) as determined by the electroretinogram is at 10^{-8} lux.

Action Spectrum for Feeding

Figure 4 shows the feeding incidence under different spectral conditions plotted on probit scale against log irradiance. The 50% feeding threshold irradiances (FT_{50}'s) are indicated. The lowest irradiance that elicits 50% feeding occurs around 530 nm, whereas much more energy is required around 370 nm and 660 nm. The 95% confidence intervals (horizontal bars) of the FT_{50}'s cover about one order of magnitude, except for the two extreme wavelength bands. In the latter, larger errors occurred because the 50% feeding thresholds had to be extrapolated beyond the range of data (as indicated by the dotted portions of the regression lines for 370 nm and 660 nm in Figure 4). This was because the apparatus did not produce sufficient

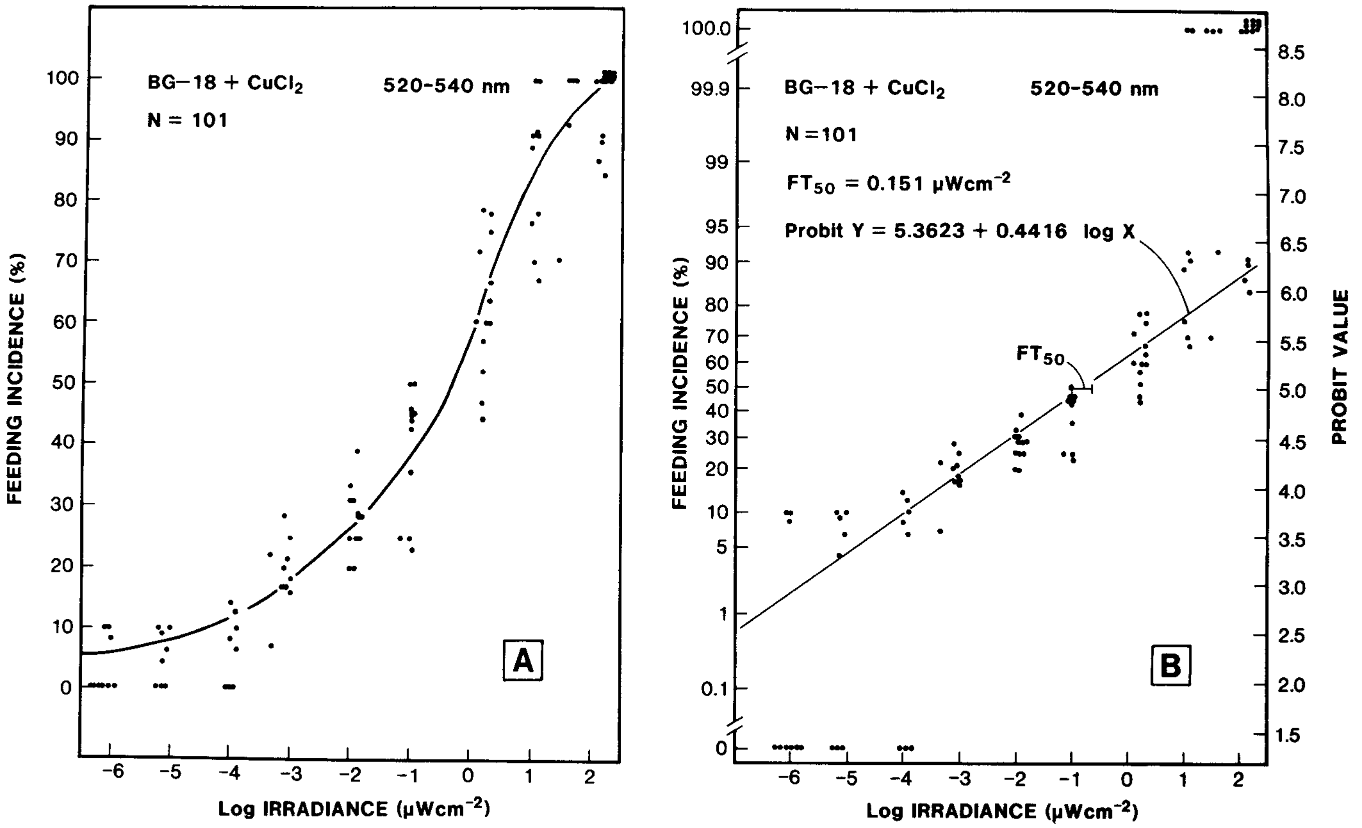

Figure 3. The incidence of feeding (percentage of larvae with two or more rotifers in the gut) under various irradiance levels of blue-green light. FT_{50} is the 50% feeding threshold; the horizontal bar indicates the 95% confidence interval using probit analysis (Finney 1971); N, the number of tests. In both graphs, the abscissa is on log scale; the ordinate is on linear scale in *A* and probit scale in *B* (with probit values given at the right.) The equation gives the regression of y = probit value on x = log irradiance.

TABLE 2
Visual Thresholds for Feeding in Fishes

Species	Length stage	Feeding threshold	Criteria	Prey	Author
Northern anchovy	6 mm	6.5 lux	50% larvae with $R \geq 1$	*Brachionus*	Hunter (unpubl)
	10-15 mm	0.6 lux	50% larvae with $R \geq 2$	*Brachionus*	This study
Herring	12-14 mm	0.13 lux	10% feeding incidence	*Artemia*	Blaxter (1966)
	12-14 mm	0.19 lux	10% feeding incidence	*Balanus*	Blaxter (1966)
	13-17 mm	0.02-0.09 lux	Number of prey taken extrapolated to zero	*Artemia*	Blaxter (1968a)
	13-17 mm	0.10-0.18 lux	Number of prey taken extrapolated to zero	*Balanus*	Blaxter (1968a)
	90-100 mm	0.036-0.007 lux	Cessation of feeding	Squid	Blaxter (1964)
Plaice	6 mm	1-10 lux	Feeding index reduced to 10%	*Artemia*	Blaxter (1968b)
	9-15 mm	0.01 lux	Feeding index raised above dark level	*Artemia*	Blaxter (1968b)
	6 mm	0.01-1 lux	Feeding index reduced to zero	*Artemia*	Blaxter (1969)
Cod	4-5 mm	0.1-0.4 lux	0 feeding incidence	*Artemia*	Ellertsen et al. (1980)
Jack mackerel	93-143 mm	6×10^{-7} ft-L	Incidence of prey in fish gut	*Artemia*	Hunter (1968)
	93-143 mm	6×10^{-5} ft-L	Incidence of 50% of prey taken in light	*Artemia*	Hunter (1968)
Pacific salmon	Young	10^{-4} ft-c	50% available prey eaten	*Daphnia*	Brett and Groot (1963)
	Fry/smolt	10^{-5} ft-c	Feeding extinguished	*Daphnia*	Ali (1959)
	Fry/smolt	0.1-1 ft-c	Feeding reaches maximum	*Daphnia*	Ali (1959)

R is the number of rotifers in the guts of anchovy larvae; 1 ft-c = 10.764 lux; under scotopic conditions, ft-c approximately equal to ft-L.

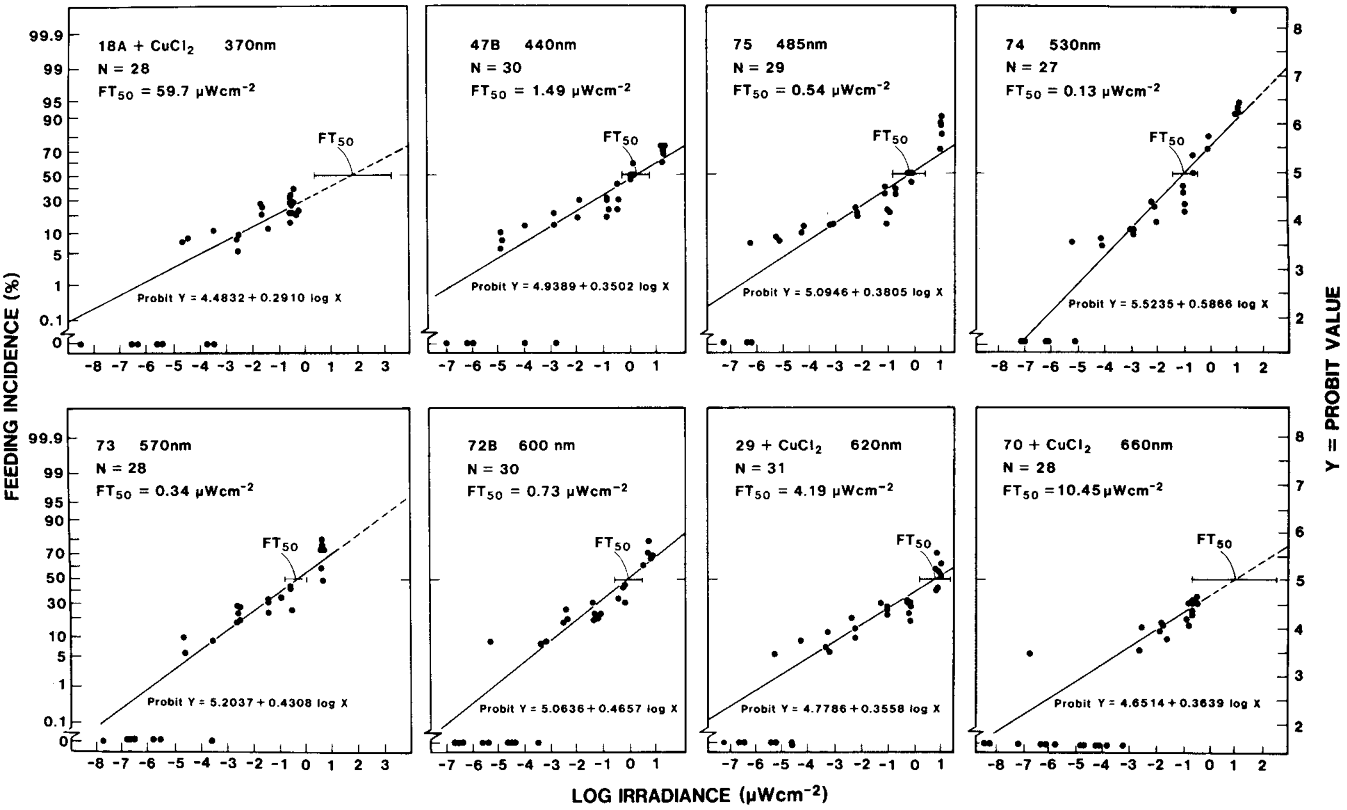

Figure 4. The incidence of feeding (percentage of larvae with two or more rotifers in the gut) under various wavelengths and irradiance levels. The filter name and peak transmission wavelength are given at the top left-hand corner. FT_{50} is the 50% feeding threshold using probit analysis (Finney 1971) (the horizontal bars indicate the 95% confidence intervals); N, the number of tests. All graphs are on logarithmic scale abscissa and probit scale ordinate (probit values at the right). Equations give the regression of y = probit value against x = log irradiance. The corrected FT_{50} for 18A is 27.7 μWcm^{-2}, and this value was used in the action spectrum.

energy to induce a 50% response at these wavelengths. The higher uncertainty at the extreme wavelengths should not detract from the overall accuracy of the action spectrum. Since the eye is essentially a log receptor, ± ½ log unit for most points is adequate precision.

Spectral sensitivity is usually expressed as the reciprocal of the threshold radiant energy. In Figure 5, we plot $1/FT_{50}$ in μWcm^{-2}, as well as in equivalent 1/photon units, to give the spectral sensitivity curve of 10-15-mm anchovy larvae. The number of photons at threshold level was obtained by multiplying the FT_{50} by the number of photons per erg at the peak wavelength (Withrow and Withrow 1956). The sensitivity curve in photons is displaced relative to that in energy units because the energy content per photon is higher in the short than in the long wavelengths. Either curve can be considered as the action spectrum of 10-15-mm anchovy for feeding on translucent prey; peak sensitivity occurs at 530 nm. The relative sensitivity coefficients are indicated on the leftmost scale in Figure 5.

The anchovy action spectrum peaks decidedly in the green part of the spectrum—between 510 nm and 550

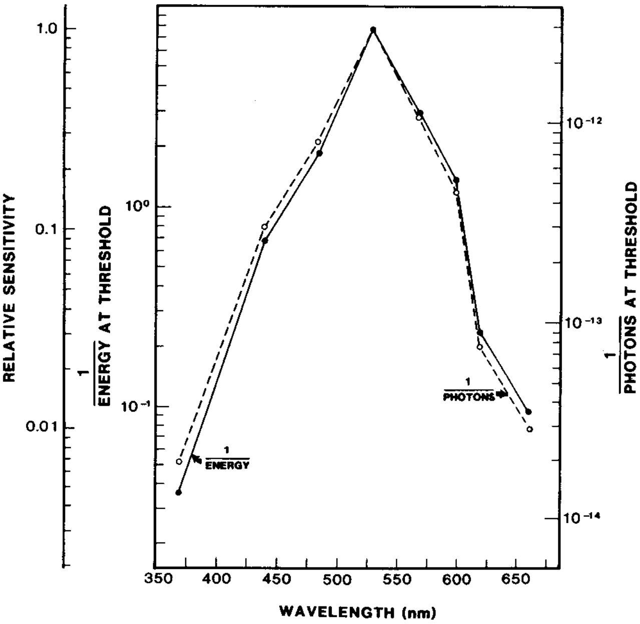

Figure 5. The action spectrum of 10-15-mm northern anchovy larvae for feeding on translucent prey, based on the reciprocals of the 50% feeding thresholds in energy and photon terms (given on log scales inside the graph). The leftmost log scale on the ordinate is the relative sensitivity of the anchovy at various wavelengths when the peak sensitivity at 530 nm is set equal to 1.0 and those at other wavelengths normalized accordingly.

nm. Northern anchovy are distributed off California and Baja California close to the coast. California waters transmit maximally in the green (Tyler 1961, 1964; Kampa 1961; Hobson et al. 1981). The larvae's increased sensitivity to green makes their environment appear relatively brighter and their prey easier to detect by contrast. The action spectrum obtained in this study may be applicable to most natural prey (primarily copepod nauplii to adults): like rotifers, they are often translucent.

Based on the FT_{50}'s, the action spectrum may be attributed to the rods, with some contribution from the cones. Most of the test irradiances were low (with energies quantitatively less than the blue-green light threshold), and in these the cones of the dark-adapted larvae were probably never activated. In the higher irradiance tests, both rods and cones may have been activated. The slopes of the probit regression lines for the various wavelength bands (Figure 4) were not homogeneous ($F=3.60$, $P=0.001$, $k=7$, $DF=215$) as they would have been if the response were due to only one visual system (rods only). Moreover, comparison of the northern anchovy larval action spectrum with the scotopic (with maximum at 500 nm) and the photopic (with maximum at 560 nm) ERG spectral curves of the adult Mediterranean anchovy (Protasov 1964) shows that it lies between the two values. The same is true in comparison with human luminosity curves. This also seems to indicate that the anchovy action spectrum for feeding has both rod and cone components.

TABLE 3
Comparison of the 50% Feeding Thresholds (FT_{50}) under Different Spectral Conditions and Weightings

		50% feeding threshold		
Peak wavelength (nm)[a]	Ratio[b]	Unweighted FT_{50} μWcm^{-2}	Weighted FT_{50} $\mu Wcm^{-2}{}_{anch\ eff}$[c]	Lux
370	0.0060	27.7	0.1662	43.21
440	0.1053	1.49	0.1569	2.79
485	0.3428	0.54	0.1851	1.54
530	0.8678	0.13	0.1128	0.79
570	0.3931	0.34	0.1336	2.04
600	0.1358	0.73	0.0991	2.70
620	0.0348	4.19	0.1458	8.38
660	0.0139	10.45	0.1453	11.09
Blue-green (broadband)	0.5092	0.15	0.0764	0.61

[a] Peak of the spectral irradiances of the filters (Figure 2).
[b] Fraction of the filter spectral irradiance effective for anchovy feeding (obtained by weighting the former against the anchovy action spectrum).
[c] The ratio in column 2 times the 50% feeding thresholds (Figure 4) gives the irradiance in anchovy effective units $\mu Wcm^{-2}{}_{anch\ eff}$).

If the form of the action spectrum were accurate, the energy at the 50% feeding incidence level would be the same value for all the spectral irradiances when these are weighted by the action spectrum. As a rough test of the action spectrum, we calculated the irradiance in anchovy effective units ($\mu Wcm^{-2}{}_{anch\ eff}$) by weighting the spectral irradiances of the various filters (Figure 2) using the anchovy action spectrum (Figure 5) and adjusting the 50% feeding thresholds. The weighted thresholds range in value from 0.10 to 0.17 $\mu Wcm^{-2}{}_{anch\ eff}$ and average 0.14 $\mu Wcm^{-2}{}_{anch\ eff}$ (Table 3). These tests are interesting but are not independent because the eight color filters were used to estimate the action spectrum. An independent test of the action spectrum for predicting 50% feeding incidence under different spectral irradiances is to convert the 50% threshold estimated under the broadband filter combination ($BG-18$ + $CuCl_2$) to anchovy effective units by weighting the spectral irradiance of the broadband filter by the anchovy action spectrum and comparing the results to the thresholds estimated for the other filters. Since the broadband filter was not used to estimate the action spectrum, this procedure is an independent measure of the accuracy of the action spectrum. Under the broadband filter the 50% feeding incidence threshold, in weighted units, was 0.076 $\mu Wcm^{-2}{}_{anch\ eff}$, which is different by only a factor of 2 from the average value for the other color filters (Table 3). Certainly this level of accuracy seems good, considering that the confidence interval around any point in the action spectrum was about an order of magnitude (Figure 4). This test indicates that the action spectrum obtained is a reliable predictor of the wavelength dependency of the feeding performance of anchovy larvae. This also means that, with an uncertainty of 2×, the feeding threshold can be estimated for any water type where the spectral irradiance is known, simply by weighting the irradiance by the action spectrum.

There appears to be a difference in the spectral sensitivity of 6-mm and 10-15-mm anchovy larvae tested under similar conditions. Younger larvae, which have cones only (O'Connell 1981), have a broader curve with two maxima at 440 nm and 600 nm (Hunter unpubl.), whereas the older larvae studied here have a narrow scotopic curve with maximum at 530 nm. This green sensitivity is also shown by adult anchovy (Loukashkin and Grant 1965). Blaxter (1964, 1968a) shows a similar development in herring: larvae with pure-cone retina have photopic curves with 1 to 3 maxima depending on the behavior and test conditions; the juveniles with rods show a scotopic maximum at 510-520 nm.

The action spectrum may be expected to reflect the absorption spectrum of the visual pigment. The visual pigment of northern anchovy has not yet been extracted but is probably similar to that of the deepbody anchovy, *Anchoa compressa*, a relative that also lives in turbid water and has an absorption maximum at 510 nm (Munz 1957). The action spectrum of 10-15-mm northern anchovy is similar to that of juvenile herring (Blaxter 1964), to the scotopic ERG spectra (with maxima at 520-540 nm) of several species of shallow-water marine and freshwater fishes studied by Kobayashi (1962) and Protasov (1964), and to the scotopic sensitivity spectrum (with peak at 525 nm) of adult *Tilapia* (Tavolga and Jacobs 1971).

Feeding in the Dark

Of the larvae kept 12-24 hr in the dark, 12% had two or more freshly ingested rotifers in the gut at high food densities (40 rotifers/ml) whereas only 3% fed in pots where the only food present was that transferred with the larvae from the rearing tank (5 rotifers/ml) (Table 4). There was no doubt that most of the food seen in the gut was recently consumed because many of the rotifers were undigested, and Theilacker (Southwest Fisheries Center, La Jolla, pers. comm.) found that the time for complete evacuation of the gut in feeding anchovy larvae less than two weeks old, as well as in herring larvae up to five weeks old, varied little from 2 hr. That the incidence of food in the gut showed a significant increase at high food densities ($x^2 = 11.53$, $p = 0.007$ when the criterion used is two or more prey per gut or $R \geqslant 2$) also clearly demonstrates that 10-15-mm larvae can feed in the dark at high food densities. The dark controls with 20-25 rotifers/ml averaged 10% feeding incidence (Table 4). It appears that the extent of dark feeding depends on the food density.

Previous work on larvae of the northern anchovy and related species has shown a marked diurnality in feeding activity, with no feeding in the dark (Berner 1959; Arthur 1976). Arthur, however, mentions a remarkable "exception": a sample taken 38 km off the coast of central Baja California approximately 6 hr after sunset and 1.5 hr after moonset (first quarter moon) contained both anchovy and sardine larvae literally crammed with the pteropod *Limacina bulminoides*. Mollusks were otherwise a rare item in the guts of these larvae. O'Connell (1981) found that the olfactory and the lateral line apparatus are present and apparently functional at hatching in anchovy; maturation of these systems continues throughout larval life. These faculties are sufficiently developed to be used by the larvae in locating prey in the dark. Olfaction may be used to locate prey patches; once in a patch, larvae could ingest food by swimming through open-mouthed or by blindly striking.

Dark feeding has been observed in other fish larvae, (Blaxter 1969; Bainbridge and McKay 1968; John and Hasler 1956; Ellertsen et al. 1980). Blaxter (1966) noted that some of the 12-14-mm herring larvae (without rods) in his dark controls fed overnight. Dempsey (1978) showed that herring respond by olfaction to washings and extracts of prey they had previously fed on, and to amino acids characteristic of these prey. Herring larvae with the eyeballs removed are able to feed at very high food densities (Hunter personal observation).

TABLE 4
Feeding Incidence in Anchovy Larvae Kept 12 hr or More in the Dark

Rotifer density (#/ml)	Number larvae	Number tests	Feeding incidence Mean ± (2SE) (%)	
			$R \geqslant 1^a$	$R \geqslant 2$
5	188	21	10.74 (5.90)	2.89 (2.41)
40	172	21	26.99 (6.92)	12.44 (5.80)
22[b]	428	37	14.49 (4.28)	9.41 (3.41)
25[c]	140	10	14.16 (7.13)	10.10 (4.29)

[a] R is the number of rotifers in the guts of larvae; $R \geqslant 1$ is the original, and $R \geqslant 2$ the modified criterion of positive feeding incidence applied to the same larvae.

[b] Dark controls for the threshold experiments in which rotifers were added 12 hr before test.

[c] Dark controls in which the rotifers were added just before test. The chi-square test shows significant differences in the frequencies of feeding larvae under low and high food density conditions: $X^2 = 11.53$, $P = 0.007$ when $R \geqslant 2$, and $X^2 = 20.66$, $P = 0.001$ when $R \geqslant 1$.

Daily Feeding Period

One of the important effects of increased visual sensitivity is the increase in the length of time that larvae are able to feed effectively (Blaxter 1966). When the sun is 6° below the horizon (civil twilight), illumination at the sea surface is about 3.4 lux (Brown 1952). This irradiance level would still enable 50% of 10-15-mm anchovy to feed, but is below the feeding threshold of the 6-mm larvae. Full moon is typically 0.1 lux, and at least some 10-15-mm larvae could feed at the surface. The broadband blue-green feeding threshold of 10-15-mm anchovy larvae, $0.15\ \mu\text{Wcm}^{-2} = 0.61$ lux $= 0.057$ ft-c, is reached at the earth's surface when the sun is 7.5° below the horizon at dusk and dawn. With the sun 6° below the horizon, we calculate that in California waters with a total attenuation coefficient of 0.152/m in January (Tyler 1961), 50% of 10-15-mm anchovy larvae could still feed at 5-m depth. At noon of a typical sunny day, when incident illumination is 11,500 ft-c at the surface (Brown 1952), 50% of 10-15-mm anchovy could feed at 74 m. Anchovy larvae are distributed from the surface down to about 100 m, with about 95% of them in the upper 60 m (Ahlstrom 1959). Larvae 10 mm and larger remain near the surface at night and descend to

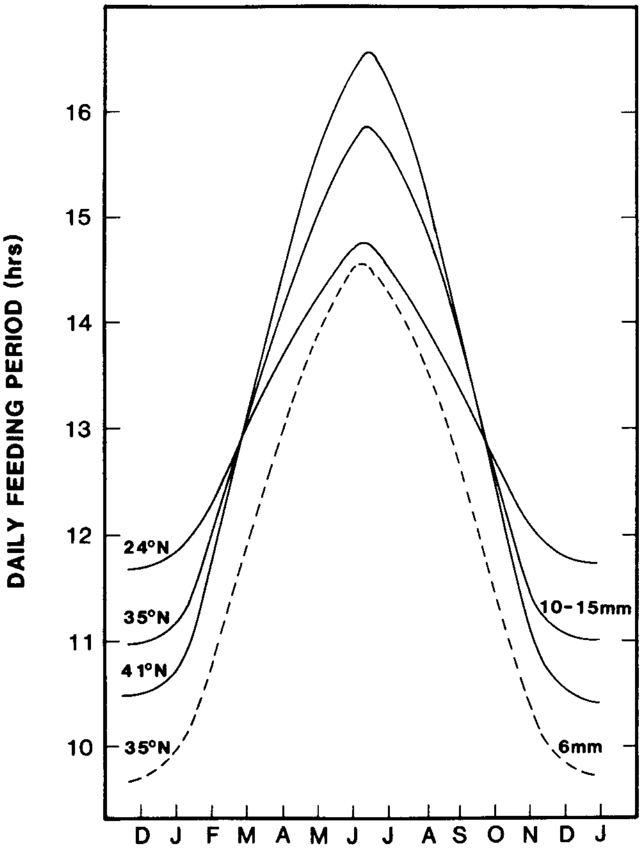

Figure 6. The daily feeding period of anchovy larvae at these selected latitudes at different times of the year.

depths down to 70 m in the day (Hunter and Sanchez 1976).

We calculated the daily feeding period of anchovy larvae (the number of hours when the light intensity at the sea surface is above the visual threshold value and the larvae are able to feed) based on Brown's (1952) Natural Illumination Charts. Figure 6 shows the daily feeding periods of 10-15-mm anchovy larvae at 41°N (Cape Mendocino), 35°N (Point Concepcion), and 24°N (Point San Juanico). It appears that in southern Baja California there is sufficient light for feeding by 10-mm anchovy larvae for 12 or more hours per day throughout the year. Southern California larvae have at least 11 hr and up to 16 hr per day. The anchovy population that occurs north of Cape Mendocino into Canada spawns in the summer, at which time there are 17-18 hr for larvae to feed (and the temperature and the food supply are favorable).

At 35°N, 10-15-mm larvae have approximately one hour more each day for feeding than the 6-mm ones, a consequence of their higher visual sensitivity. Thus, contrary to Hunter's (1972) assumption of a 10-hr feeding day, anchovy larvae have potentially much longer daily feeding periods. In March, which is the peak spawning month, 6-mm larvae can feed about 12 hr and 10-15-mm larvae 13 hr each day. This, of course, increases the possible volume of water searched by 10-15-mm larvae per day by 30% and thereby improves the chance of finding food by that amount.

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INTERACTIONS BETWEEN FISHING EFFORT AND CATCH PER UNIT EFFORT IN THE SAN PEDRO FISHERY: A STATISTICAL NOTE

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ABSTRACT

Time series methods are applied to daily data of trips and average catch per trip (effort and CPUE) for anchovy and mackerel fishing in the San Pedro, California, purse seine fishery. The study shows that high fishing effort leads to a slight increase in CPUE, whereas high CPUE attracts additional fishing effort. The data show little evidence of local stock depletion in the short run. An additional result is that forecast models of anchovy or mackerel CPUE should not be cast in a single equation framework; rather, a four-equation system simultaneously forecasting CPUE and effort for each species is the appropriate specification.

RESUMEN

Los métodos períodicos se aplican a los datos diarios de viajes y el promedio de captura por viaje (esfuerzo y captura por unidad de esfuerzo: CPUE) para las pesquerías de anchoa y jurel utilizando red de cerco, en la región de San Pedro, California. El estudio demuestra que un esfuerzo de pesca elevado incrementa ligeramente el CPUE, mientras que la elevación de la captura por unidad de esfuerzo, implica esfuerzo de pesca adicional. Los datos no señalan que exista a corto plazo, una reducción de las reservas pesqueras. Los modelos para predecir las capturas de anchoa y jurel por unidad de esfuerzo, no debían de encajarse en la rigidez de una ecuación, mas bien la apropiada especifidad requeriría de un sistema simultáneo de cuatro ecuaciones para predecir captura por unidad de esfuerzo (CPUE) y el esfuerzo, para cada una de las especies.

INTRODUCTION

The question "how does today's fishing effort ininfluence tomorrow's catch?" may receive very different answers depending on which fisheries scientist one asks.

For example, a biologist might answer that there is little or no influence unless the catch is large relative to the target school, in which case local depletion causes catch per unit effort (CPUE) to decline. Conversely, an economist might maintain that CPUE is an increasing function of effort: as the level of fishing effort increases, fishermen become more adept at finding and catching fish, and consequently average catch rises. Alternatively, one could take the fishermen's perspective and decide that the causation implied in the question is backwards; actually fishing effort has little effect on CPUE. Rather, fishing conditions today determine tomorrow's fishing activities.

These are three reasonable yet conflicting answers to the question. Although presented in a very stylized fashion, each answer has significant implications for the modeling and regulation of commercial fishing industries.

For example, if CPUE is not a function of effort, then CPUE can be forecast by regulators without simultaneously forecasting effort. This might be done towards the end of a fishing season to determine a possible closing date. On the other hand, if CPUE does depend to some extent on the level of effort, CPUE cannot be accurately predicted without incorporating into the forecasting process those economic variables that influence effort.

Perhaps of more interest to modelers is whether each species in a multiple species fishery can be regulated independently. If the CPUE for one species is influenced by the effort for a different species, then the two species must be simultaneously modeled and regulated.

In general, if there are strong influences of fishing effort on CPUE then the modeling and regulatory process can be severely complicated. (A lengthy elaboration of these points and similar issues is presented in Phillips 1982.) In this paper I present the results of an empirical analysis attempting to statistically determine the extent of CPUE and effort interactions in the San Pedro, California, anchovy and mackerel fishery, where "effort" is operationally defined as the boat-days dedicated to fishing for a given species.

The results suggest that there are definite positive interactions between fishing effort for anchovy (and mackerel) and CPUE for anchovy (and mackerel). The results also suggest some cross-effects between species. Although there is a slightly positive effect of fishing effort on CPUE, particularly for mackerel, the major effect seems to be of CPUE on fishing effort.

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DATA AND METHODOLOGY

The investigation was performed using data provided by the California Department of Fish and Game. Each day, agents of the Department of Fish and Game collect records of each commercial sale of oceanic fish in California. These records, collected at the docks, include the prices paid, the weight, and the species of fish involved. Because of the vast number of data collected, there is a substantial lag before the data are available for statistical analysis. Therefore, I used observations from the 1974, 1975, and 1976 fishing seasons.

From the raw data, I extracted daily sales by those San Pedro fishermen who earned at least 75% of their annual revenues from mackerel and anchovy. This defined a working fleet of about 30 vessels. I then aggregated these daily observations into a new data base reflecting the entire fleet's daily activities. No individual vessel's data were analyzed except in the aggregated form.

The resulting data base had 684 fishing days in the total sample. These were divided into an "in-sample" and a "postsample" group. The in-sample group of 488 observations was used for statistical estimation, and the postsample group of 196 observations was used to evaluate alternative statistical models.

The four relevant series, anchovy CPUE and fishing effort and mackerel CPUE and fishing effort, were used to fit ARIMA models using Box-Jenkins univariate modeling techniques (Box and Jenkins 1976). These estimated models were used to filter the series into "prewhitened" data. Using the estimated ARIMA models, I removed the trends and serial correlation, leaving four series-satisfying tests for white noise.

Next, I estimated cross-correlograms between the prewhitened CPUE and prewhitened effort series and used them to tentatively identify the presence of feedback and the direction of "causation"[1] between the series. The analysis in this step provides a statistical basis for answering "how today's effort influences tomorrow's catch."

RESULTS

Using the daily data, I identified univariate time series models for anchovy and mackerel effort and CPUE. In each case, the suggested model was a low-order autoregressive model. Following the Box-Jenkins algorithm for modeling such series, I estimated several alternate autoregressive, moving average, and mixed models for each series. I estimated the equations over the initial 488 observations and computed the forecast performance over the final 196 observations. The models performing best in terms of minimizing the mean-squared forecast error are the autoregressive models reported in Table 1.

TABLE 1

Let B denote the "backwards" operator such that $y^{t-1} = B^i \cdot y^t$. Let MCPUE denote mackerel CPUE, let ACPUE denote anchovy CPUE, let ME denote mackerel effort, and let AE denote anchovy effort. Let the prefix R denote "residual" to identify the prewhitened variables. The univariate linear models of the series minimizing means squared forecasting error are the following models. (Standard errors are reported.)

ACPUE

$$\begin{aligned}&(1 - \underset{(0.03575)}{0.5951849B} - \underset{(0.03746)}{0.1121908B^3} + \underset{(0.04512)}{0.1161364B^7}\\ &\qquad - \underset{(0.04396)}{0.1093452B^6})\mathrm{ACPUE}^t = 13.95966 + \mathrm{RACPUE}^t\end{aligned}$$

In sample: $N = 488$

$R^2 = 0.42426$

$\bar{R}^2 = 0.41949$

s.e. $= 20.97673$

$F = 88.98047$

AE

$$\begin{aligned}&(1 - \underset{(0.0458)}{0.5687526B} - \underset{(0.04371)}{0.1719947B^6} + \underset{(0.04464)}{0.0935268B^5}\\ &\qquad - \underset{(0.04347)}{0.13414B^3} + \underset{(0.05281)}{0.05610872B^2})\mathrm{AE}^t = 3.244975 + \mathrm{RAE}^t\end{aligned}$$

In sample: $N = 488$

$R^2 = 0.37908$

$\bar{R}^2 = 0.37264$

s.e. $= 6.91751$

$F = 58.854$

MCPUE

$$\begin{aligned}&(1 - \underset{(0.04588)}{0.3984744B} - \underset{(0.04195)}{0.1424534B^6} - \underset{(0.04306)}{0.1072012B^7})\mathrm{MCPUE}^t\\ &\qquad = 3.84161 + \mathrm{RMCPUE}^t\end{aligned}$$

In sample: $N = 488$

$R^2 = 0.1883$

$\bar{R}^2 = 0.18327$

s.e. $= 10.33098$

$F = 37.42624$

ME

$$\begin{aligned}&(1 - \underset{(0.04675)}{0.455493B} + \underset{(0.04772)}{0.0697266B^2} - \underset{(0.05507)}{0.1670767B^6} - \underset{(0.04972)}{0.199367B^7})\mathrm{ME}^t\\ &\qquad = 1.089719 + \mathrm{RME}^t\end{aligned}$$

In sample: $N = 488$

$R^2 = 0.31849$

$\bar{R}^2 = 0.31285$

s.e. $= 4.05084$

$F = 56.43089$

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[1] Using the concept of causality in the mean proposed by Granger (1969), fishing effort is said to "cause" CPUE if the mean squared forecasting error is less when the information set used for forecasting includes past values of both CPUE and effort than when the information set only includes past values of CPUE. In this application, if there is significant correlation between past value of prewhitened effort and present values of prewhitened CPUE, one tentatively identifies effort as "causing" CPUE. Note that the identification is only tentative and is relative to the particular information set used. With more information, the apparent causation might be eliminated. Two recent application papers discuss the finer details of causality testing and should be reviewed by interested practitioners: Ashley and Granger (1979), and Ashley et al. (1980).

The residuals from the estimated equations are the prewhitened variables. By construction, they approximately satisfy white noise criteria and with the estimated models contain the same information as the original data series. The next step in my analysis was to compute the cross-correlograms presented in Table 2. The correlograms show several interesting—and unexpected—relations between the series. I will first discuss the anchovy results and then the mackerel

With respect to anchovies, curiously, the only statistically significant correlations, besides at the zero lag, are at approximately ±1 week. A possible explanation for the significance of the -7 lag ($\rho = 0.10742$), is that the fishermen use more sophisticated forecasts based, perhaps, on additional information such as weather and lunar cycles. It does not seem reasonable that fishing a week ago improves fishing today while intervening fishing activity does not significantly affect CPUE. I propose that the -7 term reflects the fishermen's wider information set rather than a biological causal mechanism. The $+6$ and $+7$ lags are also significant: today's CPUE is positively correlated with fishing effort a week from now. This is consistent with the San Pedro fishermen's tendency to change nets at weekly intervals.

TABLE 2

Corr(RAE_{t+k},RACPUE)	$N = 488$ $k =$	Corr(RME_{t+k},RMCPUE)
0.10742	−7	0.01030
−0.03183	−6	−0.07330
−0.02469	−5	−0.06093
−0.01882	−4	0.04897
0.04895	−3	0.01888
−0.04371	−2	0.03568
0.08566	−1	0.17200
0.57756	0	0.37698
0.03401	1	0.13095
0.05562	2	0.03926
−0.01367	3	0.07514
0.05800	4	0.00360
−0.00516	5	−0.07646
0.12612	6	0.10683
0.10017	7	0.02349

95% critical value $\approx 2\sigma \approx \frac{2}{\sqrt{n}} = 0.09053$

The mackerel cross-correlations suggest a different explanation for that fishery. As with the anchovy, there is a significant positive correlation at about a week lead ($\rho_6 = 0.10683$), consistent with fishing effort transferring into the fishery after the usual week delay. However, there are two other statistically significant correlations, both positive and at ±1 day. The highly significant -1 lag ($\rho_{-1} = 0.17200$) is consistent with learning explanations and seems to refute short-term depletion hypotheses. The significant lag at $+1$ ($\rho_1 = 0.13095$) may be in response to the higher value of mackerel relative to anchovy: when mackerel CPUE seems to increase, more fishermen want to participate in the fishery.

As an additional experiment, I computed the cross species-effort/CPUE cross-correlations (Table 3). Besides the significant zero lag correlations, there was one other significant correlation in each cross-correlogram. The correlation between today's mackerel CPUE and the anchovy fishing effort 5 days hence is significantly negative ($\rho_5 = -0.1049$), perhaps reflecting the anchovy fishermen who stop fishing, change nets, and enter the mackerel fishery on lead 6 or 7 as seen above. The only significant nonzero lag correlation between mackerel effort and anchovy CPUE is at the -7 lag ($\rho_{-7} = 0.1211$). I have no story to explain why mackerel fishing a week ago is related to higher anchovy CPUE today.

TABLE 3

Corr(RAE_{t+k},$RMCPUE_t$)	$N = 488$ $k =$	Corr(RME_{t+k},$RACPUE_t$)
0.02707	−7	0.12110
−0.02909	−6	−0.07682
−0.08135	−5	0.02977
+0.01047	−4	0.00909
−0.01614	−3	0.03507
−0.02851	−2	0.03460
0.05008	−1	0.04919
0.20184	0	0.32219
0.04682	1	0.06772
0.02192	2	−0.06894
0.02107	3	0.04975
0.00281	4	−0.02038
−0.10490	5	−0.03269
0.04736	6	0.04031
0.05832	7	0.00545

95% critical value $\approx 2\sigma \approx \frac{2}{\sqrt{n}} = 0.09053$

CONCLUSION

The data suggest that there are statistically significant interactions between past values of fishing effort for mackerel and anchovy and the current values of mackerel and anchovy CPUE. Consequently, models of this fishery may need revision to reflect the underlying multiple species structure. An interesting area for future research would be to incorporate additional information into the underlying information set—especially spotter plane and meteorological data—to see if the cross-correlations remain significant.

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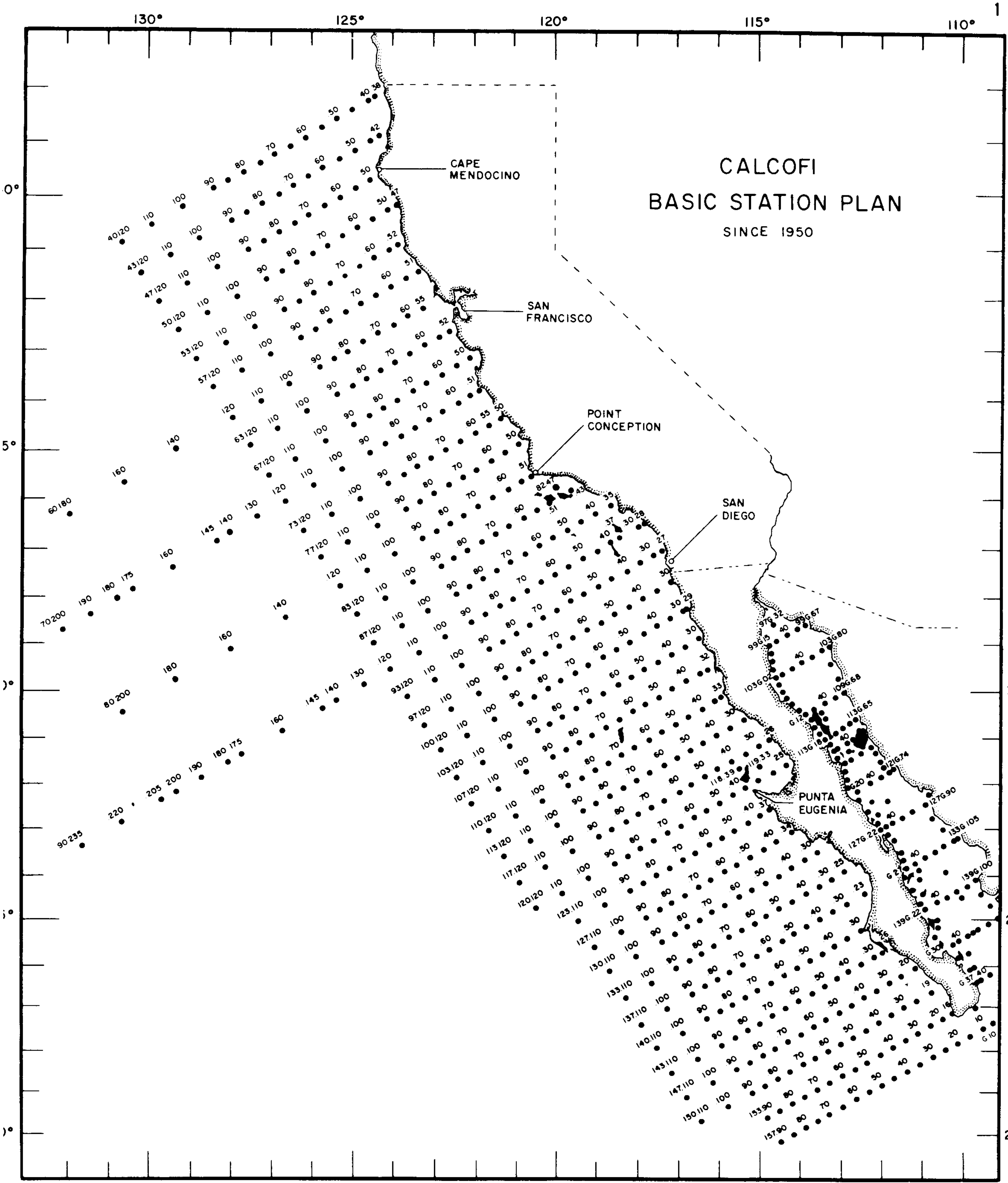

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