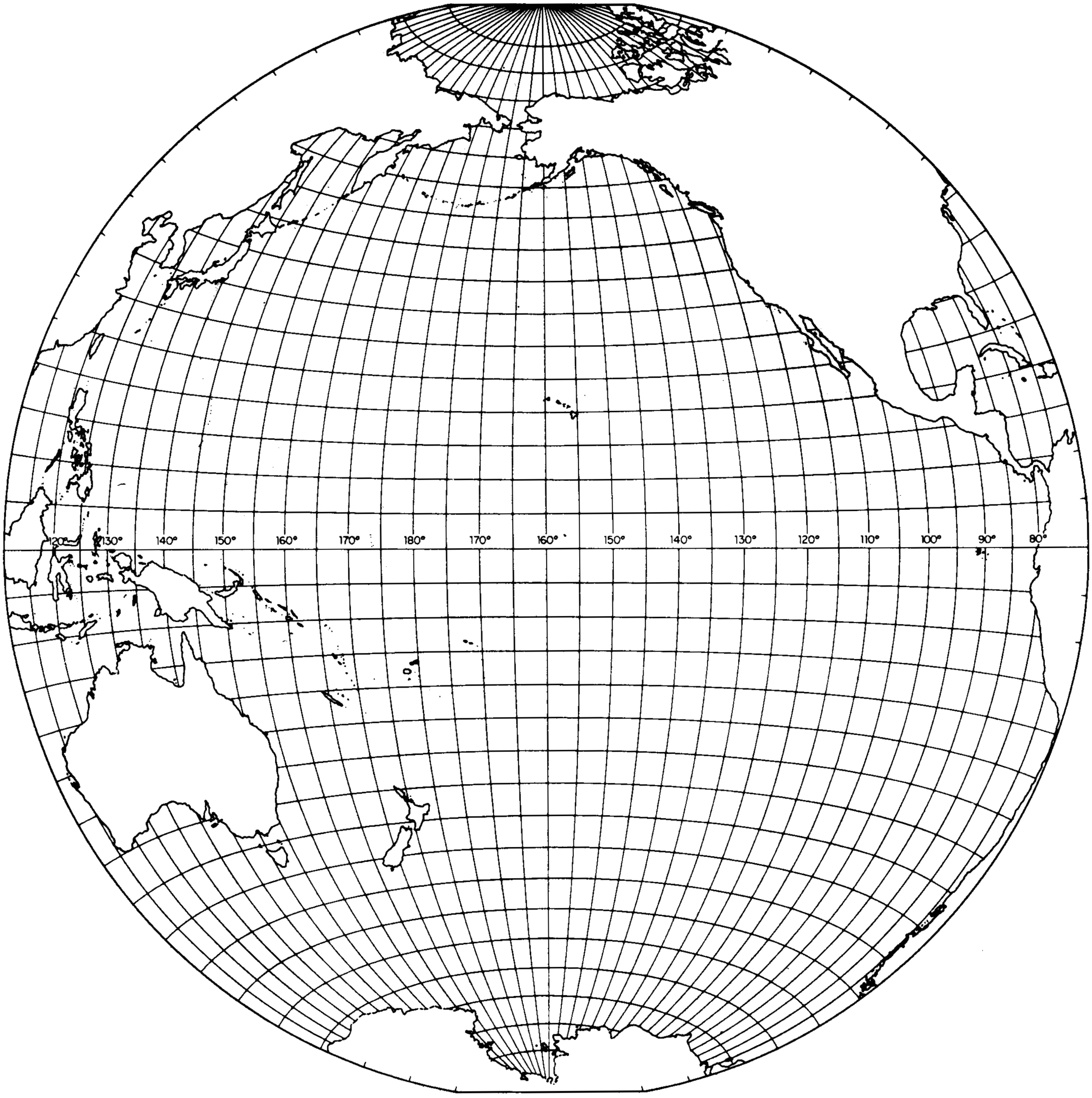

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

VOLUME XXIII
OCTOBER 1982

CALIFORNIA
COOPERATIVE
OCEANIC
FISHERIES
INVESTIGATIONS

Reports

VOLUME XXIII
January 1 to December 31, 1981

Cooperating Agencies:

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

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Published October, 1982, La Jolla, California

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IN MEMORIAM

John Radovich
April 1, 1921-June 27, 1981

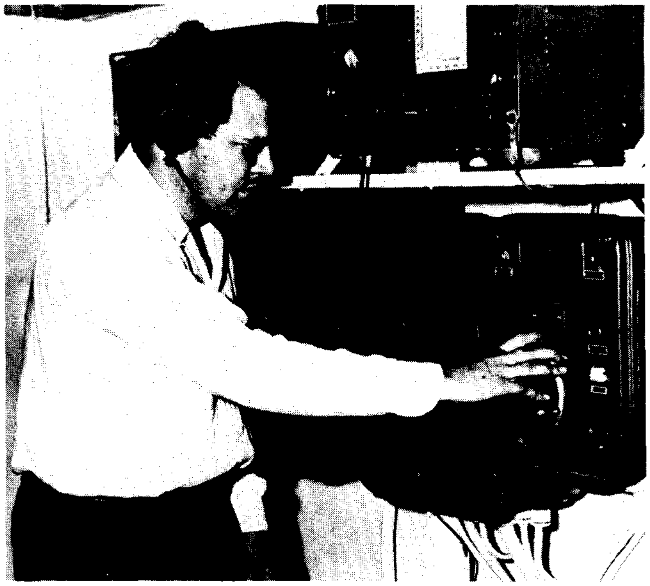
On Saturday, June 27, 1981, fishery science lost John Radovich, who died of a heart attack while playing tennis. He was 60 years old.

John Radovich's involvement with the sea began while he was in the U.S. Navy (1943-46), where he became a diver. After the war, he graduated from the University of Southern California with a degree in zoology. He later obtained a master's degree in public administration at Sacramento State University, and at the time of his death was in the latter stages of work toward a Ph.D. degree at University of California, Davis.

In 1949, John joined the California Department of Fish and Game as a seismic observer, and later became affiliated with the Sea Survey Project. He became Assistant Director of the California State Fisheries Laboratory at Terminal Island, spent 1955 in Sacramento as Assistant Marine Resources Branch Chief, and in 1956 became leader of the Pelagic Fisheries Investigations at Terminal Island. In 1963 he became Chief of Marine Resources Branch in Sacramento. Operations Resource Branch was created in 1969 with John at its helm. In 1979 he was appointed Senior Marine Advisor to the Director of the California Department of Fish and Game.

Radovich was involved with a number of professional, scientific, and fishery management organizations and committees. He was a member of the American Institute of Fishery Research Biologists and, at the time of his death, president. He was a member of the American Fisheries Society and Pacific Fisheries Biologists, as well as a Research Associate in Oceanography, Marine Life Research Group, Scripps Institution of Oceanography. He served on a number of advisory committees dealing with living marine resources research. John was a member of the Scientific and Statistical Committee of the Pacific Fisheries Management Council and was chairman of this committee at the time of his death. John was deeply involved with CalCOFI from its inception, and was a member of the CalCOFI Committee from 1957 to 1963 and from 1975 to the time of his death. Over the years, his influence and guidance helped mold CalCOFI policies and research activities.

John's numerous papers and publications concerning fisheries, population dynamics, and biological oceanography are a matter of record and need not be enumerated here.


John Radovich and sea survey equipment, 1950.

I knew John as a supervisor, a colleague, and—most of all—as a friend. He was a many-faceted individual. He had numerous interests, all of which he pursued with vigor. He was a yachtsman and a recreational fisherman. As a sports fan he was unsurpassed, especially with respect to USC. He was very competitive at tennis, both on and off the court, where he enthusiastically discussed previous or future matches. At conferences, workshops, or meetings, John's energy was very evident—be it during the meeting, while dining, in after-meeting scientific or philosophical discussions, or in recreational activities. His enthusiasm was infectious; what might start out as a rather routine discussion of a research project or proposal problem would end up with John eagerly suggesting possible approaches or solutions.

John was a gourmet, a cook, and really enjoyed both consuming and talking about fine foods and wines. He liked fine art and enjoyed viewing it. In fact, most activities in which John participated were approached with keen interest, warmth, and determination.

John Radovich—scientist, colleague, and friend—will remain deeply impressed in our memories. To his wife, Marie, and his sons, Bob and Don, I express our deep sympathy. It is with both sadness and honor that we dedicate this volume to him.

Herbert W. Frey

Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE FOR 1981

With deep regret the CalCOFI Committee reports the loss of committee member and long-time friend John Radovich of the California Department of Fish and Game. The committee respectfully dedicates this volume of the *Reports* to John, who gave himself unstintingly to CalCOFI during its formative years. We have asked new member Herbert Frey to write a memorial to John; it appears on the preceding page.

The year was one of continued evolution in California fisheries and marine science, and CalCOFI members were active in the scientific aspects of management as well as in studying the ecology of the California Current. A major CalCOFI cruise year (seven cruises) was completed with the R/V *David Starr Jordan* (NMFS) and the R/V *New Horizon* (SIO), featuring the introduction of a new anchovy biomass assessment technique necessitating nearly a thousand vertical plankton tows for anchovy eggs and early larvae. The "egg production method," as this new technique is called, also required sampling spawning females by trawl. This was accomplished by the combined efforts of the *Jordan* and a vessel chartered by the California Department of Fish and Game. Recognizing the potential widespread use of this new technique, the Coastal Division of the Southwest Fisheries Center is preparing a handbook on its use and interpretation. During the 1981 cruise year, the egg production method was calibrated with the larval census method, and the results were presented to the Pacific Fishery Management Council. This year the CalCOFI cruises added four 48-hour stations, whose objectives were to relate the larger-scale patterns of chlorophyll, productivity, and zooplankton biomass to physical structure and to compare patchiness of biological features on large and small scales.

The CalCOFI Conference this year was held at the University of Southern California's Idyllwild Conference Center and featured the symposium "Reminiscences of California Fishery Research and Management." Besides the six symposium papers reprinted in this volume, forty-three additional papers were presented. A round table discussion on the state of California fisheries was chaired by Herbert Frey of California Department of Fish and Game. A plenary session with the Eastern Pacific Oceanic Conference (EPOC) highlighted the last day of the meeting; CalCOFI Coordinator Reuben Lasker presented an overview of present and future CalCOFI activities to EPOC participants.

The CalCOFI committee has continued to pursue an introspective course in this year of shrinking budgets and greater demand for resources. The future of CalCOFI continues to be of concern. Thus letters were sent to a large list of "friends of CalCOFI" soliciting their comments on what they think the future activities of CalCOFI should be. Almost a hundred correspondents replied, and we are in the process of considering each suggestion.

In 1981 we published *CalCOFI Atlas No. 29: Teleconnections of 700 mb Height Anomalies for the Northern Hemisphere,* by Jerome Namias. No. 30 is having its final artist's review at this writing; it is *Vertical and Horizontal Distribution of Seasonal Mean Temperature, Salinity, Sigma-t, Stability, Dynamic Height, Oxygen and Oxygen Saturation, 1950-1978 in the California Current,* by Ronald Lynn, Kenneth Bliss, and Lawrence Eber of the Southwest Fisheries Center. Abraham Fleminger is the editor of the Atlas series.

The reviewers and editorial staff of this volume, particularly Julie Olfe, are to be congratulated for their excellent work.

The CalCOFI Committee
Izadore Barrett
Herbert Frey
Joseph Reid

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1980 AND 1981[1]

Total California landings for the pelagic wet fisheries in California increased in both 1980 and 1981 (Table 1). There are indications that the condition of the sardine population off the California coast may be improving. The 1981 year class of anchovies appears to be extremely weak. Pacific mackerel landings in 1981 were the highest since 1940.

Pacific Sardine

The moratorium on fishing sardines remained in effect during 1980 and 1981 because the spawning biomass was assessed to remain well below the 20,000 tons necessary to initiate a fishery.

The moratorium law does allow for the incidental catch of sardines (15% by weight tolerance) with mackerel and anchovies, but provides that sardines so caught can only be used for canning or reduction. The intent of these marketing restrictions, enacted in 1972, was to reduce local fishing pressures by cutting off sportfishermen's demand for sardines as dead bait. This demand sustained a lucrative market that insured continued fishing pressure even at extremely low biomass levels. The demand is now met with imported sardines. The incidental catch of sardines during 1980 and 1981 has given fishery managers some hope that a resurgence of the stock is still possible, and maybe even likely during the next decade.

Sardines caught incidental to mackerel fishing jumped from 17 tons in 1979 to 38 tons in 1980. Even though this figure dropped to 31 tons in 1981, the size composition of the catch during late 1981 indicates a minor resurgence is occurring. The majority of samples during this period were fish-of-the-year, and during the last 15-20 years it has been extremely rare to see 4-6-inch sardines. Optimism about resurgence is reinforced by reports from live-bait fishermen from San Diego to Port Hueneme that "fire crackers" (juvenile sardines) frequently occurred mixed with anchovy schools during the fall of 1981.

Whereas most of the incidental catches of these young sardines with mackerel and live bait have been small in quantity, both mackerel fishermen and live-bait fishermen reported sightings, sets, and dumping of "pure" schools of juvenile sardines. These reports increased in frequency during 1981, but most remain unconfirmed. Nevertheless, one mackerel purse-seine fisherman, who said he set and dumped a 50-ton school of sardines, provided the port sampler with approximately 10 pounds of 119-138-mm SL sardines.

Northern Anchovy

The anchovy landings for calendar year 1980 were 46,873 short tons statewide.

The year commenced with approximately 148,000 tons remaining on the 1979-80 season quota of 156,100 tons. Only the Monterey and Port Hueneme-based seiners had expended any fishing effort toward anchovies early in the season. The San Pedro-based boats did not participate in the reduction fishery until the season reopened in April after the February-March closure. During April and May fishing picked up significantly, with the wetfish fleet landing 2,000-3,000 tons per week. In the first week of June many undersize (less than 5 inches in total length) fish began to show up in landings, and a number of San Pedro boats were cited for illegal catches. Rather than risk further citations, the San Pedro fleet stopped fishing anchovies for the remainder of the season.

In Monterey, only 47 tons were landed after January 1, in part because of a lack of anchovy availability in Monterey Bay and because more effort was expended on the lucrative squid and herring fisheries.

Quotas for the 1980-81 reduction season were established by the U.S. Department of Commerce in July at 10,000 and 156,400 tons for the Northern and Southern Areas, respectively. The California Fish and Game Commission chose to take more restrictive measures when it established a 15,000-ton reduction processing quota for the season on August 28, 1980. This was revised upward to 80,000 tons on November 8.

The 1980-81 season opened on August 1 in the Northern Area, and the Monterey fleet began fishing at a brisk pace. By the end of October, 2,700 tons of anchovies had been landed. The fleet had difficulty finding legal-size fish in early November, and fishing stopped temporarily when one vessel was cited for having undersized fish. Good schools of legal-size anchovies were found again in mid-December, and fishing resumed at a slower pace until year's end, when some 3,200 tons had been landed.

The Southern Area season opened September 15, with Port Hueneme boats ready to fish. However, legal-size fish were difficult to find, and only 112 tons were landed through November. Meanwhile, San Pedro fishermen had not settled on an anchovy price with the canneries, and concentrated their efforts on mackerel and squid. In late November, when good legal-size schools of anchovies were found, a price agreement was reached and fishing began. At the year's end 13,700 tons had been landed in the South-

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[1] Includes review of the pelagic wet fisheries.

TABLE 1
Landings of Pelagic Wet Fishes in California in Short Tons in 1964-81

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

*Preliminary

ern Area. During 1980 the price for anchovy ranged from $49-$56 per ton in southern California.

Sampling indicated the age composition of anchovies taken by the Southern Area spring fishery was 94% 1979 and 1978 year-class fish, with very few older fish.

During 1980 an estimated 4,600 tons of anchovies were used for live bait and 1,300 tons for other nonreduction purposes.

Calendar year 1981 began with approximately 18,000 tons of the 1980-81 season quota having been taken.

Monterey area boats did not actively fish for anchovies until April. In early May effort toward anchovies stopped for the remainder of the season when market squid appeared in Monterey Bay, and this more lucrative fishery began.

The season closed with 4,736 tons (Table 2) having been landed in the Northern Area.

In the Southern Area the wetfish fleet began fishing immediately after the holiday season. With a price of $60.50 per ton, interest was high; some 27,000 tons of anchovies were landed prior to the February-March closure.

When the season resumed on April 1, fishing effort once again was brisk, even though the price had fallen to $55 per ton. Landings averaged 3,000 to 6,000 tons per week into May. As the landings approached the Southern Area reduction processing quota, on May 26 the California Fish and Game Commission authorized the California Department of Fish and Game to increase this quota to 90,000 tons, if necessary. This action was never taken, since landings dropped off dramatically the second week of June. Anchovy remained largely unavailable until the season closed June 30 with a total catch of 62,161 tons.

TABLE 2
Anchovy Landings for Reduction in the Southern and Northern Areas from 1966 to 1981, 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

*Preliminary

On July 1, the U.S. Department of Commerce established a reduction quota for the 1981-82 season at 408,100 tons. However, the Fish and Game Commission again set a lower reduction processing quota at 150,000 tons.

In the Northern Area the season opened on August 1, with Monterey fishermen showing little interest in fishing for anchovies. On September 22, two boats landed fish, and they were later joined by a third boat in November. Fishing was moderately successful, and by the end of December 3,500 tons had been landed.

In the Southern Area the 1981-82 season opened on September 15, but the wetfish fleet showed no interest in fishing for anchovies. Negotiations between fishermen, boat owners, and canneries over price and unloading rules for anchovy and mackerel continued from September through October in San Pedro; there was little fishing effort. A full strike idled the fleet for 3 weeks. It wasn't until November 7 that Port Hueneme boats began to fish for anchovy, and several weeks later they were joined by four San Pedro boats. The majority of the San Pedro fleet were unable to reach a price agreement for anchovy with their cannery, and concentrated on fishing for mackerel. By the end of December only 4,700 tons of anchovies had been landed in the Southern Area.

Sampling indicates Southern Area 1981 spring fishery landings comprised 43% 1980 year-class fish, 33% 1979 year-class fish, 22% 1978 year-class fish, with less than 3% older fish. The California Department of Fish and Game 1981 fall prerecruit sea survey indicated a weak 1981 year class.

The total reduction landings for 1981 statewide were 57,355 short tons. An estimated 6,000 tons were used for live bait and 800 tons for other nonreduction purposes. During 1981 the price for anchovy ranged from $60.50 to $46 per ton in southern California.

Jack Mackerel

In the 35 years since jack mackerel began supporting a viable fishery in 1947, it has been the dominant of the two "mackerels" in landings in all but 5 years. The years 1980 and 1981 represent the second and third year in a row that jack mackerel has contributed less than Pacific mackerel to California's "mackerel" fishery (Table 1).

During 1980, landings of jack mackerel were estimated at 22,225 tons. It dominated "mackerel" landings in only 4 months during the year, and these were the months when the California Department of Fish and Game imposed catch restrictions on Pacific mackerel. In 1981 this trend continued, with landings estimated at 15,513 tons and jack mackerel dominating the catch in only 3 months of the year.

It seems unlikely that the dominance of Pacific mackerel in recent years is related to any changes in marketability that may have caused a preference for this species by processors or fishermen. Both species are canned for human consumption and pet food production, and fishermen receive the same price for both: a price that jumped from $150 per ton in December 1979 to $190 per ton by the spring of 1981. The diminishing importance of jack mackerel recently is probably more closely associated with an extremely strong resurgence by the Pacific mackerel population, which has increased the availability of these fish to a level not evidenced since the early 1940s.

Pacific Mackerel

The year 1980 began with approximately 14,000 tons left on the 1979-80 season (October 1-September 30) quota of 25,000 tons, and with fishermen continuing to fish with no permit restrictions. On February 11, Pacific mackerel permits were amended for the purpose of slowing catch rates. Boatloads containing more than 18% by number Pacific mackerel (incidental catch tolerance) could only be possessed from 0001 hours Monday to 2400 hours Thursday and could not exceed 25 tons. The 1979-80 season was closed on May 15 when the landings reached 25,000 tons.

On May 22, 1980, the California Legislature passed Assembly Bill 2194. It established that future seasons would open on July 1 of each year, allowed the California Department of Fish and Game more flexibility in establishing interseason incidental catch tolerance levels, provided for a seasonal size limit of 10 inches fork length from January 1 to June 30, and dictated that within-season quota adjustments could only be made prior to February 1 of each year.

On July 1, the 1980-81 season opened with a 15,000-ton quota. This lower quota level was necessitated by an almost total lack of recruitment of 1-year-old fish (1979 year class). This cohort remained virtually unrepresented in samples, even though fishing was excellent during the first few months of the season. On September 19 the season was closed, with interseason restrictions allowing for 50% by number incidental catch tolerance for Pacific mackerel. Even though effort was substantially diverted from Pacific mackerel to jack mackerel for the remainder of the year, the estimated landings for 1980 of 32,349 tons are the highest annual landings since 1944.

Early in 1981 the California Department of Fish and Game, after a review of historical biomass estimates, aerial spotter relative abundance indices, and sport fishery catch-per-unit-of-effort, increased the 1980-81 season allowable catch from 15,000 to 20,000 tons, and on January 20, 1981, the "season" was reopened without permit restrictions. The additional 5,000 tons was caught in a little over a month, and on February 26 the interseason incidental catch tolerance was again set at 50% by number.

The 1981-82 season was opened on July 1, 1981, with a 33,000-ton quota amidst predictions that the 1980 year class would be the strongest since the resurgence of Pacific mackerel fishery during the mid-1970s. Although fishing was slow during the first few weeks, landings picked up dramatically in late July and fishing was excellent for the remainder of the year. Pacific mackerel were even readily available in Monterey Bay, where annual landings exceeded 1,000 tons for the first time since 1959.

By year's end, the "seasonal" catch was approaching 30,000 tons, despite a weak showing by the 1980 year class and almost no contribution by the 1979 year class. The 1978 year class was literally carrying the fishery, accounting for approximately 71%, 72%, and 46% of the tonnage landed in 1981, 1980, and 1979, respectively.

The estimated landings of 42,477 tons for 1981 are the largest since 1940, and mark the fourth straight year of an increase in catch under quota management.

Market Squid

After two excellent years the Monterey Squid fishery declined in 1980 to 6,900 tons. The fishery began in May but didn't peak until September. Over half of the annual catch was taken in August and September; normally the peak months are May and June.

The negotiated price to fishermen increased from $260 to $265 per ton for freezing, while the canning price remained $90 per ton. Santa Cruz Cannery at Moss Landing was unable to buy squid locally because fishermen would not sell their catch for the lower canning price. Consequently, the cannery trucked squid from Port Hueneme, as in previous years.

The southern California squid fishery continued to be primarily a late fall-early winter fishery during 1980, with 95% of the annual landings occurring during the months of January, February, November, and December. The estimated landings were 9,121 tons.

In 1981, the Monterey fishery rebounded, and landings increased to 13,900 tons, the second highest year on record. Thirty-five lampara boats participated in the fishery, also believed to be a record. Monterey undoubtedly had an excellent squid fishery in 1981; however, other factors must be mentioned.

Marine Patrol at Monterey found more squid in freezing plants than could be accounted for on fish receipts after the 1980 season. This case is far from going to trial, but all the squid buyers at Monterey are aware of the situation, and it is just possible that more accurate landing weights were reported this season. This may account for at least part of the record 1981 landings at Monterey. The fishery began in May and peaked in June. The fall fishery was also very good, with 6,000 tons taken from September to November. The negotiated price for freezing squid and canning increased in 1981 to $285 and $115 per ton, respectively.

Santa Cruz Cannery once again attempted to buy local squid. There were a few boats that would have fished for the cannery but were prevented from doing so by pressures exerted on them by buyers at Monterey. As the season progressed the cannery began to purchase local squid for freezing and canned at least 200 tons that it had acquired at the freezing price. Monterey Packing Company also canned some local squid this season.

Again the southern California fishery occurred primarily in early fall-late winter. The 1981 landings of 10,918 tons represent only the second time in history that southern California's landings were above 10,000 tons. The fishery seems to be continuing the very gradual growth trend that has characterized its history.

While the price for squid in Monterey has jumped considerably in recent years, prices at San Pedro have remained about the same. Generally, the ex-vessel price in southern California starts around $140-$160 per ton at the beginning of the season and declines during the season to as low as $40 per ton.

Pacific Herring

The 1979-80 and 1980-81 seasonal herring roe fishery landings were 6,430 tons and 5,826 tons, respectively. The annual herring landings encompass part of two fishing seasons and totaled a record high 7,969 tons in 1980, and then dropped to 6,198 tons in 1981. Landings declined in 1981 because of a strike by fishermen.

A system of quotas by area and gear was employed in previous seasons to regulate the fishery; it remains in effect. Quotas during the 1979-80 season were set for four areas: San Francisco Bay, 6,020 tons; Tomales and Bodega bays, 1,210 tons; Humboldt Bay, 50 tons; and Crescent City Harbor, 30 tons. The 1980-81 quota for San Francisco Bay was increased to 7,270 tons; quotas for other areas were not changed.

The roe fishery is limited to gill nets only in all areas except San Francisco Bay, where purse seines and lamparas also are used to take herring. The quotas are allocated by gear in order to eliminate competition between different gear types. Gill net boats were divided into two platoons that fished alternate weeks in order to alleviate congestion on the fishing grounds. Allocation of larger quotas and increased number of permits issued for the 1979-80 season (Table 3) and the 1980-81 season (Table 4) reflect the viability of this lucrative fishery.

When the quota for San Francisco Bay was increased in 1980, another platoon of gill net boats was allowed into the fishery. This experimental or "X" platoon is allowed to fish 3 weeks in December. The success of this early fishery was in doubt because fishermen were unsure if sufficient mature herring would be in San Francisco Bay in December. But December catch rates have been very good.

In the 1980 roe fishery, quotas were nearly taken or

TABLE 3
Permits Issued and Quotas by Gear and Area for the 1979-80 Herring Roe Fishery

Area	Gear	Permits	Quota (short tons)
San Francisco Bay	Gill net (odd)	109	1,500
	Gill net (even)	109	1,500
	Purse seine	27	1,500
	Lampara	27	1,500
Tomales and Bodega bays	Gill net (odd)	34	605
	Gill net (even)	34	605
	Beach seine	1	—
Humboldt Bay	Gill net	4	50
Crescent City	Gill net	3	30
Total		347	7,280

TABLE 4
Permits Issued and Quotas by Gear and Area for the 1980-81 Herring Roe Fishery

Area	Gear	Permits	Quota (short tons)
San Francisco Bay	Gill net (x)	100	1,250
	Gill net (even)	110	1,500
	Gill net (odd)	110	1,500
	Purse seine	23	1,500
	Lampara	29	1,500
Tomales and Bodega bays	Gill net (even)	34	600
	Gill net (odd)	34	600
	Beach seine	1	—
Humboldt Bay	Gill net	4	50
Crescent City	Gill net	3	30
Total		448	8,530

were exceeded in all areas except Tomales Bay, where only one-half the 1,210-ton quota was taken. The platoon system in Tomales Bay tends to keep the catch down because the off-week platoon is unable to fish during periods of peak spawning activity.

The 1981 roe fishery catch declined for two reasons. Herring spawned earlier in 1981, and by the time the regular season opened on January 5, over half the season's spawning had occurred. Fishing did not begin until January 16 because fishermen went on strike when herring prices were lowered. During the strike the season's largest spawn occurred simultaneously in Tomales and San Francisco bays. When fishing began after the strike, over 80% of the spawning activity had ended in San Francisco Bay, and only one large spawn occurred in Tomales Bay during the remainder of the season.

The herring spawning biomass was estimated in 1980 and 1981 for Tomales and San Francisco bays. The Tomales Bay population was estimated at 6,023 tons and 5,576 tons in 1980 and 1981. The decline in 1981 reflects normal variation around a long-term average population size of 6,000 tons. The San Francisco Bay population estimates have increased recently because of improved survey techniques, which now emphasize surveying subtidal rather than interdial spawning areas. San Francisco Bay spawning biomass estimates were 52,900 tons in 1980 and 65,400 tons in 1981.

The base price paid to fishermen peaked in 1980 at $2,000 per ton for 10% roe recovery and ranged from $1,000 to over $3,000. Gill net catches generally have a higher roe recovery than roundhaul landings.

Japanese consumers balked at retail prices for herring roe that reached $60 a pound in 1980, and the base price for herring was dropped to $1,200 per ton at the start of the 1980 season in December. When the regular season opened in January 1981, the base price for herring was dropped again to $600 per ton. Fishermen struck, and later settled on a base price of $800 per ton; this was eventually raised to $1,000 late in the season after catches declined. The roe fishery may never be as lucrative as it once was, but prices remain at a level where it is still a viable fishery, with an ex-vessel value of $6 million in 1981.

Groundfish

California commercial and recreational fishermen landed 45,309 tons of groundfish in 1980. Rockfish, Dover sole, and sablefish were the leading species in the catch, with respective landings of 16,868 tons, 8,538 tons, and 4,628 tons.

The trawler fleet landed 36,509 tons, the majority of the catch. Of this total, midwater trawlers landed 713 tons of Pacific whiting and 4,078 tons of widow rockfish. Fishermen using line, trap, and gill nets landed an estimated 5,500 tons of groundfish. This catch was predominated by rockfish and sablefish. Recreational fishermen caught an estimated total of 3,300 tons of groundfish, most of which were rockfish.

The 1980 landings were the result of increased effort by a larger fleet. Significant events in 1980 were the further development of the midwater trawl fishery and the decline in the trap fishery for sablefish.

Groundfish landings continued to increase in 1981. Landings by commercial and recreational fishermen were 48,797 tons. The major species in the catch were several species of rockfish (20,710 tons), Dover sole (10,143 tons), and sablefish (7,283 tons). Other flounders, lingcod, and Pacific whiting were also important in the catch.

The trawler fleet increased to 193 vessels; the additions were new, larger, more mobile vessels, and many were from Oregon or Washington.

The midwater trawl fishery for widow rockfish expanded in 1981. The fleet extended its operations from off Eureka to the San Francisco area. The annual catch of widow rockfish was 4,129 tons. The Pacific whiting catch declined to 2,674 tons concurrent with the increase in widow rockfish.

Sablefish landings increased to 7,283 tons, as catches by all gears increased.

The increasing trend of the groundfish fishery continued. Innovative harvesting, processing, and marketing technology contributed to its development.

Groundfish continued to be important to recreational fishermen. Rockfish and lingcod were the major species in the recreational catch.

Dungeness Crab

Statewide landings of Dungeness crab *(Cancer magister)* totalled 13.6 million pounds during the 1979-80 season, compared to 8.3 million pounds landed during the 1978-79 season.

Landings for Crescent City, Trinidad, Eureka, and Fort Bragg were 5.7, 1.1, 5.5, and 0.7 million pounds, respectively. The northern California season opened December 1, 1979, but price disputes slowed effort until December 13, when a price of 50¢ per pound was agreed upon. On February 5, 1980, the price jumped to 75¢ and remained at that level the rest of the season. Crab condition at the start of the season was good, and 85% of the season's catch came across the docks by the end of January. Only 46,000 pounds were landed during the season extension from July 16 to August 31. Approximately 380 vessels engaged in the north coast fishery.

San Francisco area landings totalled 633,000 pounds. The 1979-80 season opened on the second Tuesday in November, and price was settled the same day at $1.05 per pound. In December the price dropped to 60¢ but climbed back to $1.15 by the end of the season. Only 2,700 pounds were landed during the season extension from July 1 to 31. The season extension excluded the Bodega Bay area where soft and filling crabs were dominant during May and June.

Landings in the Monterey and Morro Bay areas totalled only 11,500 pounds.

The statewide Dungeness crab landings during the 1980-81 season totalled 12.0 million pounds.

In northern California, total landings for Crescent City, Trinidad, Eureka, and Fort Bragg were 6.4, 0.8, 3.3, and 1.0 million pounds, respectively. The season opened December 1, but gear was not set until December 2, when fishermen agreed to 59¢ per pound. Exceptionally good weather and open markets contributed to record landings of 8.2 million pounds during December. The previous high for any monthly period was 7.3 million pounds landed during December 1977. The price jumped to 75¢ in January, $1.00 in February, and leveled out at $1.25 in March. Only 1,600 pounds were landed during the season extension from July 15 to August 31. Approximately 400 boats participated in the fishery.

The central California fishery opened the second Tuesday of November, and fishermen received $1.10 per pound for crab. The price dropped to 68¢ when the northern California season opened, but reached $1.30 in February and remained there to the end of the season. Total landings for the San Francisco area were 515,000 pounds. Only 6,000 pounds were landed in the Monterey-Morro Bay areas.

Pelagic Shark and Swordfish

The number of vessels engaged in the drift gill net fishery for shark grew rapidly in 1980 to 116 from 30-40 the previous year. As a result, total shark landings in southern California climbed from 2.3 million pounds in 1979 to 3.2 million pounds in 1980. Peak shark catches occurred in August and September.

The composition of the catch was 58% thresher shark, 10% swordfish, 3% bonito shark, and 29% blue shark. The blue shark catch prompted most drift gill netters to increase mesh size of their nets: some to as large as 20 inches stretched mesh, from an initial size of only 8 inches. The most popular sizes appear to be 14 and 16 inches.

Harpoon swordfish landings reached 1.2 million pounds in 1980, about one-third higher than the previous 10-year average.

Harpoon success, which is associated with the "finning" behavior of swordfish, was greatest during the months of July through November, with peak success in September.

Gill net swordfish landings occurred somewhat later, with peak success in November. Prior to the drift gill net fishery, it had been assumed that when swordfish were no longer seen "finning," they had left local waters. It now appears that swordfish may remain in local waters in large numbers as much as 2 months longer than was previously believed.

In September 1980 California Assembly Bill 2564 passed, restricting the number of drift gill net permits that could be issued. By the end of the 1981 fishing season 150 vessels had participated in this fishery.

Shark landings declined in 1981. The southern California season total amounted to 1.9 million pounds. The season looked promising in April through June, with a good showing of fish; however, beginning in July catches slowed to the point where most boats discontinued fishing.

Very few fish "finned" for the harpoon fleet in

1981. There were only 2,200 swordfish harpooned during the entire season. If the harpoon fleet's success was the only indicator of seasonal abundance of swordfish in local waters, then one might conclude that few fish migrated into California waters in 1981. However, beginning in September, the drift gill net fleet began catching subsurface swordfish in large numbers. By the end of October swordfish landings by drift gill nets had exceeded the entire season harpoon catch by a factor of two. November, which normally represents the peak in gill net landings, would likely have doubled the catch again, but the Director of the Department of Fish and Game closed the season in response to a quota established by Assembly Bill 2564. This quota is based upon the success of the harpoon fishery and not upon the condition of the swordfish resource.

Southern California Recreational Fishery

Commercial Passenger Fishing Vessel (CPFV) anglers in southern California enjoyed good fishing for surface species during 1980. Pacific bonito contributed heavily to landings, with over 561,000 taken. The moderately strong 1979 year class made up most of the catch and enabled bonito landings to reach a 5-year high. Fishing for kelp bass and sand bass improved over the previous 5-year average (498,000), with 585,000 landed. Improved sand bass catches were responsible for most of the increase; kelp bass catches remained relatively stable. Pacific mackerel landings continued to increase from a low point of 51,000 in 1976. By year's end, they had reached 1,315,000 because of large landings of 1976 and 1978 year-class fish.

Fishing for albacore improved from the previous year, with 21,000 landed—double the 1979 catch. Albacore catches were depressed because of warm water conditions, the same phenomenon that accounted for good fishing on other surface species.

Catches of two species with low population levels continued to decline. California barracuda landings tumbled to a 4-year low of 28,000 fish. White seabass catches were also depressed, with 1,000 landed. Only 1978 produced fewer fish for CPFV anglers. Rockfish catches also were down in 1980, with 3,300,000 landed, well below the previous year's mean of 3,700,000.

Throughout the year the California Department of Fish and Game, under a contract with the National Marine Fisheries Service, conducted the California segment of the National Marine Fisheries Statistics Survey. The study was designed to estimate catch and effort for ocean anglers. Preliminary estimates of angler effort showed there were between 8.18 and 9.08 million angler-trips in southern California during 1980. Catch data were not available.

Partyboat anglers continued to do well as 1981 turned into a near repeat of 1980. Surface fish were still abundant, and anglers' catches reflected that fact. Most 1981 partyboat data have been processed and are available for analysis, but information for several months is still unprocessed and not available in a usable form. Preliminary data from CPFV showed bonito landings were down 20% from the previous year but were still expected to reach 454,000. Fishing for kelp bass and sand bass improved by 21%, with the catch expected to reach 702,000 fish. The entire increase can be attributed to improved kelp bass landings. Landings of Pacific mackerel declined significantly, with only 1,004,000 fish taken, 21% below the 1980 take. Lack of a strong incoming year class to replace the 1976 and 1978 year classes is responsible for this.

California halibut catches doubled from the previous year, with over 13,000 expected to have been landed. Strict enforcement of the 22" size limit is apparently adding substantially to catches in the fishery. Landings of California barracuda increased dramatically, with the catch projected to reach 77,000 for the year. Increased catches can be attributed to an influx of adult fish from Mexico, because of warm water, rather than to an increase in the local population. White seabass landings also benefited from warm water, with an anticipated 1,600 fish taken, up 60% from the previous year.

Albacore fishing improved slightly, with approximately 22,000 fish landed. The season was short; most fish were taken during July and August. Anglers who sought rockfishes were rewarded with improved catches. The 1981 catch should approach the previous 5-year mean of 3.7 million fish.

Marlin fishing off southern California was exceptionally good during 1981. The season started the earliest on record (June 27) and ran through November. In total, 1,540 marlin were taken, with the month of September producing 790 fish, a normal season's catch under average conditions. Offshore anglers also were rewarded with exceptional bigeye tuna fishing during the summer. Although the number of fish landed was small (approximately 500), their large size (50 to 250 pounds) made most fishermen happy.

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THE NORTHERN ANCHOVY SPAWNING BIOMASS FOR THE 1981-82 CALIFORNIA FISHING SEASON

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ABSTRACT

The biomass of the central subpopulation of the northern anchovy during the 1981 spawning season is estimated to be 2,803,000 short tons, based on the larva census method. Anchovy stock was surveyed over its geographic range on four cruises during the six-month period from January to June. The anchovy larvae in the plankton samples were sorted, counted, and measured, and the data were summarized to form larva census information for estimating the anchovy spawning biomass. The resulting 1981 estimate of 2,803,000 tons is approximately 58 percent greater than the 1980 estimate of 1,775,000 tons. The optimum yield for the central subpopulation in the 1981-82 fishing season is 601,000 short tons, as specified by the yield formula given in the Pacific Fishery Management Council's Northern Anchovy Fishery Management Plan. Within the U.S. 200-mile Fishery Conservation Zone, the optimum yield is 420,700 tons.

RESUMEN

La biomasa de la subpoblación de *Engraulis mordax* durante la temporada del desove en 1981 se calculó ser de 2,803,000 toneladas cortas, basado en el método de censo de larvas. La existencia de anchoveta fue reconocida durante cuatro cruceros por toda su extensión geográfica, durante un período de seis meses entre enero y junio. Las larvas de anchoveta en las muestras de plancton fueron separadas, contadas, y medidas, y los datos fueron resumidos para formar la información del censo de larvas para estimar la biomasa de desove de anchovetas. La estimación resultante para 1981 de 2,803,000 toneladas es aproximadamente el 58 por ciento más que la de 1980, de 1,775,000 toneladas. El rendimiento óptimo para la subpoblación central durante la temporada de pesca en 1981-82 es 601,000 toneladas cortas, especificado por la fórmula de rendimiento presentada por el Pacific Fishery Management Council en su Plan de Administración de la Pesquería de Anchoveta del Norte. Dentro de las 200 millas que abarca la Zona de Conservación de la Pesquería de los EE.UU., el rendimiento óptimo es 420,700 toneladas.

INTRODUCTION

The harvest plan for northern anchovy, *Engraulis mordax,* in California is specified in the Pacific Fishery Management Council's (PFMC) Northern Anchovy Fishery Management Plan (FMP), first implemented in 1978. The optimum yield for the U.S. fishing season is set according to the optimum yield formula given in the FMP and based on the current estimate of the spawning biomass. The purpose of this annual report, the fourth in a series, is to document the 1981 estimate of the spawning biomass of northern anchovy for the 1981-82 California fishing season. The 1981 biomass estimate is derived by the larva census procedure first developed by Smith (1972) and documented in Appendix I of the Anchovy FMP (PFMC 1978). Stauffer and Parker (1980) later developed the calibration for an annual larva census from the six-month winter-spring larva census. The 1981 anchovy larva data were collected on four cruises during winter and spring in the 1981 California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larva survey. This survey was directed by the National Marine Fisheries Service, Southwest Fisheries Center (SWFC). Other agencies cooperating in the multicruise survey were Scripps Institution of Oceanography (SIO), Instituto Nacional de Pesca, Mexico (INP), and National Ocean Survey (NOS). Samples from Mexican waters were taken by permission of the Secretaria de Relaciones Exteriores under diplomatic note numbers 315052, 315576, 315611, 315984, and 316422.

LARVA SURVEY

The 1981 egg and larva survey of the central subpopulation of the northern anchovy was part of the 1981 triennial CalCOFI survey of the California Current region. The 1981 CalCOFI survey comprised six multiship cruises and sampled CalCOFI stations from line 60 at 38°N off San Francisco to line 137 at 25°N off central Baja California, Mexico, out to station 90—160 to 240 nautical miles offshore (Figure 1). To survey and estimate the spawning biomass of the central subpopulation of northern anchovies by July 1, 1981, as required by the FMP, we processed and analyzed plankton samples from only eight of the twenty-four CalCOFI regions (4, 5, 7, 8, 9, 11, 13,

[Manuscript received February 12, 1982.]

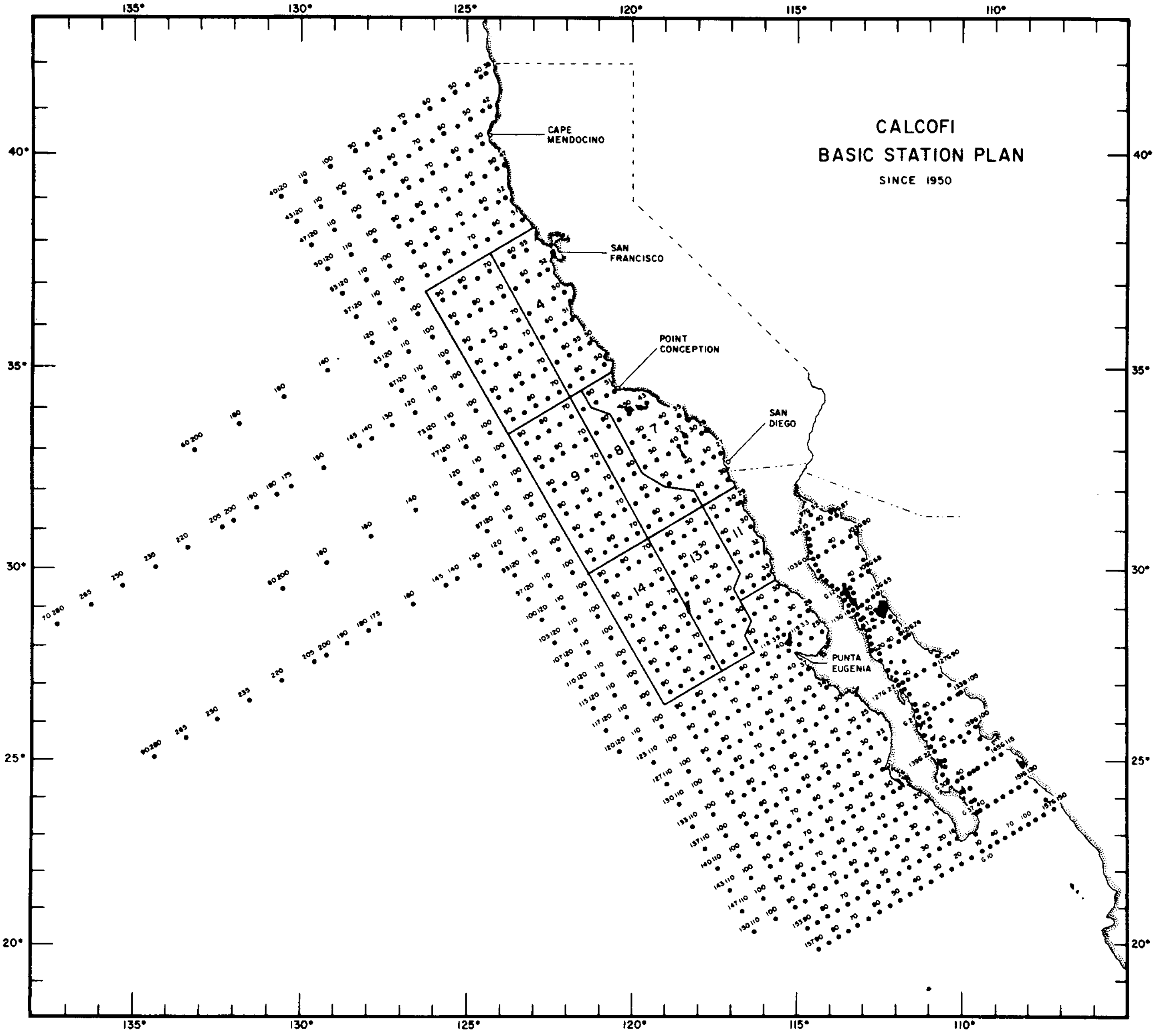

Figure 1. CalCOFI basic station plan. The geographic range of the central subpopulation of northern anchovy is within the eight numbered regions.

and 14) and from the four cruises conducted in the winter and spring. Approximately 130 CalCOFI stations were routinely occupied per cruise within these eight regions. As outlined in Figure 1, these geographic regions coincide with the range of the central subpopulation (Vrooman et al. 1980). The four winter and spring cruises covered the major portion of the anchovy spawning season (Stauffer and Parker 1980).

The anchovy survey cruises were scheduled at approximately six-week intervals beginning in early January (Table 1). Each cruise was about four weeks long. The January cruise was conducted over CalCOFI lines 110 through 60 by the R/V *David Starr Jordan* from January 7 to February 1. The second cruise,

TABLE 1
Schedule of the 1981 Egg and Larva Cruises

Cruise number	Cruise month	Survey quarter	Vessel name	Date	CalCOFI area
8101	January	Winter	*Jordan*	1/7-2/1	Lines 110 to 60
8102	February	Winter	(1) *Jordan*	2/12-3/10	Lines 110 to 60 within regions 4,7,8,11, and 13
			(2) *New Horizon*	2/12-3/8	Lines 60 to 110 within regions 5,9, and 14; lines 113 to 130
8104	April	Spring	(1) *Jordan*	3/31-4/27	Lines 110 to 100 in region 11; lines 97 to 60
			(2) *New Horizon*	4/7-4/28	Lines 100 to 133
8105	May	Spring	(1) *Jordan*	5/18-6/13	Lines 90 to 110
			(2) *New Horizon*	5/19-6/8	Lines 87 to 60

8102, was run with two ships, *Jordan* and R/V *New Horizon,* beginning February 12 and finishing March 10. The cruise plan for the *Jordan* included an egg survey of CalCOFI regions 4, 7, 8, 11, and 13 to estimate the anchovy biomass by the egg production method (Parker 1980). Stormy weather in February prevented the ship from surveying the stations in region 9 during cruise 8102. The first cruise of the spring quarter, 8104, began March 31 and ended April 28. The *Jordan,* conducting a second egg survey in regions 7, 8, and 11, occupied inshore stations on lines 110 to 100 and all routine stations on lines 97 to 60. The *New Horizon* surveyed the southern lines beginning with line 100, duplicating occupancy of region 11. The last cruise, 8105, began May 18 and ended June 13. The *Jordan* surveyed from lines 90 to 110, the *New Horizon* from lines 87 to 60.

The plankton samples were collected and processed with methods identical to the 1979 and 1980 surveys reported by Stauffer (1980) and Stauffer and Picquelle (1981). The plankton was sampled with a CalCOFI bongo net towed at a 45° angle from a maximum depth of 200 meters (Smith and Richardson 1977). The plankton samples from the starboard half of the bongo net were sorted. All of the plankton in a sample was sorted if the station was beyond 200 miles from shore or if the plankton volume was less than 26 ml; otherwise, a 50 percent aliquot of the sample was sorted. In all, 534 samples were collected and processed. Nineteen stations in region 11 were occupied twice during cruise 8104. The larva counts for these paired samples were averaged for the cruise. Because cruise 8105 ended June 13, time was too short to sort all the plankton samples for the July 1 deadline. Therefore, samples were not sorted for the stations in region 5 offshore of central California—a region with few anchovy larvae in May in the past. The larva data were entered into the computerized CalCOFI data management system where the data are edited, filed, processed, and summarized into larva census values for winter and spring quarters.

SURVEY RESULTS

The geographic distribution of anchovy larvae in 1981 has expanded somewhat farther offshore compared to the past three years. The number of larvae per station was low in the January cruise. The number of larvae per station in the February-March cruise increased tenfold over the January samples. The peak occurred in the April cruise, with the number of larvae 50 percent greater than in the February-March cruise. By May-June the number of larvae per station had decreased to a level similar to that in January. As shown in Figure 2, larvae in northern regions 4 and 5 were most abundant in the winter quarter cruises. Off Baja California, anchovy larvae were most abundant during March and April. Few larvae were taken there in the January and June cruises. The Southern California Bight, represented by region 7, contained the largest portion of the anchovy larvae. For the first time since 1975, a number of anchovy larvae were found in offshore region 9 during the April cruise. Unfortunately, stations in region 9 were not occupied during the February-March cruise. The large size of the larvae in region 9 suggests that the larvae were relatively old and were probably carried offshore by the California Current and upwelling plumes arising off central California. The first major upwelling of the 1981 season occurred from March 26 to April 9 off central and southern California (A. Bakun, Pacific Environmental Group, pers. comm.).

Of the 255 stations occupied in the winter quarter, 56 percent, or 143 contained anchovy larvae. For the spring quarter, 51 percent, or 134 out of 260 stations contained anchovy larvae. The larva census compiled for the eight regions of the central subpopulations is $11{,}127.4 \times 10^9$ larvae for the winter quarter and $14{,}164.3 \times 10^9$ larvae for the spring quarter. The combined winter-spring larva census, L_{WS}, is $25{,}921.7 \times 10^9$ larvae (Table 2).

TABLE 2
Estimated Larval Abundance (10^{12} larvae) for the Central Subpopulation from Appendix I, Table 2, FMP

Year	Winter	Spring	Winter & spring	Annual	Spawner biomass in millions of short tons
1951	.298	.690	.988	1.841	.180
1952	.407	.457	.864	1.600	.156
1953	1.210	.373	1.583	5.208	.510
1954	4.469	.988	5.457	7.838	.768
1955	5.588	1.709	7.297	8.618	.845
1956	1.911	1.206	3.117	4.944	.485
1957	5.954	4.308	10.262	11.960	1.172
1958	8.114	5.236	13.350	15.087	1.479
1959	6.341	8.155	14.496	15.440	1.514
1960	7.552	7.547	15.099	15.713	1.540
1961	.992	6.714	7.706	11.827	1.159
1962	4.814	23.567	28.381	30.478	2.986
1963	17.377	24.818	42.195	43.407	4.254
1964	8.941	14.383	23.324	29.599	2.901
1965	19.155	22.690	41.845	47.540	4.659
1966	15.103	15.865	30.968	36.452	3.572
1969	19.756	6.538	26.294	30.594	2.998
1972	8.213	14.335	22.548	28.373	2.781
1975	29.754	4.071	33.825	36.768	3.603
1978	6.704	4.184	10.888	13.306	1.304
1979	6.546	9.124	15.670	17.580	1.723[1]
1980	—	—	—	18.110	1.775[2]
1981	11.127	14.164	25.292	28.603	2.803[3]

Spawner biomass in tons is calculated from annual larvae abundance; spawner biomass = $9.8 \times 10^{-8} \times$ larvae abundance, from Smith 1972.
[1] Stauffer and Parker 1980
[2] Stauffer 1980
[3] Stauffer and Picquelle 1981.

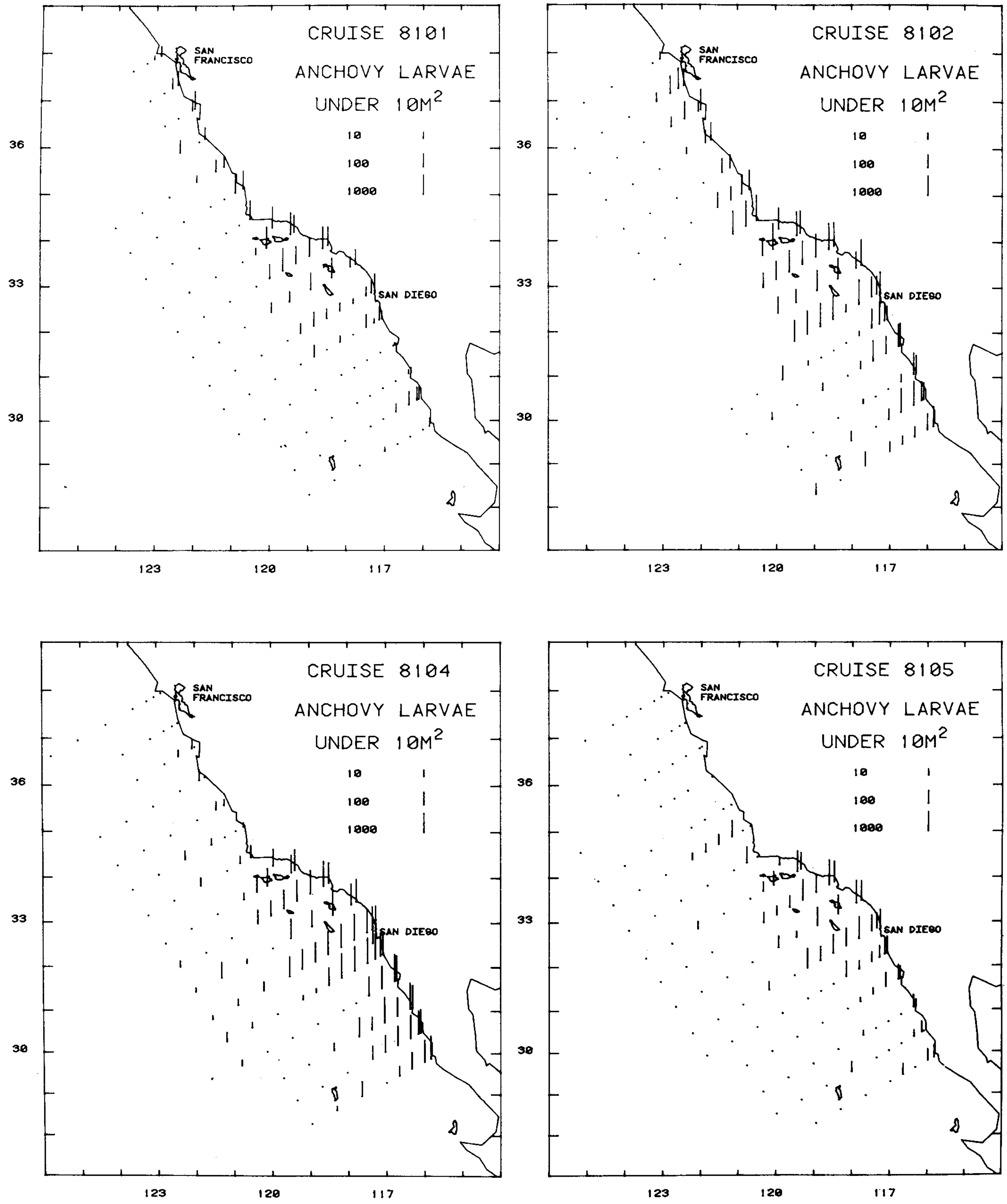

Figure 2. Occupied stations for the 1981 cruises, and geographic distribution of anchovy larvae for the central subpopulation in the winter and spring. The vertical bars represent the logarithm of the number of larvae under 10 m^2 of sea surface.

BIOMASS ESTIMATE

The larva census estimates of anchovy biomass for the years 1951–69 developed by Smith (1972) are based on annual larva census values. Stauffer and Parker (1980) expanded the winter-spring larva census to an annual larva census, L, with the regression equation,

$$L = 1.062\, L_{WS} + 1{,}743 \times 10^{9}.$$

The equation is based on larva census data for 1951–75 summarized by CalCOFI regions as outlined in Figure 1. From this equation, the 1981 annual larva census is $28{,}602.7 \times 10^{9}$ larvae. The estimate of the 1981 spawning biomass, with Smith's (1972) equation,

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

is 2,803,000 short tons. This is a 58 percent increase over the 1980 estimate of 1,775,000 tons, and is the third consecutive year with an increase in the biomass estimate since the 1978 low of 1,304,000 tons (Figure 3). The 1981 larva census values for the winter and spring quarters and the resulting biomass estimate are nearly identical to survey results for 1964 and, more recently, 1972.

OPTIMUM YIELD

The optimum yield for the 1981-82 fishing season for the estimated biomass of 2,803,000 tons is 601,000 tons based on the formula specified in the Northern Anchovy FMP (PFMC 1978). The optimum yield in the U.S. Fishery Conservation Zone (FCZ) is 70 percent or 420,700 short tons, The U.S. capacity to process anchovies, including live bait, is estimated to be 371,885 tons. The difference of 48,815 tons is available to joint ventures or to foreign fisheries within the U.S. FCZ as TALFF (Total Allowable Level of Foreign Fishing). The 1981–82 quota for the U.S. commercial fishery was set at 359,285 tons by National Marine Fisheries Service. However, the California Fish and Game Commission established a 150,000 short-ton limit on the amount of northern anchovy that could be processed by shore-based reduction plants in California because of the discrepancy between the 1980 estimates of biomass using the larva census method and the newly developed egg production method (Stauffer and Picquelle 1981).

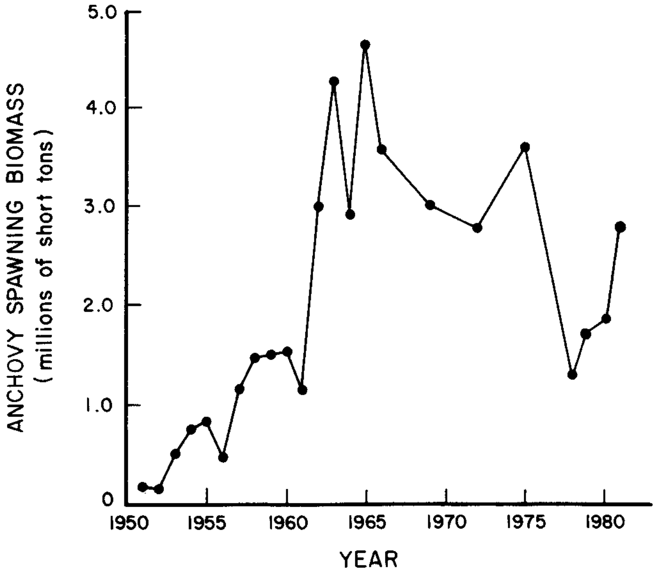

Figure 3. Estimated spawning biomass for the central subpopulation of northern anchovies, 1951–81.

ACKNOWLEDGMENTS

We thank many people for their efforts in collecting and processing the CalCOFI egg and larva data used in this estimation. They include Scripps Institution of Oceanography (SIO) plankton sorting group,Southwest Fisheries Center CalCOFI group, and crews of NOAA Ship R/V *David Starr Jordan* and SIO R/V *New Horizon*. We could not have accomplished this task without everyone's full cooperation and extra effort.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

IDYLLWILD, CALIFORNIA

OCTOBER 27, 1981

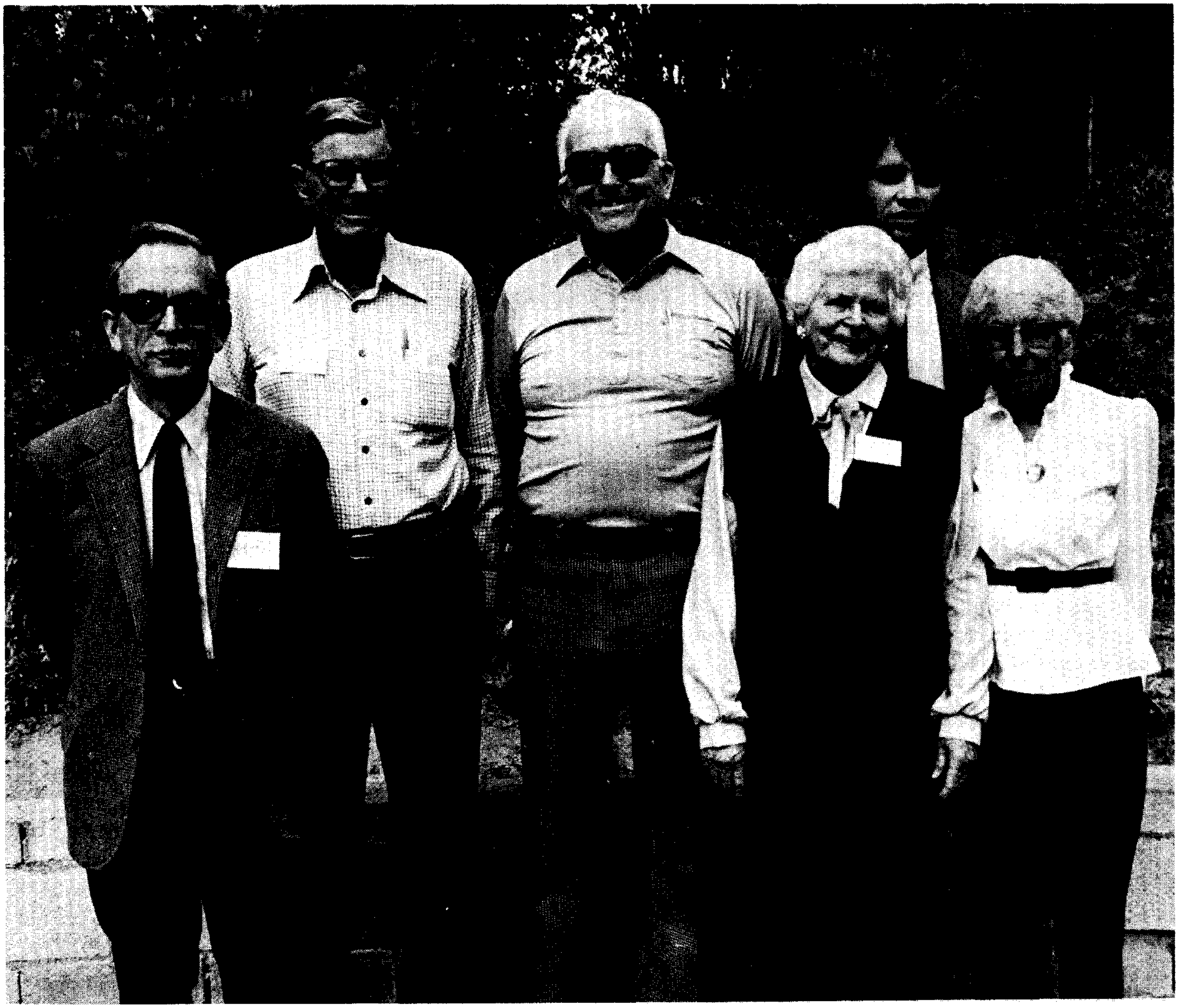
REMINISCENCES OF CALIFORNIA FISHERY RESEARCH AND MANAGEMENT

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) as an organized program is a little over thirty years old. Yet the groundwork for CalCOFI was laid many years earlier by a group of dedicated fishery biologists and oceanographers in the California Department of Fish and Game, the Scripps Institution of Oceanography, and the former Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service. The desire to know how CalCOFI came to be the organization it is and what role it has played in the fisheries science of California prompted the CalCOFI Committee to invite a select group of people to review this history in a symposium called "Reminiscences of California Fishery Research and Management." The symposium was convened by CalCOFI Coordinator Reuben Lasker.

Speaking at the symposium were Frances Clark, former director of the marine division of California Department of Fish and Game; Richard Croker, former chief of the marine resources branch of California Department of Fish and Game; John Baxter, regional manager of the Marine Resources Region of the California Department of Fish and Game; Patricia Powell, former California Department of Fish and Game librarian; and Arthur McEvoy of Northwestern University, who is studying the history of California fisheries. Another speaker, and also the chairman of the proceedings, was Joseph Reid, oceanographer and director of the Marine Life Research Group at the Scripps Institution of Oceanography.

The CalCOFI Committee recorded the talks given at this symposium; the tapes were transcribed by the Regional Oral History Office of the University of California, Berkeley. Each paper was edited and annotated by the speaker and appears here in its amended version. Arthur McEvoy chose to write and submit his as a formal paper. The University of California's Institute of Marine Resources (IMR), with a grant from the Van Camp Foundation, provided the funds for transcribing, editing, and typing the symposium papers. We thank Fred Spiess, director of IMR, for his help in this regard. We received permission from John Wiley & Sons, publishers, to reprint the excellent 1981 article by John Radovich, "The Collapse of the California Sardine Fishery. What Have We Learned?" John's insight and knowledge of the science and politics of this fishery add immeasurably to the historical usefulness of this symposium collection.

The CalCOFI Committee



Participants in the 1981 Symposium of the CalCOFI Conference are, from left to right, Joseph Reid, Richard Croker, John Baxter, Patricia Powell, Arthur McEvoy, and Frances Clark.

CALIFORNIA MARINE FISHERIES INVESTIGATIONS, 1914–1939

FRANCES N. CLARK

These are exciting times. But also there is much in the past, and I want to go back about sixty years. To you that is probably a long time; it's just yesterday to me.

Fish and game studies in California started in 1914. At that time, there was a Fish Commission composed of five men who decided that there must be a marine fisheries investigation. So they organized a Department of Commercial Fisheries and named Norman Bishop Scofield its administrator. The responsibilities of this investigation were to gather statistics, to study fishing methods, fish processing and handling, and to learn about fishes, their habits, how they migrated, where they appeared on the fishing grounds, when they spawned—just the little minor details. We're still struggling!

Norman Bishop Scofield, to me, was the father of commercial fisheries investigation in California. He was born in 1869 in the Midwest and had a bachelor's degree in biology before he came to California about 1890. He was known throughout the years as N.B., so from now on he probably will be N.B. when I refer to him.

When N.B. came to California he registered at Stanford as a graduate student, and in 1895 was awarded a master's degree with Stanford's first graduating class. While he was a student at Stanford, he studied some of the San Francisco Bay and central California fisheries under Dr. Charles Henry Gilbert. You people probably know that Gilbert was the man who determined, in general, that Pacific Coast salmon return to spawn in the streams in which they hatched.

Because of N.B.'s interests and his work as a student, he was employed by the Department of Fish and Game from 1897 to 1899. Then he dropped out of the picture for several years. He was in the East doing some business; I don't know what. But California seemed to be his love, and he came back and was employed again by the Department of Fish and Game from 1908 until he retired in 1939.

He was a man who had the imagination to know what needed to be done, and the ability to find out how to do it and to provide the means for doing it. He took over the direction of this new fisheries investigation in 1915, supposedly to study statistics. You can't study statistics without information and figures. So in 1915 a law was passed that required fish buyers to issue receipts, and that was the beginning of our figures on the catch.

By 1917 N.B. discovered that you can't do fisheries investigations without money. California at that time sold licenses for commercial fishing, for sport fishing and for hunting. That was the department's revenue. But more money was needed, so a law was passed requiring the dealers to pay two-and-a-half cents per pound for all fish they bought. This, plus the sale of fishing licenses, was the sole support for the Department of Fish and Game for quite a number of years. Nothing came from the general fund. As the years went by, the price per pound was increased, and more money came in.

By this time Scofield had gotten things organized. There was a way of getting information, and there was some money, so he looked around to find somebody to direct this new investigation. He selected William Francis Thompson, who is known to all of us for his work throughout the years. He had done some studies on the halibut in Washington and in the northern area, and Scofield admired his work. So Thompson was hired and started at Monterey. He stayed there for a year or two and then decided that the center of California fisheries was going to be in southern California.

Thompson employed William Lancelot Scofield, known as Lance Scofield to all of us, to study sardines and other fisheries in the Monterey area. Thompson transferred to southern California, where he employed Elmer Higgins and a few other people and started the work in that area. Thompson and Higgins used patrol boats to try to explore some of the waters off southern California. Thompson mentioned in some of his laboratory notes that they had taken eggs that he thought might be sardines. But his chief interest in this exploration was to try to learn about albacore. At that time the albacore canning industry was expanding rapidly.

By 1918 Thompson and Scofield realized that the information they were getting from the dealers and their receipts was not adequate. They needed more information for a fisheries investigation. So they set up what we have called the pink-ticket system. It required three receipts: one to the fisherman; a pink copy to Fish and Game—that's the origin of the term "pink ticket"; and a third copy kept by the dealers.

Again, I want to give a little credit to another man, H.B. Nidever. He was working for patrol, first in the San Francisco area. There he had worked with N.B. when N.B. was first employed. Nidever had tremendous admiration for the biologists. In fact, he had us up on a pedestal, which was not justified. But he had the ability to work with people, and when he went out to arrest the fishermen, he could almost make the fishermen like him for doing it!

So when Nidever and N.B. felt that we needed this detailed information, they drew up the plan for the pink-ticket system, which is the basis for much of the detail that we have from our fisheries. Thus things were under way, going nicely. Higgins and Thompson were working. They also employed students for a short time during the summer vacation and occasionally for longer terms.

By 1920, Oscar Elton Sette was working with Thompson, also Harlan Holmes, Tage Scogsberg, whom some of you probably know as the man who was with Hopkins Marine Station doing biological work in Monterey Bay for a number of years, and Lance Scofield. Thompson realized then that they must have permanent quarters, and the plan for the California State Fisheries Laboratory at Terminal Island was drawn up. The building was constructed and subsequently occupied in November 1921.

Things were going along nicely, but by 1922 there were hard times. The depression that followed the First World War was with us. At the same time, the cost of living was rising rapidly. Doesn't that sound familiar? But the price of fish dropped rapidly. The revenue to the California Department of Fish and Game was falling off. The fishermen weren't fishing; they weren't being paid; and yet the cost of living was going up. The biologists just couldn't afford to work: they weren't paid enough.

At the same time, the federal government was paying its biologists more than the California Department of Fish and Game was paying. So things fell off. Sette and Higgins left for the Atlantic Coast to work for the federal government; Holmes went to Seattle to work for the federal government; and there were very few working at the laboratory. That led Thompson and N.B. to realize that California was the training ground for marine fisheries students. They took the matter up with the federal government and got some agreement. It was decided that the government would pay part of the salary of a few people. I don't know how it was paid, how much it was, whether it was a lump sum to the Department of Fish and Game, or whether it was a part of individual salaries. But I do know that George Rounsefell and Bill Herrington worked a year or two and then went back into federal government.

Then we carry on to mid-1920, when, because the economy was looking up, money came in and the program was going along nicely. In 1924, the North Pacific Fisheries Treaty with Japan was signed. Then in 1926 the United States and Mexico formed an International Fishing Commission. I am sure that this was largely the work of N.B. Scofield, who was made the commission's director. They started an investigation, and several people were employed.

In 1926 Thompson went to Seattle and took over the work for the fisheries investigation with the United States and Japan. Lance Scofield, who had been working at Monterey, was transferred to southern California and became director of the work in California.

By 1928 things were expanding. Julie Phillips was employed, as were Dick Croker, Don Fry, and Harry Godsil. They used the patrol boats to investigate the local waters and the populations of sardine, albacore, and other fish along the coast.

The commission with Mexico did not prove successful and had faded away by 1929. Some of its staff were transferred to the California Department of Fish and Game. Among them were Bert Walford and Geraldine Conner. Walford worked with different fisheries and did quite a bit with the barracuda. Geraldine Conner had been a secretary to N.B. for many years, and had been the secretary for the International Fishing Commission. Now she took over the pink tickets, a mass of which had been collected. If a biologist wanted to learn what certain fishing boats had caught, all he had to do was to go through this mass of tickets and try to find the boats he was interested in.

Geraldine Conner is another person for whom I have great admiration. Her training had been limited, yet she was the person who had the ability, when there was a job to do, to know how to do it, and to go ahead and do it. She set up a program to sort and file the pink tickets and make their figures available with details of boat catches and kinds of fish.

That is a quick summary of the first fifteen years. We might pause a moment to consider what had been learned, for in the beginning practically nothing was known about our fisheries. A little had been learned about albacore. Thompson had indicated that there was some relation between albacore catch and the temperatures of the water. Gene Scofield, a young son of N.B., was doing work with the patrol boat *Bluefin* and some of the smaller boats, and had found and identified sardine eggs and larvae.

The fishing grounds for sardines and mackerel off California had been well defined. The staff had learned the sizes of the fish that were being taken, the fact that spawning abundance varied from year to year, and that there were differences in the sizes of year classes. They knew that fish taken on the fishing grounds in central and southern California varied to some extent. The time of the appearance in the fisheries varied for both sardines and albacore. Quite a bit had been learned about tuna. Studies of the barracuda had been made, and of the white sea bass, the Pismo clam, and several of the other fisheries along the coast.

That takes care of the first fifteen years, and we'll start a new decade. In 1930 the government of Canada and the provincial government of British Columbia started a sardine investigation headed by John Hart, again a man of great ability. He came to California, talked with the people investigating here, and kept in touch by correspondence so that the work in Canada was integrated with that in California.

In 1931 it was realized that something must be done about the mass of pink tickets. Their information still was not being made available quickly enough. So the punch-card system, as we called it, started up. It was really the beginning of computers, again a tribute to Gerry Conner who started the program that developed into a computer program; she got the machines set up to punch the records, sort them, and make all the records available on printed copies.

In 1931 the sport-fish catch records were started. The *Bluefin*, the patrol boat that did much of the first oceanographic work, had explored California and Mexican waters. At this time, it was discovered that the value of fish oil and meal was greater than the value of canned fish. Up to this time, California had ruled that no whole fish could be directly reduced to fish meal and oil: only the trimmings, the offal, and fish that were too crushed or too small for canning. In addition, the commission stated that any processor could reduce only a certain percentage of his total catch. Because the demand for fish meal and oil was so great, the processors appealed to the Department of Fish and Game and obtained a grant of 130,000 additional tons for use in reducing whole fish into meal and oil.

At this time, in order to get around the department's control, two ships had been organized to go offshore and reduce fish into meal and oil beyond the state's jurisdiction. So the pressure for the use of sardines, especially, for fish meal and oil was becoming very heavy. In 1933 the law restricting the amount of tonnage used for fish meal and oil was removed. Then the pressure to increase the reduction of sardines mounted rapidly.

By 1933 Don Fry had found, reared, and identified mackerel eggs and had established knowledge about mackerel spawning. Compared to all of the mechanical equipment we have now, there wasn't much in those days. Don reared his mackerel eggs, it's rumored, in the home bathtub. That's the way he was able to keep the eggs and larvae until they reached a size large enough for them to be identified.

In 1934 the *Bluefin* made five cruises. They were in local and southern California waters south to La Paz, and out to Tanner Bank. Much of this was under the direction of Harry Godsil, but all of the other biologists worked at turns on these different projects. Then in 1934 Gene Scofield brought out his report that sardine eggs and larvae were taken from San Francisco south to Cape San Lucas, and offshore for about a hundred miles.

In 1935 the tagging of tuna was started, again under the direction of Harry Godsil. In 1936 Fry brought out the summary of what he had learned about the mackerel spawning. Phil Roedel was employed in 1936. In 1937 sardine tagging was started off British Columbia, Washington, Oregon, and California. John Janssen was in charge of that program. The California Department of Fish and Game and Scripps Institution of Oceanography had released drift bottles off southern California to learn something about the surface drifts in the area.

By 1938 the sardine tagging was producing evidence that sardines were moving up the coast as far as British Columbia and south to Baja California waters. The tuna and mackerel taggings were bringing good results. It was particularly exciting in 1938 when about thirty-five small sardines, thirty-four to thirty-five millimeters in length, were taken in an albacore stomach about thirty miles off the mouth of the Columbia River and sent to California biologists, thus proving that baby sardines at times occurred even that far north.

The pressure to use sardines for fish meal and oil was tremendous. The industry claimed that California had no justification in trying to hold the total catch down to a basic 200,000 tons a year. Whether that was too small or too large no one knew, and probably will never know. The processors, the reduction people, were vociferous in their resistance to the California Department of Fish and Game's attempt to hold down the catch. Very unpleasant things were said about the biologists' bringing out statements and not knowing the truth about the facts they had. They couldn't be proved and probably never can be. The processors were certainly far from polite in the things they said to us, and they brought pressure on the federal government to have somebody come and really learn something about sardines! So Elton Sette transferred back to California and set up a program to study sardines. I'm sure Sette did not relish this problem. The California biologists obviously had a very big chip on their shoulders. Their feelings had been seriously hurt. They resisted somebody else's coming in and showing them that they didn't know anything.

So there were many heated meetings. There was much discussion and final realization that the thing to do was to learn to work together and fuse the two programs so they would not overlap, but supplement each other. Thus with all the pangs, finally CalCOFI was born. It rapidly became a very lusty infant.

Also, in December of 1935 the *N.B. Scofield* research vessel was launched. This is the only time the California Department of Fish and Game has ever named one of its boats for anything but a fish, but it was certainly a wonderful tribute to the work that N.B. had done. In 1939 the *N.B. Scofield* made six cruises, traveled 16,000 miles from northern California to Central America, and took albacore 800 miles offshore. In the fall of 1939 N.B. Scofield retired, and here ends my account of the first twenty-five years of fisheries investigation.

* * *

Question: Tell us something about what you did, Frances.

Clark: I came to work for the Department of Fish and Game in 1921, shortly before the move into the State Fisheries Laboratory. I stayed through to 1922, when people left because of lack of funds. I went to the University of Michigan to study for my doctorate under Alexander Ruthven and Carl Hubbs. I returned to the California Department of Fish and Game as a fisheries biologist in 1926 and continued on until I retired in 1957.

Here is a little anecdote about the beginning. I had an A.B. in biology from Stanford but was hired as a secretary and librarian. I had a very limited knowledge of shorthand; I knew nothing about library work. But I fortunately found that Thompson apparently didn't care to dictate letters, and he asked me if I would rather have him dictate or write the letters myself for him to sign. That was much more fun. For two mornings a week I went into Los Angeles to a library school and learned the rudiments of library work, and in that way the extensive library developed by Pat Powell got under way.

Question: I'd like to ask you, Dr. Clark, what was the public's reaction to the factory ships offshore?

Clark: I have a feeling that, aside from the fisheries people and the industry, people didn't pay much attention. It was not a major California problem. As you probably know, they did pass a law that fish meal and oil processed outside of California waters could not be delivered at California ports. This, in part, shut down the offshore fish processing. But the thing that really stopped it was employment. The people who were working on the ships offshore worked twenty-four hours a day; the union said that they could not work longer than eight hours a day, and the wages had to be increased. That financially broke the reduction ships, and they had to give up.

Question: Through your career did you face any discrimination? I assume at that time you were one of the few women working in the field of fishery biology.

Clark: My personal experience is not that people didn't *want* to employ women, they just never *thought* of doing so!

Blanca Rojas de Mendiola: I am from the Instituto del Mar de Perú. I want to tell something about Dr. Frances Clark. She was in Perú in 1953 and in the beginning of 1954. We learned a lot from her, and all of the people who had the opportunity to work with her at that time appreciate it.

AN ICONOCLAST'S VIEW OF CALIFORNIA FISHERIES RESEARCH, 1929–1962

RICHARD S. CROKER

I'm going to talk about the early days of fisheries and research in California from a somewhat different viewpoint than anybody else, I'm sure. It just happens that Herb Frey's round table, giving some idea of the hazards and pitfalls of fisheries research and management, and Frances's historical review fit in perfectly. We didn't get together on this, but it just works out fine.

In answer to some of the questions, though, about Frances, let's just say that the fisheries research field was exactly sixty years ahead of the Supreme Court. I think it's a credit to the people in our field that we did get that head start.

I'm going to talk somewhat about myself, not because of any egotistical trait, but because I want to put things into perspective, and maybe you will get an idea of my philosophy. An iconoclast originally was somebody who smashed the icons in the Russian churches and went to jail for it. I like to smash a lot of things, but I never went to jail for it.

But looking back, after Reuben talked me into this presentation, I began to think that things are kind of a pattern; things are kind of funny. But I might say that all this time I have been marching to a different drumbeat than a lot of people, except that since I married a Scottish girl, let's say that I've been marching to a different bagpipe! So three times I listened to that internal bagpipe and marched off.

The first time, to give you a little background, I marched off to World War II. The bagpipes always stirred me, and I envisioned myself as climbing out of the trenches and slaughtering the enemy. Anyway, I marched off. I'll give you a little anecdote, and it's a true one, too. Strangely enough, I was taken in to see my new commanding officer at my first station. The adjutant introduced me, and the grim-visaged colonel said, "Major, what is his background?" The adjutant said, "He's a fisheries biologist, sir." The colonel said, "For Christ's sake!" I heard him muttering, "What are we going to do with this bastard?" Then he looked at me, and said, "Lieutenant, have you ever commanded troops?" I said, "No, sir!" in my most military manner. He looked at me with that well-known steely eye, and with precise, grammatical English he said, "If I were to ask you this question twenty-four hours from now the answer would be, 'Yes, sir.' You are as of now in command of Student Squadron 57."

So from then on, his and my careers both went rapidly downhill. Not long after, he was court-martialed for accepting bribes from civilian contractors. In disgrace, he committed suicide, and in disgrace his son had to resign from the Army.

As for me, when I came back from the service, I was made a fisheries administrator with California Fish and Game. That was a quick step from a mediocre biologist to a harassed administrator, and that's one step below even a lousy biologist. But I want to make the usual disavowal. Any remarks I may make from now on do not reflect the views of any agency or company for which I have worked, and my comments have not been cleared by any of my past bosses, one of whom was too modest to mention it to you—Frances herself. So here we go.

When I came to work, it was actually a college vacation in 1928. In 1929 I was a full-time temporary. Like a temporary World War II building, a temporary appointment in state service often becomes permanent. There weren't very many of us, just a handful, and we all knew each other. We weren't pioneers by any means. I'm not sure whether we were second or third generation, but there weren't many ahead of us, and most of them, as Frances mentioned, were the greats who laid the groundwork of early fisheries research.

In the early thirties there was an extreme shortage of qualified personnel. I was working, but I wasn't qualified. There was a great shortage of public support, and there was a great shortage of funds. Frances alluded to the modern equipment that's now available. You should have seen what we had. If you will look at the pictures in that book over there, you will see Harry Godsil and me hauling a net. I'd like to tell you about that day for several reasons. This was in 1934, off Coronado Strand. We were after young sardines. The boat we had was the *Bluefin,* the patrol boat. We got it for about one week a month or so, and the rest of the time it was used to harass illegal fishermen.

We also had what we called *Bluefin, Jr.,* a skiff that must have weighed a ton, dead weight with nothing in it. It was a horrible thing, with an outboard motor that we had to operate in a well amidships to avoid fouling the net as it was shot off the stern. Harry and I went out with a four-man lampara net, and one day before lunch the two of us made eleven sets on sardines. Now, the reason that Harry and I did it and not somebody else was that Harry was short, and I was tall, and our fannies fitted perfectly on the stern of this boat, one above the other! You can see it in the picture.

Anyway, we made eleven sets, and we caught sardines in every set. We took them back to the *Bluefin* and measured them for some reason that is now obscure. We had lunch and then went out in the afternoon and made eleven *more* sets. That's how hard we had to work with the equipment we had. Every set we made, while Harry laid out the net, I had to row on the one side with a great big old oar because we couldn't make the tight circle with the motor in the middle of the boat.

Now, there are several significant things about this. One is that there were enough sardines this size to catch some every time we put the net in the water in broad daylight. There were enough sardines there to support a small but flourishing canning industry in San Diego. Del Monte packed small sardines in oil, in quarter-pound cans, and the fishermen called small-sized sardines "quarter oils." Del Monte used to keep the cans a year before putting them on the market, to let the flavor set, and those sardines were superb. To this day—and I have sampled every kind of sardine, everywhere in the world, I've only found one pack that would even compare in excellence. I encountered the closest thing in 1966 in Ensenada at a plant called Conservas del Pacífico, known as COPASA. They packed a Spanish-style sardine. The fish were caught off Mazatlan and shipped all the way up to Ensenada by reefer truck. COPASA also put up the best white and red wine produced in Mexico—from the same plant!

Anyway, it was rather significant that that was the kind of equipment we had. Another example is the story of Don Fry and the bathtub that Frances told. However, it was not mackerel, but lobsters he raised in the bathtub; he and his wife had to come to our house to take a bath.

One time we went out on the *Junior,* which by now had an inboard motor with a big flywheel. Frances, Don Fry, and I went out to tag mackerel off the outer Long Beach breakwater. The first thing that came right by us—of course, if they had known we were Fish and Game they would have stayed away—was a purse seiner. It swamped our engine, and there we were stranded, and the three of us sat there. Don and I pulled our arms off on the great flywheel. Finally, I got mad and said, "Excuse me, Frances"—or "Clarkey," as we called her in those days. I sat up on the bow and I cursed that engine until I was blue in the face. Then I marched back to the engine and gave it one turn and chug-chug-chug-chug. Frances said, "I never knew that swearing was any good at all!"

After we finished tagging mackerel, we had made such slow progress getting out there that we knew the bottom was fouled. Anyway it had been a long day, and there were no accommodations on board, so we'd go over the side to scrape the seaweed and the growth off the bottom. In those days one never mentioned going to the bathroom when in a situation like that, so we could do it while we were scraping off the bottom.

So that's the kind of thing we had to do. One day, the fellow over at the dock where we kept this *Junior* phoned me up and said, "Mr. Croker?" I said, "Yeah." "I'd like to tell you that the boat *Junior* sank at the dock." I just said, "Good," and hung up. That's the kind of equipment we had to work with. This wasn't pioneering; this was second-, third-generation stuff.

As I said, there was no respect for us, except among ourselves and our colleagues up and down the coast. We were sort of second-class citizens, and no one took us at all seriously, no matter what we had to say. You've seen that television comedian who always says, "I don't get no respect." Well, that was us. . . . Maybe we still don't.

We didn't have much contact with the outside world except through literature and correspondence. Frances mentioned the library, and Pat will be too modest to indicate the part it played, but it eventually became the finest fishery library in the world. Occasionally big shots even in those ancient days would come by, and we'd have a little seminar. In fact, I remember one embarrassing situation when I fell asleep during a talk. Gee, did I catch hell.

There were our cruises down off the Mexican coast that Frances mentioned and our contacts at Seattle, so we knew that our world really extended from Puget Sound to Cape San Lucas. It was kind of a parochial situation; I guess the people in New Brunswick and in Hull or Lowestoft in England were the same way.

The first profound interrelationship was the sardine group of British Columbia, Washington, Oregon, and California. As the sardines were progressively fished farther north, we got together. One way or another, the laboratory and the library achieved a growing respect abroad, but still none at home. We were just like an expert: the farther from home he is, the better he is rated.

As Frances said, during those prewar years the state fishery laboratory was sort of a prep school for federal jobs. People just graduated and went on, and when they left, they always thought—I remember one of them telling me—that they were the top people, and they left the scum behind. That didn't go over very well with us. There was—Frances alluded to it, but I'm going to talk about it—a growing rivalry between the federal Fish and Wildlife Service and the three Pacific states. It was not California alone. Oregon and Washington were even more bitter. We were trying to do something the federals weren't doing, and that was to conduct research and manage the fisheries at the same time, which was quite different—as I am going to expound upon—from just conducting research.

Up until World War II the fish stocks, in general, were in pretty good shape. Some of the minor fisheries needed and received some conservation protection. We achieved quite a few things, largely through N.B. Scofield's influence in Sacramento. He was universally respected, and he could get some things done. But he couldn't buck the big canning industry. About that time, everybody was beginning to worry if the salmon could survive both heavy fishing pressure and the destruction of the environment. There was a great deal of interest in salmon at this time. But out on the coast the sardine was king.

World War II was an interruption in several ways, and I'll list about four of them. First, the demand for food caused intensification of fishing. Many of the tuna boats and the crews were drafted into the armed forces, so the tuna fishery stopped short. All of the other fisheries expanded greatly, however, to meet the demand, and perhaps some of them kind of overdid it, as in the case of the soupfin shark, for example. Overfishing was the name of the game. Many of the fisheries biologists and the state's two research vessels went off to war, leaving behind only a small, dedicated group to hold the research program together.

Another result of the war was that our horizons were broadened. The biologists returned from service all over the world having seen how the rest of the world lived and died, having observed fisheries in the field, and having met foreign scientists. It was a broadening episode in all our lives—traumatic, in fact. A worldwide view of the fisheries began to emerge. We began to realize that fish were being caught everywhere and that fish respected no national boundaries.

Another result, only in California, really, was a tremendous growth in population that resulted from the war. It was unequalled by any migration of western peoples in historical times, I guess. I could see it while I was still in the service, even overseas. I don't know how many service people I met who planned to move to California, especially Texans. I like Texas actually. It was great, no kidding! I love the Texans, too. They knew exactly how much they could take you for, and they told you. I remember my corporal in Texas said once, "Lieutenant, don't tell anybody, but I'm sick and tired of hillbilly music"—he played the guitar—"and I am going to throw the damn thing away. As soon as this war is over, I'm coming to California." These new residents overtaxed all public services, causing water pollution, water shortages, destruction of aquatic habitat, and most of them fished; it all put a strain on our marine resources.

After World War II, and now we're getting places, not only was there the broadening I just mentioned, but there also came a change in thinking. Instead of single-species research, a gradual change took place, and we began to think in terms of multiple-species fisheries. The multidiscipline concept of the total ocean emerged; we began to think more of the whole picture. The same occurred in game work and in freshwater work, too.

One place where two disciplines got together was funny: we'd always laugh. We could always tell an oceanographer by his beard and, before we knew it, the biologists were wearing them, and we couldn't tell them apart! Even some of the oceanographers shaved theirs off. I don't know whether that had any meaning or not, but they did begin to work together.

The several Pacific Coast agencies began to cooperate and formed the Pacific Marine Fisheries Commission. It included the states of California, Oregon, and Washington, and was approved by Congress. It was either the first or second of the present three interstate commissions. There are now five states in our commission.

The Canadians were invited to sit in, and they contributed greatly. The U.S. Fish and Wildlife Service was also an invited participant. But most of us realized, though we never said it out loud, that the interstate commission was in part created to keep the feds from assuming too big a role.

Incidentally, the federal agency changed its name so often that I can't keep track of it. But we'll call them the feds and, a sort of pejorative, *los federales*. Those of you from Mexico, particularly, will know how esteemed *los federales* were!

Back to the Pacific Marine Commission: at first the commission was heavily involved with sardines. That didn't last long because the fisheries progressively collapsed from north to south: B.C., Washington, Oregon, California. Then emphasis shifted to fisheries still of mutual concern to the three states and B.C.—the Dungeness crab, the albacore, the bottom fisheries, shrimps, and so on. But from the beginning, really, salmon was the big deal, and the federal salmon program became closely integrated with state programs. Instead of being kept out, the federal people were brought in, and a marvelous working relationship developed.

In California, everyone began to wonder if the sardine supply really was inexhaustible. Some people were genuinely concerned, but many in the industry refused to worry. They were making big money and couldn't care less about the future. Others wanted to stay in business, and they just desired to learn if the collapse was temporary, what caused it, and what, if anything, could be done to bring back the sardines. Eveything you can imagine was blamed, including the scientists, ocean currents, water temperature, sea lions, offshore oil exploration, and all sorts of flights of fancy. But nobody would even dream of saying out loud that it might be heavy fishing, because depletion was a dirty word.

After countless meetings of everyone involved, the Marine Research Committee was formed. The industry proposed it and funded it, and for thirty years you might say the industry has been the sponsor of a world-acclaimed ocean research program.

We all entered into the new concept with disparate motives and mixed emotions, but there was always a surprisingly good program even if it didn't save the sardine fishery or bring back the sardine. In fact, an underlying reason that it was started was to discredit those fishery scientists whose studies had led them to believe that the resource could and should be safeguarded by imposing moderate restraints on overfishing.

Meanwhile, a number of us went abroad to see how foreign fisheries were operated and to help the developing countries manage their fisheries. It became almost unwritten policy to hire scientists who had had overseas service, or to grant leaves of absence so that researchers could get the experience that overseas work involved.

Now, let's list the participating agencies. The several agencies that were brought together and literally forced to cooperate, kicking and screaming, had different viewpoints and responsibilities that were bound to result in friction. It was indeed remarkable that their research staffs could swallow their pride and subordinate their feelings to work together.

First was California Fish and Game: this agency had, and still has, a dual responsibility under state law, as Miss Clark stated, to study all aspects of the state fisheries and recommend appropriate conservation measures even if the state legislature is under no mandate to heed any such recommendations. State scientists accepted the new setup as a slap in the face, as it was intended to be, and kept right on working. Very little of Marine Research Committee funds ever filtered down to California Fish and Game because, after all, if the sardines disappear, it's the fault of California Fish and Game.

Personally, a second drumbeat sounded when I came back and took an administrative job. I heard the bagpipes. When I signed on back there, like the air traffic controllers, I had to take an oath to do my job, and that job was to save the fishery resources. I didn't, and that made a profound impression on me. If I sometimes sound a little bitter, I am, because I couldn't find any way to save the sardine resource from disappearing. Maybe nobody could anyway. I took it personally and waited for the next bagpipe.

The second agency was the federal Fisheries Service, which, as I said, we called *los federales*. This staff had no management responsibility or expertise. Remember now, the Fish and Wildlife Service didn't manage or regulate any fishery except in Alaska, and the less said about their efforts up there the better! (Not that the state of Alaska has done too much better.) I mean the Fish and Wildlife Service just wasn't set up for managerial responsibility. They were responsible to no one for anything except their conduct of research, at which they were and still are good—better than good. If the sardines disappear, too bad, but the research was good, and this was a great way to get a foothold in California anyway.

The third participant was the university and academy group—Hopkins Marine Station, Cal Academy, and Scripps. Their staffs conducted pure research on the fish and the ocean, and this was a good way to get outside funds, which were indeed put to good use. Their research was and is of top quality. We must note that one agency was included largely so its very wise and diplomatic director could act as an arbitrator and peacemaker among the big three. Now I'd like to express my thanks to Bob Miller for a job done well above and beyond the call of duty, and for keeping the brass working together.

There came a change in attitudes toward Fish and Game biologists. I'm speaking of the working stiffs. As a result of the long, drawn-out death agonies of the sardine fisheries, there was a great change in the relationship between the staff of Fish and Game and its constituents—the fishing industry and the sports fishermen. After all is said and done, these two groups paid the salaries of the state biologists through various user fees, so how the fishing public perceived the staff, no matter right or wrong, is important to all concerned.

In general, before World War II the biologists were more or less tolerated with amusement. We liked our customers, and they sort of liked us. We were welcome in each other's homes and on their fishing boats. The legislature rather ignored us, but our bosses pushed through much useful conservation legislation with respect to several minor fisheries—those in which the participants didn't have much political clout. Many of these fisheries, including the salmon and trawl fisheries, whose fishermen actually asked for more restrictions, continued to fare well.

I would like to put in a word for fishermen. I said that we liked them and they liked us. I can honestly say now I don't think there is any greater bunch of people to work with, whether you are for them or against them, than fishermen—sport fishermen or commercial fishermen, and the fish packers and dealers and the whole rigmarole. I have worked with these people literally all over the world, and there are no people like fishermen. You can make friends with them, you can empathize with them, and sympathize with them, and they with you, I think. To reiterate more or less what the people up here said earlier, we're working with people, not fish. If you are in management research, and I think maybe ivory tower research, too, there are people involved. You run into people as you go along, and you have great times ahead of you working with the fishing industry and the sports fishermen.

I remember once when there was some kind of hassle up in the legislature, and the then assemblyman from San Pedro, good old Vince Thomas, had a bright idea. He invited the assembly committee to go out on a Fish and Game boat and observe a commercial fishing boat in action. So special permission was granted to a purse seiner to set a net in a closed area in Catalina because it would be calm and the legislators wouldn't get seasick. The fishermen chose a crew composed entirely of old captains, all Yugoslav and Italian boat captains. So when they set the net, I could see how incompetent we were. They could do everything right when it came to locating the fish and starting the set, but, boy, when they started to haul them in, they weren't as good as their crewmen.

But anyway, the assemblymen and assemblywomen that were there were very impressed by the rapport that existed between our patrol, enforcement, and research personnel and the fishermen. Some of our people, both on enforcement and research, had taken the trouble to learn enough Serbo-Croatian to talk with the Yugoslav fishermen and enough Italian or Sicilian to talk with the Italian fishermen. We went aboard each other's ships, the purse seiner and the *Scofield,* or it might have been the *Yellowfin.* We ate in the galleys of the fishermen and on our boat. The legislators were impressed with that rapport, even though we were on opposite sides during some squabbles. I think that's important, and you all have a great opportunity to make real friends. Some of them are miserable rascals and, you can imagine, crooks. But they were great guys!

I met a man from the Better Business Bureau once who said that the most charming people he ever met were bunco artists. And some of the fish canners were. So there was a friendly feeling at first, and it persisted on a personal basis. But as the sardine industry faltered, attitudes changed. The state biologists stepped up their talk about the need for catch restrictions, based on what seemed to them to be a classic and actual drop in sardine abundance.

This was threatening to the sardine industry. If the recommendations were put into effect, their money-making machine would have to slow down. The industry took various delaying actions. One was to convince the legislature that the scarcity was temporary. Another was to fish even harder, following the old Japanese theory of conservation, which is "wise use" interpreted as "catch the fish before someone else does." We call it the Alaska ethic. If it moves, shoot it or catch it. If it doesn't move, chop it down or dig it up! Since the new administration came to Washington, we call it the James Watt syndrome.

The crowning success of the sardine industry was to bring in outside scientists who might, just might, endorse the theory that ocean fisheries are inexhaustible. To cloud the picture and cast doubt on the management biologists, the Marine Research Committee was established. It was founded on the premise that research should be stepped up and carried on until the sardine is wiped out, no matter what wipes it out, and by then no one would care.

In any event, the research goes on, and now we're in a peculiar position. Herb Frey mentioned to me this morning that if the sardines did reappear, the industry wouldn't know what to do with them. They've lost their markets; the fish would just be a nuisance. There are lines set up for mackerel and tuna, mostly tuna, and maybe if the sardines came back, nobody would really care except the sport fishermen and the bait haulers.

Meanwhile, the Department of Fish and Game's other customers—the sport and commercial fishermen who fish for the predatory fish that depend on sardines for food—were screaming at the department for not doing something to save the sardines. Right or wrong, those fishermen were convinced that the purse seine fleet was destroying the sardine resource, not to mention the mackerel.

This morning Paul Smith mentioned something I had completely forgotten: that there was once an initiative measure on the ballot to prohibit all purse seining south of central California, and it won a million yes votes. A million out of three million voters wanted to do away with purse seiners altogether. So there was some very large public appreciation of trouble, trouble, trouble. The sportsmen pounded us and gave us hell for letting it happen.

By now—about 1960—instead of being ignored or tolerated, the state biologists were denounced from both sides. It became frustrating to watch an industry die while we continued really useful research, which was doomed from the start never to answer to everyone's satisfaction the simple question: where have the sardines gone and why?

About then I heard the third skirl of the bagpipes. I had become aware of the world crisis in resources and environment, and world hunger and shortage of water, and all those things. I marched off again to try to do something, and I found I couldn't even lick that. So finally I gave up. I said to hell with it and I'll go fishing!

* * *

Question: What was the role that Wib Chapman played in the organization of the association between the feds and the state and the academic people?

Croker: You're asking a complex question about a very complex person: a man of vision, one of my best friends, the man with whom I have disagreed more than anyone else. As far as I know, at least in his productive years, he never worked for the feds or the Fish and Wildlife people. He never worked for Cal Fish and Game. In fact, he was at the Academy of Sciences in San Francisco and later was to become the fisheries honcho, head man in the U.S. Department of State. He left State and turned it over to Bill Herrington, who also got his schooling in San Pedro, right near the lab. Then Wib went to work for the tuna people. It was while he was with the Academy that he helped bring the various agencies together.

I remember one enlightening conversation I had with him during his tuna industry days. He was being very antagonistic toward what he called, in his inimitable way, our parochialism. He spoke in lofty terms of five hundred, a thousand million tons, and how the world is full of fish, and people have got to eat, and we in California were so parochial.

Then I said to him, "Wib, remember, as you stream around the world writing your wonderful long letters and flying on exotic airlines, you're in the jet set, and here I am, stuck in California. I too spend time in the jet set, but mostly I am in the DC-3 set. I have to take care of the salmon and the shrimp and the crab and the sport fisherman and all the nitty gritty. I just can't afford to spend all of my time in a 707 or a DC-8 like you can." Wib realized what I meant, that he could take care of the big world picture without being on the firing line, while my staff and I had to stay home and fight the local wars. He thought about it for a while, and we saw eye-to-eye from that time on. But I never could swallow his idea that the total supply of all kinds of fish in the world was inexhaustible, and we could expand world fisheries *ad infinitum*. There we had to disagree.

From the time we had this little conversation, he did everything in his power to bring all the agencies closer together. He was not a disruptive factor as far as I was concerned.

Clark: Although my answer was, no, Wib Chapman never worked with us, many times he did work *for* us, and in his wonderful way he did a great deal for us.

Question: Is this Gilbert whose name came up today the same one who conducted the Philippine fish survey?

Croker: Yes. Several people pioneered ichthyological research and laid the groundwork for Carl Hubbs to carry on for so long; they were Gilbert, Evermann, Jordan, and, a little bit later, Snyder. Snyder once told me about a trip to Kodiak or somewhere where the crew kept drinking all of his alcohol for preserving specimens. So he put some formaldehyde in the alcohol and put a big sign on it that said, "I have added formaldehyde; it will poison you," and the entire crew got sick!

I remember a scientist from Montana who was, I think, with Gilbert during early work in the Philippines. He got so seasick that when they put ashore, he somehow got home—I don't know how—and he never again left Montana. He gave up fisheries work! Seasick all the way to Manila. So those were the pioneering days.

Question: Dick, I would be awfully disappointed if you didn't tell the folks your perception of how people felt about a fishery biologist back in the early years. You know what I mean.

Croker: Oh, this is going to be tough on the interpreter, but I'll give it in English. I told you that we didn't get no respect. That double negative is all right in Spanish. One of our fellows received a letter from his mother asking, "Son, what are you doing now?" It's alleged that he was so ashamed to admit being a fishery biologist that he wrote, "Dear Mom, I am sure you would be happy to know that I am the piano player in a whorehouse." Times have changed, I hope!

THE ROLE OF THE MARINE RESEARCH COMMITTEE AND CalCOFI

JOHN L. BAXTER

I feel quite honored to be on a panel with Frances N. Clark and Richard S. Croker. Clark hired me, and at that time she was director of the California State Fisheries Laboratory, and on a pedestal much higher than I could reach. And Croker was the chief of the then Marine Fisheries Branch, a very important job indeed. So, as you can see, I feel a little bit out of place here, but I acknowledge that I am a second stringer. Actually, they intended this speaker to be Phil Roedel, and that would have been much more appropriate. I am like the baseball player who was inserted in the eighth inning and then was pinch hit for in the ninth. So that's a good analogy for my relationship with CalCOFI.

My talk is titled "The Role of the Marine Research Committee and CalCOFI," and results from a lot of library research that I hope will make sense to you and will fit in with this symposium. The Marine Research Committee (MRC) was established by an act of the legislature in 1947. Croker generally covered the reasons and some of the behind-the-scenes occurrences that led to its establishment. The statute described it as consisting of nine members, three of whom were *ex officio* members with the same rights and powers as the other members. The three were the president of the Fish and Game Commission, the executive secretary of the then Division of Fish and Game and later the director of the Department of Fish and Game (DFG), and one employee of DFG designated by the Fish and Game Commission. This member was, from the very start, Dick Croker. Of the other six members, at least five were to be experienced in and actively engaged in the canning or reduction of California sardines.

Members served without compensation. An added tax of fifty cents per ton or a fraction of each ton of sardines purchased, received, or taken was levied against the industry. That money was put into the Fish and Game Preservation Fund and dispersed by the majority of the Marine Research Committee solely to finance research in developing the commercial fisheries of the Pacific Ocean and developing marine products susceptible to being made available to Californians.

In 1953, this law was changed. The tax was increased to a dollar a ton for sardines and, in addition, the dollar a ton was levied on Pacific mackerel, jack mackerel, squid, Pacific herring, and anchovies. Beginning in 1956 the membership of the committee was changed. The three *ex officio* members representing the Fish and Game Commission and the Department of Fish and Game were replaced. The six members representing the industry remained, but one member from the public at large, one from organized labor, and one to represent organized sportsmen were added.

The first meeting of MRC was held on April 28, 1948, at the California Academy of Sciences (CAS) in San Francisco. At that meeting, Julian Burnette, an old reductionist, was elected chairman of MRC, a position he held until February of 1967, when he was replaced by Charles R. Carry. Julian was the only member who served during the entire thirty-one-year life of MRC. Mr. Carry continued as chairman until its final meeting, which was held June 29, 1978, in Long Beach. Incidentally, Dick Croker was elected secretary at that first meeting in 1948, and he held that position until 1962 when he retired. He was followed by Phil Roedel, Doyle Gates, Laura Richardson, and Herb Frey.

During the thirty-one years that the MRC was in existence, revenues collected under the special tax totaled only $3,350,000. Of this, approximately $923,000 came from sardines, $977,000 from the mackerels, $1,200,000 from anchovies, $231,000 from herring, and $215,000 from the squid fishery. The largest budget ever adopted by MRC was $185,000 in 1970-71, and more than half of this was from carry-over funds that hadn't been expended earlier. This, incidentally, was during the time the anchovy fishery was growing at a pretty good rate.

Of course, this money represents only a small part of the total picture. It has been estimated by many that the "seed money" provided by MRC was important in stimulating revenues that in recent years have greatly increased. The CalCOFI program has been over $4,000,000 a year. That $4,000,000 per year from other sources was all spent on things over which MRC exercised some purview.

In the early years, the MRC funds ranged from about $65,000 to $180,000; they played a very important part in keeping the cooperative sardine program going. They assisted the U.S. Bureau of Commercial Fisheries (BCF) through some tough years with its boat schedules, and provided assistance for boat crews for the DFG. The majority of MRC's monies in the first five years went to those kinds of programs.

From 1950 through 1960, Scripps Institution of Oceanography (SIO) used from $30,000 to $70,000 per year, to assist with research. It's obvious that although the budget of MRC was rather small, it helped the research organizations over some tough financial times in the early years. In the later years, MRC served as a rather small tail wagging a rather large dog, which the CalCOFI program has become.

Also, this influential group of men, particularly the industry representatives, played a large part in encouraging the University of California to fund SIO for its CalCOFI part of the program. MRC members could talk to the president of the University of California, and also they played a large part in the founding of the Institute of Marine Resources (IMR). Whereas in 1949-50, MRC funding was $97,500, the three major agencies by that time were expending about $600,000 a year on the cooperative sardine fishery investigation. Ten years later, in July of 1960, MRC was supplying about $60,000 to Scripps, Fish and Game, and BCF, and their budgets for the program totaled $950,000. As pointed out earlier, the CalCOFI program is today about $4,000,000 per year.

Through the forties and fifties, the major differences among scientists working on sardines hindered the implementation of management measures. Although I don't pretend to understand the total picture, the basic difference between BCF and DFG scientists was that BCF held that year-class size was independent of spawning-stock size. This basic disagreement was later softened when different leadership, upon further examination of the data, reached a decision more compatible with the DFG's views.

The matter was finally put to rest by Garth Murphy in his 1966 thesis on sardine population biology. He stated: "Thus, the long series of poor year classes (1949-1963) at small stock sizes in the face of varying oceanic climate suggests that Marr's conclusion that year-class size is independent of stock size is untenable." Further, "it seems clear that the population was overfished in an economic sense, and overfished in the biological sense, too, in that the heavy mortality induced by the fishery removed the 'cushion' against poor spawning success provided by older fish."

The net effect of this disagreement between major agencies over the relation of spawning-stock size and year-class size, in my view, continued overfishing of sardines until they were driven to the critically low point where the population is today. The first legislation restricting the size of the sardine catch was passed in 1969. MRC at last passed a motion recommending a complete moratorium on the take of sardines at their September 1967 meeting. This legislation was strengthened in 1974 by further restricting the uses of incidentally caught sardines.

Now, back to the beginnings. On May 19, 1948, the MRC met in La Jolla. At that time, Robert C. Miller was chairman of the Technical Committee (he is the one Dick Croker referred to as having a very large part in holding this thing together in the early years). Bob outlined the following lines of research to be pursued by the then California Cooperative Sardine Research Program: (1) physical-chemical conditions in the sea; (2) organic productivity of the sea; (3) spawning survival and recruitment of sardines; (4) availability of the stock to fishermen, that is, the behavior of the fish as it affects catch, abundance, distribution, and migration; (5) fishing methods in relation to availability; and (6) dynamics of the sardine population and fishery.

This forerunner of the later CalCOFI program was made up of representatives from SIO, CAS, BCF, and DFG. The California Cooperative Sardine Research Program was renamed the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in June of 1953 to recognize the expansion of the sardine program to include work on other species. In 1952, the Hopkins Marine Station of Stanford University (HMS) joined the program. In 1965 or '66, San Diego State College was included. In 1974, HMS dropped out of the MRC part of the program, and its work in Monterey Bay was taken over by Moss Landing Marine Laboratories. From 1974 through 1977, MRC funded phytoplankton studies by UC Santa Cruz in Monterey Bay. These, then, have been the agencies that benefited from MRC's funds over the years.

Informal cooperative scientific studies between CalCOFI and Mexican scientists were begun in the fall of 1971 and continue to this day.

Much of the future course of CalCOFI was determined in the late 1950s. At the May 3, 1957, MRC meeting a special technical committee was appointed by the chairman to examine the objectives of CalCOFI, to define the problems involved in attaining these objectives, to assess progress on the solution of problems, and to assign priorities to the remaining problems. This committee was affectionately known as the Three John Committee and was made up of John Isaacs of SIO, John Marr of BCF, and John Radovich of DFG. Elton Sette was named as an independent scientist to serve as special advisor to the chairman of MRC and to attend all meetings of the special technical committee to offer his advice and comments whenever he considered it necessary to expedite progress or agreement. Jack Marr was the chairman of this committee.

At the December meeting of MRC, the special technical committee presented its report, which noted that the research program of CalCOFI, conducted by the five agencies under MRC, had made real contributions toward understanding the fisheries but lacked effective coordination. To remedy these shortcomings, the committee recommended that control of the program be vested in a four-person committee. There would be one member each from DFG, from BCF, and from SIO. Each committee member would be the person actively directing his agency's share of the CalCOFI program. The fourth member and chairman would be a full-time scientific advisor hired by the MRC for this purpose. MRC and the three major agencies endorsed the plan, and thus was born the CalCOFI Committee.

The high priorities proposed by the Three John Committee were (1) to further describe and investigate the causes of the sardine's catastrophic decline; (2) to determine the population subgroups and their rate of intermixing; (3) to further study the dynamics to determine the vital statistics of the sardine population; that is, to derive an independent measure of recruitment and appraise the best methods for determining the size of the spawning stock to a degree of accuracy consistent with other associated measures; and (4) to complete descriptive oceanographic studies of the general circulation and of seasonal and other changes.

An early objective of the California Cooperative Sardine Investigation, the forerunner of CalCOFI, was to seek out the underlying principles that governed the Pacific sardine's behavior, availability, and total abundance. By 1960 the CalCOFI Committee formulated slightly different objectives: to acquire knowledge and understanding of the factors governing the abundance, distribution, and variation of the pelagic marine fishes, emphasizing the oceanographic and biological factors affecting the sardine and its ecological associates in the California Current system. The ultimate aim of the investigation was to obtain an understanding sufficient to predict, thus permitting efficient use of the species and perhaps manipulation of the population. These restated objectives formalized some aspects of the research that had long been recognized: (1) that no pelagic fish such as the sardine can be studied in nature as a creature isolated from its natural associates, (2) that such research is ultimately responsible to the needs of society, and (3) that the ultimate goal of this responsibility is attaining sufficient understanding to guide society in using the resource. Quite a change from earlier objectives.

After a year of search, Garth Murphy was selected as coordinator in November 1958. His chief responsibilities were to coordinate the agency programs through the CalCOFI Committee and to look into the sardine problem. His studies on sardine population dynamics culminated in a 1965 Ph.D. dissertation entitled "Population Biology of the Pacific Sardine *(Sardinops caerulea)*." This study showed that the maximum sustainable yield of the pre-1949 sardine population was 471,000 tons for a spawning population size of about 1,000,000 tons. During this period the catch averaged 570,000 tons. In addition, the heavy fishing left too few older individuals to cushion the population against reproductive failure. The maximum sustainable yield of the 1960s population was 57,000 tons for a population of 178,000 tons.

During his work with CalCOFI, Murphy received data indicating that the rise of the anchovy was apparently in response to an environmental void created by the decline of the sardine. Murphy states, "If this is so, the validity of a sustainable yield of sardines can be questioned, for the reduced sardine population required to generate the yield would also release resources to the anchovies. The subsequent increase of the anchovy would surely alter the parameters of the sardine population in such a way as to reduce the maximum sustainable yield. As a converse, the present situation is not likely to alter rapidly, even if sardine fishing is stopped, unless man or nature acts to reduce the anchovy population somewhat. It appears that judicious use of all ecologically similar species within the trophic level offers the only hope of sustained yield."

As a result of Murphy's work, and that of many others in CalCOFI's other agencies, the CalCOFI Committee proposed the famous anchovy experiment in March of 1964. At that time, the CalCOFI Committee was made up of Garth Murphy, coordinator; John Isaacs from SIO; E.H. Ahlstrom from BCF, who replaced Marr in 1959; and Baxter, from DFG, who replaced Radovich in 1963.

This proposal was developed considering the following three factors: (1) the basis for the suggested experiment, although the most complete ever achieved, still is not precise enough to foresee exactly how many anchovies and sardines should ultimately be taken; (2) a careful stepwise approach, such as was used in South Africa, is the only defensible experiment; and (3) there are time lags in response of sardine and anchovy populations to new factors. Their life histories suggest that at least three years would be required for population responses to be detected, even in a regime of favorable environment, and there are also time lags in scientific analysis, especially when dealing with new problems. Thus it is necessary to carry out measurements that can follow events closely and that will yield results that are readily interpreted.

With these three factors in mind, the approach was divided into three phases. The CalCOFI Committee believed three years was the minimum for each phase. In phase I, the objective was to initiate a conservative fishery on anchovies and reduce sardine fishing just enough to produce an observable change in the system and just enough to improve our preliminary appraisals of the magnitude of the anchovy resource. During this phase, a limit of 200,000 tons should be placed on the anchovy fishery, and the sardine fishery should be limited to 10,000 tons. Percentages were also established for north and south of the Baja California border.

The amounts to be removed during phase II, and the areal distribution of the limits of these *species* must await the results of phase I. We hazarded a guess at that time that during phase II the anchovy quota might be raised about fifty percent, providing the results of phase I are not widely different from preliminary expectations.

Phase III, we felt, couldn't be specified at all beyond indicating its objective, which was to restore the predecline balance between sardines and anchovies and maximize the harvest consistent with all uses—food, recreation, and so forth.

Although the great experiment really has never come off, as a result of CalCOFI's and MRC's active participation in the program, the Fish and Game Commission took a big step in 1964. They changed their policy on allowing the reduction of anchovies, which had been banned since about 1920, and permitted a quota of 75,000 tons. Because of many restrictions and small fishing zones, it was almost impossible for the fishery to really develop.

A fishery has continued since, with catches of up to 165,000 tons. Opposition by sportsmen and even other commercial groups was so great over the years that the fishery has never operated as the "experiment" that the proposal called for.

Anyway, shortly after receiving his Ph.D. in late 1965, Murphy left CalCOFI and took a position at the University of Hawaii. In fact, I am told he is the only person known who went from a graduate student to a full professor and took a cut in pay! Phil Roedel, who really should be up here instead of me, succeeded Dick Croker as secretary of MRC and was named the acting coordinator after Murphy left, a position he held until the mid-seventies. Then Marston Sargent came on and served as the MRC coordinator from mid-1971 until his retirement in 1974. Thereafter, I guess a number of people have served as coordinator—Herb Frey, I know, for a number of years, then George Hemingway, and now Reuben Lasker.

I was asked to speak on the role of MRC and CalCOFI, and what I have discussed is a combination of their roles and a history of their activities. The Marine Research Committee was established at a time when the sardine fishery was showing very strong signs of overfishing. California Fish and Game was urging curtailment of the catch, and had been for a number of years. Others were questioning that fishing was the cause of the failure of the sardine fishery. The industry agreed to tax itself to fund needed studies. What started as a delaying tactic to avoid management resulted in a research program that has provided much better understanding of the California Current system, and technological development that otherwise might not have been possible.

Of course, we lost the sardine, and I leave it to you to decide whether it was all worth it. CalCOFI continues today even without MRC. Would it have gotten started and prospered as it has without the small start MRC provided, without the coordination made possible by MRC, without the political clout that MRC and its members exerted, which resulted in added funding from other sources for furthering the CalCOFI research program? Again, you decide. Thank you.

* * *

Lasker: Jack, I wonder if you would consider today's very large anchovy fishery as the experiment you were talking about, considering that a total of 300,000 tons of anchovy is now being taken from both sides of the border.

Baxter: I considered that, and I conveniently left it out, but, yes, I agree. Of course, it hasn't gone on for three years. We haven't monitored as closely, I think, as our origial experiment envisioned. But even with the drop in anchovy biomass on our side of the border in recent years, the sardine has failed to reestablish itself. It makes me wonder, too, but I still think it was worth the try.

Question: Jack, may I answer Lasker's question? The reason we can't really come off with the experiment is that there are not enough sardines left. Remember that we were going to cut the harvest of the sardines to 10,000 tons. At this time I don't think there are 10,000 tons or close to 10,000 tons of spawning biomass left.

Comment: It's too small to measure by our present methods anyway.

AN OCEANOGRAPHER'S PERSPECTIVE

JOSEPH L. REID

I suppose it's my turn now to add what I can about an oceanographer's perspective on this system. I think perhaps I'd better say how I got into the trade, because I came in sideways and unexpectedly. I entered Scripps as a graduate student in physical oceanography in 1948, my interest in the ocean having been engendered by some naval service. I was a student of Walter Munk's for a while, but he couldn't quite keep up with me, so I got some half-time research support, the usual kind a graduate student gets, from Marine Life Research.

About 1950 or '51 I began to attend these conferences. Well, I felt myself a very sharp young physical oceanographer who was certain to straighten these people out in a very short period of time. I could not understand—as you will, I think, from having heard what these people have said, particularly Jack Baxter—why all of these people, the feds on one side and the loosely called confederates on the other side, were having such terrible battles. I really thought they assembled annually to hear me tell them about the physical oceanography of the California Current. It took me a while to come up to speed on this.

But the format of the conference was a little different in those days. There was a higher proportion of business discussed at that time, although the papers given still dominated the sessions. I would usually give a paper, and being very full of the kind of research that could be done in physical oceanography, I would talk for fifteen minutes or so about geomagnetic electrokinetographs (GEK's), acceleration potential, geopotential anomalies, electromotive forces, and things of that kind. About half-way through my talk, Frances would look at me and say, "Joe, what do you really mean?" . . . I think it might be useful if questions of that nature were asked more frequently in the middle of these presentations. Of course I did have something to say, but I need not have said it quite in those words. By the time I thought about it and expressed it in a more rational way, nobody had any trouble understanding it. It really wasn't all that complicated. In fact, I think some biologists read my papers in physical oceanography in preference to others because at least they can understand what I'm saying, and if they can, they should thank Frances.

Then I would finally get to the end of my spiel, and Roger Revelle would get up and say, "That's not so." And I would say, "Yes, it is!" And we would argue. Here I was, the lowest graduate student on the totem pole at Scripps. I don't mean to imply that Roger was always wrong or always right, but in those days, it didn't matter at all whether Roger was right or wrong; he would win those arguments. There was just no question of it. I would look out into the audience, and there would be Ahlie Ahlstrom and Dick Croker and the like, grinning like apes at my discomfiture, of course. Then as I left the stage, Frances would look at me with her kind, sweet smile and pat me on the back. Our technical director, Bob Miller, whose name has come up before, would take me out and buy me a drink. That was, I guess, one of his job requirements under those circumstances, one of his many functions to keep the place going. Then we would be ready to continue.

What was oceanography in those days, and what were we doing? I suppose the state of physical oceanography in that period—and, in fact, of oceanography in general—could be summed up in the 1942 work of Sverdrup, Johnson, and Fleming because, of course, the war had intervened, and very little had been done in most fields of oceanography during that period. It was Harald Sverdrup himself who started the work in physical oceanography here, and he was one of the major protagonists in the proposals that got CalCOFI started. We began with his ideas and the people that he had trained or had begun to train. The physical oceanographers in those days were Bob Reid and Paul Horrer and Warren Wooster, who had come a little earlier than I had, joined shortly by Feenan Jennings. I don't know what you think of this motley crew, but that's what was assembled out at the Scripps Field Annex at Point Loma in those days.

What was there to work with? Up to that time oceanography had been dominated almost entirely by the work of the Scandinavians and more lately by the Germans, with some from the U.S. The work was either large-scale exploration—the *Dana* expeditions, the *Carnegie*, the *Deutschland*, trying to get at the general circumstances of the ocean—or of localized bays and estuaries. Nansen had done his work on the source waters of the North Atlantic; Brennecke had worked on the source at the other end, in the Weddell Sea; and we knew at least that the major deep water masses of the world ocean were formed mostly in the Atlantic. But the kinds of studies that they were able to make were limited to statements about the general circulation or the mean flow, with little time or money for finer-scale work on variability.

However, these people were very sharp. In fact, there is a wonderful paper by Helland-Hansen and

Nansen in 1909. They had gone to sea making traditional hydrographic casts, measuring what they could, and when they analyzed their data, they found not large-scale smooth fields but rather wobbly ones. There would be a station-to-station variation of the depth of various isotherms. Of course, they didn't get to sea very often, and they couldn't repeat their measurements as much as they liked, but they at least thought about them and wrote about the patterns. They didn't know whether the patterns represented mean flows on a smaller scale than people had supposed, or were waves of some kind, huge solitary waves, or were little anticyclonic and cyclonic gyres. They were able to repeat a few of their lines here and there and found that things changed in time as well as in space. Their work was limited by the facilities at hand, but they did say such things as, "Gee, it looks different from time to time. We really should try to augment our work and repeat lines whenever we can, make our observations as close together as possible to avoid aliasing, and whenever possible, stay in one place for a while, repeating the observation to get some feeling for the time variation." That was 1909. Now, that would have been a perfect prospectus for the Atlantic MODE operation if anyone in the MODE group had ever read the paper, but I don't think they had.

That was the background in which we were working. Some notions of the general circulation were at hand in 1948 when the cruises were planned, but we had little feeling for the kind of spacing required to define the field of flow and patterns of the other characteristics, and at what intervals we would have to occupy these stations to follow their time-fluctuations.

Cruise I of MLR and CalCOFI went out in March of 1949, and I was on the *Horizon* (the old *Horizon*, not the *New Horizon*). We also had in that early period such ships as the *Paolina-T* and the *Crest*. May I have a show of hands of people in this group who were ever at sea on the *Paolina-T*? Bravo. Well, I don't have to tell you what she was like. She was a perfectly seaworthy vessel. She would never sink—though we kept hoping! She just didn't care which end was up.

You remember perhaps what our 1949 pattern was like. We had about twelve lines spaced 120 miles apart going offshore from the west coast of North America, and the stations were spaced about forty to sixty miles apart along each line. We found out from the first few cruises that we hadn't done it quite right. We discovered by our own examination, not from anyone else's sage advice, that we would have to tighten this line of stations and spacing in order to get what we were after. I think I'm talking mostly about the physical oceanographic aspects of it, but it certainly proved to be true, and perhaps might have been noticed even earlier, in the egg and larva work. I'm not going to criticize the biologists at this stage; I am sure there are enough of them to do it for each other.

But this was a primitive period of physical oceanography. Out in the California Current we found strange shapes that did not fit any of the concepts we had in mind. There were unexpected loops and whorls in the temperature field on various scales. We calculated that the topography of this sea surface had undulations on a scale that we hadn't anticipated. And what were these?

At that time, someone decided they must be internal waves of a semidiurnal period, and we invited a very distinguished Austrian oceanographer, Albert Defant, to come and work on it. He came for a year or so and tried to make some accounting in terms of the concept of semidiurnal internal waves, but that wasn't the right answer. In fact, when he left, I was assigned to carry out, on the later cruises, the same kind of calculations that he had made for the earlier ones. But it seemed obvious to me that this was wrong, and I was able by that time—believe it or not, with Frances's encouragement and Roger Revelle's education—to approach people in the right way and say that we should not do this sort of smoothing any more.

The program, of course, was not just physical oceanography, but was intended to include biology and chemistry as well. Warren Wooster was a chemical oceanographer in those days before he moved more into the physical end. We did try to measure oxygen, which we did successfully. We were not so successful with nutrients at that time. We tried in the first year or so, in fact, to measure chlorophyll, but our primitive techniques were not good enough. Finally, the chlorophyll program was dropped and only recently reinstituted.

We did, on the basis of, say, the first ten years of data, begin to find some reasonable patterns relating some variables to others. As you recall from reading the proceedings of the 1958 Rancho Santa Fe Symposium *(CalCOFI Reports, Vol. VII),* people such as John Radovich had even then been able to establish relations between some patterns of fish distributions and the sea surface temperature anomalies. There were relations between those two and various kinds of fish that were taken both commercially and by the sports fishermen; that is, there were nonseasonal northward and southward movements of various species that tied in rather well with variations in the physical characteristics of the ocean.

Also, even at that period, the data showed an inverse relation between the temperature and the zooplankton volume. With only seven or eight years of data, the statistics were not as convincing as one would like, but I think both of those conjectures have been borne out by the following twenty years of data, as shown in the recent studies by Bernal and Chelton. So we have accomplished some things and established some relations and patterns, but we haven't learned everything. We certainly have not yet learned enough about the system to make a firm prediction about the success of each year class of the major fisheries.

Now, does that make us unique in studying the ocean? I don't know. We've done a number of things in the California Current domain, including work with drogues and direct measurements of flow with GEK's. We've studied such things as inertial rotation and upwelling; I won't try to list all of the things the biologists have done in this program.

But in general, what have the CalCOFI meetings achieved? What has been discussed or, to put it another way, what has not been discussed at these meetings in the thirty years that I have been attending them? I remember that, at the time, the earlier conferences seemed to be dominated by minutely detailed presentations of successions of year classes of various species beginning from before the time of the Flood. After all, I suppose Noah was the first oceanographer. (I mean Noah the biblical character, not the governmental body. But I think the record shows that after only one major cruise he left the field and took up growing grapes.) But as a newcomer to the field, I found some of those presentations as dreadful a bore as some of my discussions of the GEK must have seemed to Dick Croker and to Ahlie and others.

After all, I expected that the physical oceanographers would have the whole problem solved within a year or two. (I was very young.) But after a while it began to appear that the problem was a great deal more complicated, difficult, and in fact much more interesting than I had imagined. The sum of all of those charts on long, long sheets of butcher paper (audiovisual aids were rather primitive at that time) began to take some kind of effect.

The term *ecology* was not used so frequently or so lightly in those days, but is that what we were up to, even then, whether we recognized it or not? The topics discussed covered everything—winds, currents, temperatures, eggs and larvae, salinities, nutrients, chlorophyll, oxygen, food webs, internal waves, diurnal migration, inshore and offshore populations, eddies, spawning seasons, upwelling, narrow- and wide-ranging species, larval survival, catch per unit effort, competition among species, chlorophyll maximum, and light penetration. I know I've left out a number of items, but we can't go on all day with this.

How many times have you heard someone in this field suggest that there should be a meeting involving people in all of the disciplines appropriate to fisheries, or to ocean circulation, or to the nutrient distributions, or to ocean productivity? Anyone who has attended CalCOFI meetings for any length of time and listened carefully would have learned that no one of these problems can be attacked separately. We must take bits of information from all of these fields and put them together. Each contributes to the understanding of the others. They are simply different aspects of the same problem.

At CalCOFI we have for years maintained a breadth of view and assembled a range of disciplines and interests that is outstanding among the meetings I attend. Indeed, so many scientific meetings are becoming more and more narrowly focused. This may be proper in some cases, of course, but we should at least see that some meetings are broad enough to encourage people from wide ranges of disciplines to attend and exchange information and ideas.

At last year's meeting, we had an excellent, concise presentation on the state of the fisheries, with some historical review. Later John Hunter stated, among other things, that the anchovy population off southern California eats about thirty million tons of copepods each year. Now, it's not the first time I had heard that, or analogous information, but somehow the context in which his facts were put really got to me. All of a sudden, I realized that what we have done in CalCOFI's history is to assemble the world's greatest and most nearly complete set of background information bearing upon an ecosystem of this scale. Of course we've not done enough. The word *ecology* has been used much too lightly by many people, and we are not yet ready to say that we understand this ecosystem—that is, that of the waters off the Californias—but are we not in a much better position than most such groups?

This may be what the creators of this program had in mind, or they might have, more than thirty years ago, expected easier and narrower solutions. I don't know, but in any case, I think they have built very well. It is our turn now to continue putting these many pieces of information together to try to understand the system. I think the burden is on us for two reasons. One is that we owe it to the people who created and supported the program. The other is that we may already be closer to understanding our system than any other group is for its own particular part of the ocean. It would be dreadful if we fell behind.

I would like to mention a little more about the people who have spoken today. As I said, in her presentation Frances did not talk very much about the science she did. She made very little reference to her science, though she has done a great deal. Instead, she and the others have talked mostly about the beginnings of this field, the means by which these programs were created, funds obtained, equipment arranged for, labors of Hercules performed, problems faced at each stage.

Now, I and many of you have made no such contributions as yet. We've been simply riding along on their shoulders. They've made it possible for us to do what we have done and to continue doing what we are doing. They know this. Do you? If you do, do you make the mistake of thinking that all of their efforts were spent in management and none in science? If so, look at the record and think again.

PERSONALITIES IN CALIFORNIA FISHERY RESEARCH

P. PATRICIA POWELL

Good afternoon, my friends. I've attended many CalCOFI meetings, but this is the first time I have participated in the program. I am very honored to be here, and I thank Dr. Lasker for inviting me.

I feel inadequate in the presence of all these people whose brilliant scientific research, compassion, understanding, and ideas have made this conference significant in developing ocean research in the eastern tropical Pacific. I've only been an observer who has been included as part of this team. I am very grateful for this. To me, CalCOFI is a group of people who have worked together in spite of their personal differences, and anyone who has been associated with them in their work has been considered part of the team. Looking at the 1950 progress report, which was the first one published, I was delighted to find my name listed in the back as one of the people working on the program together with the most prominent scientists, the ship cooks, the crew, clerical assistants, technicians, and all persons who contributed to the launching of CalCOFI. I thought this was beautiful.

When I was twelve years old, I had to write a paper for some school assignment, and it just so happened I came across a description of Scripps Institution of Oceanography. I wrote about it, and I felt I'd love to work there. To me, assisting this institution would be the most wonderful thing I could do. Well, twenty-five or more years later, I began to work with the Department of Fish and Game, California State Fisheries Laboratory, which was engaged, in part, in similar research. I felt like a pilgrim who had come home when I began to participate, such as I did, with this research. I was hired as a librarian. I knew nothing about biology or marine science. But I had the whole wealth of published research in these fields to organize, index, and pass on to persons engaged in marine research. I felt that I finally was participating in the work that I really wanted to do.

There is a saying that what mind can conceive, man can achieve. CalCOFI to me is an example of that. Also it is said that when there is an idea whose time has come, it will come about. The idea for expanded, cooperative ocean research came in the postwar years, and the timing was right. Dick Croker said today that many people who had served in World War II had traveled far from their home localities and jobs, from a routine or sometimes sedentary existence. They had been exposed to many peoples and many different kinds of activities and places. Also, World War II made this a nation that worked together as a team. We came out of the war with a feeling of exultation at having won. The Californians in the field of marine science came back to settle down to their jobs, with expanded concepts of research. They were the Wib Chapmans, the Benny Schaefers, the Dick Crokers, and numerous others who would probably have gone their separate ways had it not been for the war.

There was an excitement in the air in the late 1940s. New activities, new opportunities opened up in many fields. The fishing industry was bursting wide open. People used to come into our laboratory and our library, looking for information on the fishing industry, boat building, marine research of all kinds. They wanted to go into fishing. They wanted to learn about it and expand it. Students wanted to take up marine biology or oceanography as a profession. The time really was right for expansion. And the right people happened to be at the right place at the right time to bring it about. The failure of the sardine fishery was the crisis that brought together the fishing industry, businessmen, and the scientific community, and evolved the present CalCOFI program.

Again I refer to Wib Chapman, Elton Sette, Ahlie Ahlstrom, John Isaacs, and many, many others. Wib Chapman was working as curator at the California Academy of Sciences. He envisioned feeding the world through expanding fisheries. He became a crusader while he was at the California Academy of Sciences, writing letter after letter to people in places of importance, saying that there should be a national oceanographic program. I remember one letter which said that we were the only country in the world that did not have a research program to study ocean currents, the fluctuations of fisheries, and our marine resources.

When the sardine fishery failed, the fishing industry formed a California Fishing Product Institute. Dr. Sette was engaged as its consultant. Dr. Chapman and Dr. Sette worked together to organize a multidisciplinary cooperative research program that would expand throughout the entire North Pacific Ocean and include physical oceanography, biological oceanography, meteorology, and geophysics. All significant research and industry personnel in these fields were contacted and asked to cooperate.

One of the first meetings of these groups is described in a letter written on January 20, 1947, by a Colonel I. M. Isaac, chairman of the California Fishing Products Industries, to Don Loper, lobbyist for the sardine industry. Colonel Isaac said, "A recent meeting which was held at the California State Fisheries Laboratory included Dr. H. U. Sverdrup of the Scripps Institution; W. M. Chapman at the California Academy of Sciences; Dr. Frances N. Clark and R. F. Croker, California Fish and Game; Montgomery Phister, Van Camp Seafood Company; and Mr. Dave Rubinette, I. M. Isaac, W. M. Morehead, and D. T. Saxby, all from the research committee of California Sardine Products. It was a unanimous opinion of all authorities present at this meeting that expanded oceanographic research was imperative if the important fisheries resources of the Pacific Ocean are to be on a competitive footing with those of foreign countries."

Now, that meeting took place in late 1946. It was perhaps the first time industry personnel and scientists sat down together to find political and economic means of solving this problem and to bring about action in the California legislature to create a marine research committee and to propose a tax of fifty cents a pound on sardine landings. Well, this isn't the subject of my talk, but that meeting really stirred my imagination and aroused my excitement. It was held in my library, and I was present as an uninvited observer.

Dr. Frances Clark is a brilliant scientist. She was my boss and exceptionally patient. She had been interested in the library and organized it herself according to standard library procedures. For the first three years I worked there, she taught me marine biology. I asked her a million questions, and she never once was impatient or annoyed, although she was very, very busy. Then she felt that I should extend my knowledge and attend the meetings about fisheries research to find out what was going on, so I would know what to buy for the library, what to catalog and index, and how to meet the needs of not only our scientists but also of outside agencies. Dr. Clark is extremely modest about her accomplishments, but many young biologists came to me and said they wanted to work with the Department of Fish and Game because they wanted to work under her and be trained by her, which is a very great compliment to a wonderful lady.

Dr. Chapman used to come to our library; he loved literature and was an inveterate collector of books, reprints, reports, and any publication containing ocean science or fisheries information. He would tell me of new laboratories that had opened and how I could get material from them. So he and I established a rapport, as I had with Dr. Benny Schaefer and others who loved to acquire information and get it to the attention of others who wanted or needed it. Dr. Chapman was constantly going from country to country, promoting marine research, but often he would take the time to write me a note or to send me documents and papers from meetings he attended that I could not get otherwise. I found him a most human, warm, and interesting person. Dr. Clark told me this story about him: she said that when she was acting chief of the Bureau of Marine Fisheries in San Francisco, and they sometimes tended to forget her, Wib Chapman always made sure that she was never overlooked in any conversation or discussion or any situation that arose. That was typical of the man.

One of the things that I loved about CalCOFI was the meetings. I attended them in the daytime, listened intently, and diligently took notes, trying to be quiet. It was not until the happy hour, when I could sit at the table and talk with people, that I really came to life, and it wasn't the fruit of the vine that did it. It was the stimulation of talking to these people and asking them questions and getting answers to things that any high school student should have known, but I didn't know. All my questions were patiently and fully answered. It was my first graduate education in fisheries and scientific research, so to speak, and it was a delightful one. But, also, I'm a very outspoken person. So I didn't hesitate to express my own thoughts on what they were doing and how the research should go; of course this was very presumptuous, but I never once was put down. I was politely listened to, and sometimes my advice was taken, which was very surprising! My library work supplied me with a wonderful source of knowledge about fisheries.

After the happy hour and dinner, the group would retire to the conference room, and then there would be an open discussion led by Professor Isaacs, Dr. Wooster, Dr. Ahlstrom, Dr. Tully, and many others. Anyone present participated in these meetings. You could say what you pleased, and attention would be paid to anything that was said. The ideas that came out of those meetings were absolutely fascinating. I can remember when Professor Isaacs first brought up the idea of an unmanned buoy. Surprisingly enough, everybody accepted it. Well, it was surprising to me. The idea became a significant part of later research programs. But in the beginning it was just thrown out by Professor Isaacs in one of those evening discussions the way you throw a bone to a dog to gnaw on. He just wanted to get some feedback on it, which he did.

Another time he said that since there was a water shortage in California we ought to lasso an iceberg and haul it to southern California and anchor it offshore as a source of fresh water. Since then I have found quite a few papers expounding such plans as practical, particularly in the Red Sea area and in the parts of other continents where water is scarce. I don't know whether it could be done or not, but it has been taken seriously. Those meetings would go on until ten or eleven o'clock at night. When people who had conceived the CalCOFI program got together, there was seldom friction in their differences of opinion. Yet there was an abundance of divergent ideas.

I also was impressed that published reports, such as the Three Johns Report discussed earlier, were expected to be unanimous before they were presented to the chairman of the Marine Research Committee. When groups that have widely diverse ideas of what should be done can come up with a unanimous opinion, it is remarkable. This reflects the caliber of the personalities involved.

Dr. Chapman, as you have said, had joined the jet set. I was fortunate enough to go to Ghana at the request of that government to organize a fisheries library and set up a system of obtaining information to continue it. Later, I went to all the west coast countries of Africa to see what marine fisheries information facilities they had. While I was in Abidjan for two days, to my surprise Dr. Chapman came on FAO business. He arrived about eight o'clock one night. He saw me in the hotel lobby, came up and put his arms around me and gave me a great big bear hug. He turned to the people with him and he said, "Take her to the bar. As soon as I get into something comfortable, I'll be down." So for the next two hours, we talked about CalCOFI and the work that was being done and had been done and what future plans were; it was a delightful evening. I thought I was a nobody compared to the people who formed CalCOFI, but to him I was an interested participant, and my interest merited attention.

Dr. Ahlstrom was conservative, but open-minded and a very disciplined scientist. I had great respect for his ideas. He wasn't outgoing like Dr. Chapman, but he never hesitated to speak up and say what he wanted to say. One morning at one of the CalCOFI meetings he called me to one side and told me about the new laboratory that had just been built in La Jolla. He said, "Pat, I would like you to be our librarian." Well, this startled me. I was speechless for once. The rest of the day I was on cloud nine and didn't hear what was said—not that I wanted to leave my job, but I thought this was a great honor.

During the next few weeks, I filled out the forms that the federal government required, and he offered me the job at a high government rating. He had told me that I would have a chance for advancement, that I could attend meetings, and would not be inhibited in any way. I could run the library to suit myself. Dr. Clark and Dick Croker and my other supervisors in California Fish and Game had always given me a free hand. I didn't consider I was under supervision. That was my library, and I was going to see that it was run the way I thought it should be.

When it came down to really deciding, I found I couldn't leave my library. I couldn't leave the people I had worked with. I was part of their team, and the hardest thing that I ever had to do was to tell Dr. Ahlstrom that I couldn't accept the job, but would help in any way I could. He was so gracious in his acceptance that from that time on whenever I saw him, I always felt a warm rapport with him.

Dr. Sette was an entirely different person. He was, to me, an intellectual giant, very quiet, but—as the saying goes—still waters run deep. I was fascinated by the way he would conduct his meetings, and by his comments. I would get into a discussion with him when he had the time, and he, too, showed me all the patience in the world.

I got to know Dr. Sette very well, particularly after he retired and had his office in our Menlo Park Laboratory. One of the great loves of his life was his library. It was well organized and documented, especially his extensive reprint collection. Whenever I was in Menlo Park, he would ask me to lunch, always a different place, and discuss the disposition of his library. I told Dr. Sette I would do what I could to help keep his collection intact. I visited him in the hospital a few days before he died. He could barely speak. He looked up at me with those big blue eyes of his, and I said, "Can I do anything for you?" He nodded and said, "Yes, take care of my library," which touched me very much.

His reprint collection is intact, and his index cards are located in the Marine Resources Library in Long Beach. We had no room for the bound volumes there, but they are in Menlo Park, at the California Marine Resources Laboratory. There is a listing of all his material. Most is bound volumes, like the *Journal of Marine Research* of the Sears Foundation, and can be found in major university libraries. This list can be useful in checking on literature sources he used in his research.

John Isaacs just delighted my heart, too. He was a brilliant man whose ideas came fast and furiously, and he was flamboyant in the way he expressed himself and in the things that he did. I used to be amused at the CalCOFI evening meetings when he would suggest seemingly impossible ideas to be researched, or make comment on others' ideas just to throw them off balance. He was annoyed when addressed as Dr. Isaacs. He said he was a professor, didn't want to be called a doctor, and didn't wish to have his name associated with a doctoral degree.

Once we had a meeting at Goleta. I always went out for early morning walks; I loved to bird-watch. Also, many wonderful people in CalCOFI would get up at six o'clock in the morning to go walking before the meeting began. Frances Clark started me birdwatching and helped introduce me to birds, trees, wild flowers, and many other interesting aspects of nature. Often others joined us. As usual, at Goleta I was out early one morning, and met Professor Isaacs. As we walked along together he said, "Pat, you must be one of the original women's libbers." I said, "No, I'm not a women's libber. I enjoy my status as a woman and the courtesies that men show me." We went into the cafeteria for breakfast. When we went to pay our bill, he said, "Pat, since you're not a women's libber, I'll pay for your breakfast, and I'll carry your tray for you!"

Later that evening, before the social hour, he came to me and asked, "Did you bring any liquid refreshment?" I said, "No, I didn't have time to get any." He said, "I have my car here. Let's go into town." So we went in and found a store and he bought all sorts of crackers and nuts and goodies and a quart of Wild Turkey. When we got back to the dormitory, he handed me the package, saying, "Now, why don't you take this to your room and invite people in. I'm sorry, I have some business to attend to, but I'll stop by later on." It's a side of him that I think many people did not get to know.

I was national chairman of the biological sciences section for the Special Libraries Association one year, and part of my job was to set up a program including tours and a luncheon with a keynote speaker. It was to be at the Hilton Hotel in San Francisco. About six months before the meeting I saw Professor Isaacs at our Long Beach laboratory. I asked if he would be the keynote speaker for the meeting. His answer was, "Pat, I'll be glad to. I like librarians. Check with my secretary to see if that day is free."

The day was free and the day came. I met him at the airport and took him into San Francisco, where we had provided accommodations for him. He would not accept an honorarium. On the way into town, I said, "Professor Isaacs, please don't talk down to this group. These special librarians are experts in their fields." He looked at me very seriously and said, "Pat, I never talk down to anyone."

He gave a talk that the librarians would never forget. He brought his underwater pictures of fish. Everybody was fascinated. Years later people have told me how much they enjoyed his presentation.

He told me at the time that he and his sister had run a boutique in Maiden Lane in San Francisco, which rather surprised me. Later on, Mrs. Isaacs, a member of the People-to-People organization in La Jolla, asked me to help get books together for the marine school in Ensenada. When the time came to deliver the books, she asked me to come down and have dinner with her one Sunday and spend the night. Professor Isaacs was away. I went and had a delightful weekend and enjoyed their home very much.

That night when I went to bed, on my bedside table was a book of short stories by Saki (H. H. Munro), who was one of my favorite English writers. The next morning I commented on it, as well as the fact that the room was full of books of significant literature, of poetry, travel writings, and biographies, as well as light fiction. I commented on the fact that the short stories by Saki were by my bedside. She said, "Oh, yes, that was one of Professor Isaacs' favorites, and mine too. We used to go salmon fishing when we were first married, and I would read him those stories and the poetry he loves while we were fishing."

At another time, at a San Clemente conference, Paul Smith told me that Roger Hewitt was writing a history of CalCOFI, and that he was a young lieutenant, fresh out of the Navy. I thought, "What does he know about CalCOFI? Who is he to be writing a history of CalCOFI? He has no idea of all that has gone before, and he really has no access to some vital information." Much to my regret, I told him my opinion of his lack of background for such an undertaking. I really embarrassed myself. Well, I apologized, but he told me today that I could tell this, and he said that what I really asked him was what right did he have to write about history if he hadn't lived through it! I felt so strongly that any history of CalCOFI should have a personality reflecting the personalities of all the wonderful people that created and guided it so brilliantly and successfully.

Now, I would like to tell another story. I want to tell you about Dr. Schaefer. When he used to come to the California State Fisheries Laboratory to see Dr. Clark and others, he never failed to come into the library to say "hello." Then, since he read Russian fluently, he would translate all of the titles of Russian publications in the library into English for me. Finally one day he said, "Pat, I learned how to read Russian in six hours, and you can do the same if you put your mind to it." He overestimated my ability, but he never failed to try to help, if he could, in any way.

Another story I think is interesting concerns Anatole Loukashkin, from the California Academy of Sciences. Anatole is such a conservative, perfect individual. He always appeared correctly dressed, and he would never say anything off color. CalCOFI met in Avalon one year in December, and Anatole was there wearing the long coat and black hat that he always wore. He customarily carried a little container of brandy in his vest pocket. After the luncheon meeting one day, he brought out the brandy. Gertrude Cutler, Laura Richardson, and I were there, and he shared it with us. Then we walked back to town from the meeting, which was up the hill in the clubhouse. Since it was close to Christmas, and having had the brandy, we started singing Christmas carols. We went all over Avalon, belting out Christmas carols at the top of our voices, with Anatole singing as loudly as we were. I thought this was a charming insight into the dignified Anatole.

Another thing I want to say—one night, and I think it was at Torrey Pines, we moved from room to room where there were still drinks available. I walked into a room where Joe Reid and Professor Isaacs were lying on the floor on their backs, with their heads against the entrance to the bathroom, stretched out. They had their socks off and two peanuts, which they maneuvered with their big toes. They were trying to see who could be the first to get his peanut to the entrance of the room. I think Isaacs won because he was longer than Joe, and his toe was bigger!

Well, I know my time is up. I could go on indefinitely, telling stories, but these are some of the things that have made CalCOFI very special to me. In fact, I've had a love affair with it for thirty-four years. Thank you for having me here!

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Reid: I believe that Dick Croker wants to interject one more sentence into his diatribe.

Croker: When I heard from Reuben that they were going to write all this stuff down, I remember that I woke up during the night and thought of a sentence that goes like this: With all of the trials and tribulations and frustrations and minor victories, I enjoyed almost every minute of my career, and I would start right where I did a second time around and go through it again.

SCIENTIFIC RESEARCH AND THE TWENTIETH-CENTURY FISHING INDUSTRY

ARTHUR F. McEVOY*

The 1981-82 California Sea Grant College Program directory includes two projects devoted to the history of public policymaking for the fisheries.[1] This indicates, I think, a new and salutary trend in the study and management of natural resources in the public domain. Long isolated in their various specializations, scientists and scholars interested in natural resources have, since the 1960s, begun to look across disciplinary boundaries for new perspectives on problems that draw their common concern. They have also begun to examine their own role in the making of policy—analyzing the ways in which scientists and other scholars, successfully or not, have tried at various stages in our history to contribute their expertise to developing government policy for resource use.

For students of law and society, J. Willard Hurst of the University of Wisconsin Law School set the example in 1964 with the publication of his monumental study of the role of law in the history of the Wisconsin lumber industry.[2] Hurst's work moved beyond the more typical, doctrinal study of legal change to analyze the ways in which law worked in society, both as an instrument and as a measure of social change. Harry N. Scheiber of the School of Law at the University of California, Berkeley, is likewise well known for his studies of property law and police power, and is currently completing a major work on the development of natural resource law in California.[3] My own work on law, ecology, and economic development in the California fisheries builds on the foundation laid by Hurst, Scheiber, and others, and accords the resources themselves their rightful places as independent agents of historical change.

Clearly, natural resources are more than mere commodities to be brought into the market as technology and demand dictate. They have histories of their own: they influence the course of human affairs through their independent dynamism and through their characteristic responses to human activities. In much the same way as Hurst and his followers have changed the study of law and society, several historians since 1970 have begun to move away from the traditional emphasis in environmental studies on intellectuals' ideas about their natural surroundings. These historians are making an effort to understand (1) how the ecology of natural resources affects their use and (2) the development of social institutions governing that use.[4]

Among natural scientists, Ciriacy-Wantrup set a similar example in a 1952 text on resource conservation, defining *conservation* as a dynamic process influenced by social, economic, and political institutions as much as by the character of the resources themselves.[5] More recently, Richard A. Walker admonished us not to forget that we do not address resource policy questions innocent of history, politics, or of "commitments to pre-existing threads of ideology passed down from those who have grappled with similar problems before."[6] Walker trenchantly observed that effective resource management requires the understanding and manipulation of the human processes that lead people to use nature in particular ways, as well as of the physical and biological processes that we try to harness to our advantage.[7]

Fishery science also has begun to take these issues seriously. The awakening here began soon after World War II, when economists interested in the "common property" problem pointed out that fishery depletion was as much a matter of economic institutions as it was one of biology or population dynamics.[8] The Fisheries Conservation and Management Act of 1976 (FCMA) institutionalized this awareness by mandating the harvest of socially and economically optimized yields (OY) from the stocks under its view.[9] Unlike the earlier, more "objective" concept of maximum sustainable yield (MSY), OY is by itself a slippery and ill-defined standard for policy, but it does oblige lawmakers to make explicit decisions about social and economic concerns—to look at the human side of resource use—when they set guidelines for industry.

All of these developments have their roots in the increasing postwar awareness of the interdependence of different economic activities and of the economy and the environment from which it draws resources. The 1970s, especially, brought a great blossoming of integrated research and legislation along these lines, in many areas of resource policy. The inflation of energy prices, the collapse of the international monetary system, and the emergence of major problems in agriculture and the fisheries worldwide stimulated the new developments of the last decade.[10]

In spite of these advances, however, there remains the old problem of bringing scientific knowledge of natural resources to bear on the legal processes it is designed to inform. Governments and universities invest a great deal of money and energy to illuminate alternatives available to policymakers, but as often as not they have little practical effect. Nowhere is this

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[1] Please see "Literature Cited," at the end of this paper, for all numbered references.

more apparent than in the area of fisheries management—a uniquely public concern, but one heavily burdened with traditional ideologies and vested interests that make it almost impossible for government to act effectively on the basis of scientific information of whatever character. Scientists in the pay of the California Fish and Game Commission, for example, pointed repeatedly to the impending collapse of the state's sardine fishery and pleaded annually for harvest restrictions for many years before the stocks finally did collapse in the late 1940s. What was it about the character of government research and policymaking, and the relationship between them, that prevented enlightened administration of the public's trust in this valuable resource?

California's public effort to adapt modern, integrated scientific research to the management of commercial fisheries began during the World War I era. The institutional structure of modern, industrial-bureaucratic fishery management took shape during this period, when technological progress and growing markets gave birth to the motorized, oceangoing fisheries of the twentieth century. From the very outset of the modern regime, there have been repeated calls from biologists, politicians, and even the industry itself for a coherent, scientific approach to fishery management, although it is only in the last decade or so that we have seen much real progress toward that end. The obstacles to integrated research and policymaking that scientists and lawmakers of the World War I era faced, moreover, were identical to those that confront their modern heirs. Many of the ideological and institutional stumbling blocks that thwarted effective use of scientific knowledge in the century's second and third decades were inherited from the nineteenth century, and continued through the twentieth to hamper California's efforts to undertake the multidisciplinary, integrated research and policymaking that its modern fisheries needed.

The scientists who came during the World War I era to study management problems in California's then-new tuna, sardine, and other pelagic fisheries brought a legacy of more than a century of government-sponsored efforts to apply scientific knowledge to the lawmaking process. According to Hurst, indeed, "no part of the legal history of the United States is more important than the relation between substantive public policy and the acquisition and application of scientific and technical knowledge."[11] The United States has a long history of cooperation between scientists and government. It began in the very earliest years of the republic, when the Jefferson administration established the Army Corps of Engineers in 1802 and in the following year packed Lewis and Clark off to take stock of the Louisiana bargain. The Smithsonian Institution, the National Academy of Sciences, and the colleges of agriculture all date from the Civil War years or earlier.[12] Efforts at wildlife conservation began at midcentury, when the environmental costs of industrialization began coming due. As pollution and waterpower development began to take their toll on the salmon fisheries of the Northeast in the 1860s, New England state governments founded administrative agencies to study fishery problems and draft remedial statutes.[13] In 1870 California organized its own State Board of Fish Commissioners, which quickly became one of the most progressive and most emulated in the country.[14] A year later, the federal government founded the United States Fish Commission as an arm of the Smithsonian Institution. In 1903, on the eve of the industrial revolution in fishing, Congress transferred the federal fishery agency to the Commerce Department, where it now survives as the National Marine Fisheries Service.[15]

State and federal governments conceived of their constitutional obligation to secure the blessings of liberty for their constituents in two ways. On the one hand, to be sure, liberty meant the pursuit of profitable self-expression unhampered by arbitrary incursions of state power. The California Constitution of 1879, for example, protected citizens' right to enter public lands and lands sold by the state to private owners in order to fish the waters that flowed through them.[16] Liberty also meant, on the other hand, possessing options, or being free to choose from a wide range of opportunities to make one's fortune.[17] Here lay the *raison d'être* of government-sponsored research and development in the nineteenth century: to provide citizens with technical information and access to tools and resources with which to increase their mastery over their physical and market environments.

Beginning in the Civil War era, as Hurst observed, the people of this nation began to realize that the most important limitations on their opportunities to use natural resources stemmed not from the sheer physical difficulty of recovering them and bringing them to market, but rather from their ignorance of how the natural environment worked and how most efficiently to work with it.[18] From this first acquaintance with the complexity of resource ecology came the approach of the early fishery agencies, with their emphases on describing the morphology and life histories of important species, transplanting exotic varieties to depleted or unproductive waters, and artificially propagating the salmon and trout species most in demand.[19]

There were serious deficiencies, however, in the structure of nineteenth-century public resource agencies and the methods they used—deficiencies that would make heavy baggage indeed for fishery managers in the industrial age. One was that, with few exceptions, neither state nor federal governments made any effort to coordinate the research and development activities of their constituent agencies across related resource policy fields, nor any effort to establish explicit priorities for their work.[20] Related to this was the problem of divided jurisdiction: each agency had its own narrow policy concerns and its own goals and tactics for implementing them. This often led to interagency conflict, which in turn permitted special interests to harness particular agencies to their own purposes.[21]

Finally, and most important, a fundamental weakness in the nineteenth-century approach was that the primary objective of public research was to create opportunities for continued economic growth rather than to discover where the ecology of natural resources obstructed increasing harvests of timber, fisheries, and other resources. Recognizing inherent limitations in the use of particular resources and their interrelatedness with others would have obliged public agencies to make conscious trade-offs between increasing the yield of one resource or another, or between increasing yields in the short term and conserving a resource's productivity for future use. Governments, though, justified the regulatory power they vested in their administrative agencies by maintaining that they gave to industry as well as took away from it, that in addition to policing industry's use of natural resources they also created opportunities for industry to use resources in new and more efficient ways and thus to grow. Promotion and regulation thus went hand in hand in the public management of natural resources. American citizens believed they paid taxes so that government could expand their field of options, not restrict it. This would create serious political problems for twentieth-century agencies like the California Fish and Game Commission or the federal Environmental Protection Agency, which tend to be both regulatory and inhibitive, rather than promotional, *vis-à-vis* the economy.

John Radovich pointed out, for example, that the federal and California state fishery agencies have from the outset had two very different missions: that of the federal has been to promote the development of the fishing industry; that of the state has been, in the words of its charter, to "restore and preserve the fish in state waters."[22] The contrast stems from the difference in each agency's charter and in the opposing constituencies that each of them served. Federal involvement in the fisheries dates from early in the Republic, when Congress generously subsidized the cod fisheries because it believed they were strategically valuable nurseries of seamen for the navy and the merchant marine. In return for bounties on the catch, Congress demanded that the industry conform to federal regulations as to vessel safety, the citizenship of crews, and the like; the industry was in surprising degree federally controlled. Whaling, likewise, benefited from federal subsidies to U.S. shipping because it was an important source of foreign exchange in the early economy.[23] The state agency, on the other hand, was the child of well-to-do sportfishing enthusiasts who wished to restrict access to game fish to ensure an adequate supply for their purposes. These sportsmen have always played major roles on fish and game commissions in California, though at no time as significantly as they did in the commission's first half-century or so.[24]

The interests of these two groups and their captive agencies converged in the late nineteenth century. Each took a great deal of satisfaction from artificial propagation, for example, because it seemed so miraculously to keep fishermen employed and sportsmen entertained. Hatcheries, indeed, consumed by far the largest share of state and federal fishery agencies' fiscal resources until well into the twentieth century, though there was not a shred of hard evidence that they had the slightest effect on the abundance of the stocks concerned.[25] There were good, objective reasons for this emphasis. The empirical, unsophisticated character of most nineteenth-century research meant that most advances in fishery management came not from specialists but from interested amateurs like Livingston Stone, a Unitarian preacher who took up field research in California for his health, and became the guiding force of the country's hatchery movement.[26] Stone persisted in what John N. Cobb later called an "idolatrous" faith in the hatchery panacea because, as Stone put it, "should the Commission make a success of a single river . . . it would pay for all that has been expended in this direction."[27]

That public promotional-regulatory efforts could replace what economic profligacy had destroyed became a shibboleth of U.S. natural resource policy that proved very hard to discredit. A U.S. Bureau of Fisheries agent, for example, observed in the early years of the twentieth century that "through restrictive legislation and artificial propagation," California had maintained the productivity of its salmon fisheries "in the face of most unfavorable conditions."[28] Perhaps the most significant legacy from nineteenth-century fishery managers to their harassed industrial-era successors was this faith in the ability of public agencies and their scientific hirelings to rehabilitate damaged natural systems, abetted largely by economic and ecological circumstances only remotely related to the fisheries themselves. (These included changes in temperatures and precipitation, the decline of hydraulic mining in the Sacramento watershed, and other factors.)[29]

Weaknesses built into the structure of public resource administration during the nineteenth century came into sharp focus during the early years of the twentieth, when state and national governments made new efforts to incorporate deliberate planning and advanced scientific research into the regulation of extractive industries for the now-mature industrial economy. Theodore Roosevelt's administration, highly touted for this conservationism by contemporary partisans and by historians, made concerted efforts to bring interagency coordination and expert planning to natural resource development, especially in forestry and watershed reclamation. In forestry, these efforts failed to surmount competition between special interests entrenched in the USDA's Forest Service and in the Department of the Interior. Efforts at planned, multiple-purpose watershed development fell before the resistance of the U.S. Army Corps of Engineers, the oldest expert agency in government. The Corps' opposition was crucial to the defeat of the multiple-use concept in the Water Power Act of 1920; Samuel P. Hays marked this defeat as the end of the Progressive Conservation movement.[30] During the New Deal, likewise, the Tennessee Valley Authority began as a multipurpose, multiple-agency program to enhance economic development and social welfare in a chronically impoverished area, but quickly became little more than just another power company.[31] On the West Coast, the California Fish and Game Commission entered the century "one of the oldest and most highly respected public agencies in state government" anywhere, but by the end of the World War I period was one of the most harassed.[32]

Public research and administration efforts did increase greatly in sophistication with the onset of the new age, however, especially in the fisheries. By 1910 serious declines in the productivity of fisheries in the North Sea and on the west coast of North America finally made clear to anyone who would pay attention that unregulated harvesting could in fact destroy valuable fisheries.[33] This realization, coupled with the phenomenal growth that motorized, seagoing vessels and wartime demand for processed food brought to California fisheries, led to major changes in the structure of the state's fishery management effort and brought it forward into what became essentially its modern form.[34]

The Fish and Game Commission began by retaining William F. Thompson, who in 1915 had published a pathbreaking study of the North Pacific halibut fishery for the government of British Columbia. Thompson was the first to incorporate some knowledge of economic development into his treatment of fishery problems.[35] Charged with researching the now-important sardine fishery and ensconced in a new laboratory at San Pedro, Thompson hired a skilled team of young biologists with training at California universities, including Frances N. Clark, John O. Snyder, and F.C. Weymouth. Thompson's team introduced California to the catch-per-unit-effort measure—an economic index as opposed to a strictly biological or physical one—and stressed for the first time the critical importance of analyzing natural fluctuations in sardine populations and their potential impact on the industry. The team's mission was to try to pinpoint the fishery's sustainable yield and sound the warning to the commission when the industry reached it.[36]

Other areas of government became interested in fisheries research, as well. USDA, in the service of a rapidly modernizing agricultural sector, commissioned several studies during the World War I era on the use of fishery byproducts for fertilizer and feedstocks.[37] USDA's efforts, begun in an attempt to find profitable uses for cannery waste and for species with little or no commercial value, ironically generated a huge industry devoted to producing fishmeal from whole sardines as well as from cannery offal. This new interest became one of the Fish and Game Commission's most intransigent foes during the interwar period and was ultimately responsible for the demise of the sardine stocks.[38] The California State Board of Health, after several people in other states succumbed to botulism from canned California sardines, worked with the canning industry to establish and enforce quality control standards for sardines.[39] The U.S. Bureau of Fisheries, meanwhile, experimented with processing methods for different species of fish that it felt had commercial potential. The bureau worked throughout the 1920s to improve the technology of sardine canning to help the industry provide a cheaper and better product.[40] Supposedly, this would have fattened the canners' profit margins and relieved them of their dependence on the more profitable and resource-intensive production of fishmeal, but in the absence of meaningful state controls on byproduct manufacture the bureau's promotional effort came to naught.[41]

All of these other agencies' efforts served particular constituencies desiring a steadily increasing supply of cheap raw material from the fisheries. Originally formed to serve a small group of well-to-do sportsmen, the Fish and Game Commission stood alone against these powerful and focused interests and had sole responsibility for recommending to the legislature where limits might be set. The commission's mandate, "to restore and preserve the fish in state waters," was too broad to achieve without specific legislative priorities and adequate resources for meeting them. Thus, whatever conclusions scientists could draw from their rudimentary study of such a complex ecological system as the California Current proved vulnerable to focused political attack from industrial and agricultural interests, all with coherent programs of their own and many friends in government. "Must the scientist always be on the defensive?" complained an anonymous researcher in the commission's quarterly magazine, *California Fish and Game*.[42] "There is probably no division of state government," wailed the commissioners themselves in 1928, "confronted with such difficult and uphill problems, and yet more subject to critical scrutiny, than the Division of Fish and Game."[43] The interwar commissioners might have remembered the cry of their similarly beleaguered predecessors early in the agency's history, who observed that "neither the fish, the public, nor the future of the business appear to have many friends."[44] Faced with so powerful an array of special interests, all demanding that the government promote increased harvests, the commission could do little but plead with the legislature for restrictions. Thompson admitted as much in 1919. "As in the case of the great meat packing corporations," he wrote,

> the public is demanding an actual regulation of the whole fishing industry . . . The question of economic control is, however, not at present placed in the hands of the Fish and Game Commission. It is the Commission's concern to insure a supply, then to aid in its proper and efficient use, and not—at present—to exercise any legal control over the economic phases of the industries.[45]

In defense of the badly damaged inland salmon fisheries, likewise, the Fish and Game Commission pleaded with the California State Division of Water Rights to guarantee minimum stream flows in salmon rivers, but to no avail.[46]

There were demands like those to which Thompson referred, however. Market fishermen in the Bay Area wanted the state to manage the industry so that they might be freed from the power of wholesale fish distributors to fix ex-vessel prices at low levels. Consumers, outraged at the high cost and low quality of both fishery and agricultural produce, demanded public markets for those commodities. Within the Fish and Game Commission, scientists, lawyers, and commissioners pointed repeatedly to the futility of undertaking conservation research without the power to promulgate even emergency conservation measures, and repeatedly asked for authority to set catch limits on sardines and salmon. Bills toward these ends passed the state legislature in 1915 and 1919, but met both times with gubernatorial vetoes.[47] As the sardine fishery collapsed in the mid-1940s, the commission finally asked for power to limit the number of plants producing fishmeal so that a smaller number of firms might more profitably share the reduced supply and thus have less incentive to deplete the stocks still further. The state Attorney General again informed the commission that it did not have the power to regulate economic conditions in the fishery, even if to conservationist ends.[48]

Milner B. Schaefer pointed out in the 1960s that the commission's early disquiet with the fishmeal industry stemmed from its knowledge that the state lacked the capacity to regulate an industry of the scale that fishmeal production was assuming in the 1920s.[49] This was, in fact, the root of the state's inability to save the sardine, despite the certain knowledge of its scientists that the sardine would not long support harvests as intense as those the processors were taking, that increasing harvests were bringing only steady or decreasing catches per unit effort, and despite the annual warnings after 1930 that the fishery's collapse might be imminent. When it came, the collapse was spectacular. The shadow of this failure of the state to translate knowledge into effective law hangs over the commission, through no fault of its own, to this day.

The great growth in the funding, reach, and power of public resource agencies like the California Fish and Game Commission that took place during the World War I era left unsolved two fundamental problems. First, the fragmented structure of decision-making in public resource management served to diffuse responsibility for making policy in areas that, under the pressure of economic growth and technological change, were steadily becoming more interdependent. This decreased the likelihood that prudent, informed policymaking would take place in any of them. The traditional quid pro quo of police regulation to promote economic growth gave interests favoring intensified harvesting of depletable resources a distinct advantage over those whose mission was to limit exploitation within ecologically prudent bounds. Second, this dispersion of authority among several agencies—and the consequent ability of growth-oriented, narrow interests to capture and use them to focus their political power onto the lawmaking process—made it ever less likely that a broad range of interests would be represented fairly.[50] In the case of the fisheries, the underrepresented interests included those of the consumers, the fishermen, future generations of Californians, and even, in the last analysis, the producers and consumers of fishmeal themselves.

Much progress toward solving these problems has taken place since World War II. Economists, natural scientists, and legal scholars have begun to convince lawmakers that the fisheries and other resource industries are, in fact, human industries and that their regulation is a social and economic problem as well as a mathematical or biological one. Since the late 1960s fishery agencies have abandoned MSY as an objective of fishery regulation.[51] FCMA, like most of the environmental legislation of the 1970s, enjoins management agencies to consider the social, political, and economic interests of all the constituencies affected by their industrial policing. FCMA also, as John E. Kelly pointed out, provides an institutional framework for balancing conflicting local and national interests. Power to set optimum yields is vested in regional councils representing affected constituencies, and power to promulgate actual regulations lies at the federal level, where each of these functions might most effectively be carried out.[52]

Scientific policymaking is not and never has been a "scientific," politically neutral process. Samuel P. Hays, in *Conservation and the Gospel of Efficiency,* showed how delegating power over the economic use of resources to technically expert agencies has profoundly antidemocratic implications.[53] But, as Hurst reminded us, democracy and liberty have two aspects: they entail both being left alone in the pursuit of profit, and having options to pursue it. Two hundred years ago proponents of the new, more powerful central government outlined in the 1787 constitution answered the fears of local interests by observing that uncoordinated, decentralized government in the states had in fact failed to protect the liberty and security that the states felt were threatened by powerful national government.[54] At this point, it should be clear that only by rationally planning resource use, by severely restricting citizens' license to use the fisheries and other resources, can government hope to preserve the opportunities of future citizens to use them at all.

We should also remember, when we quail at the power of recently established environmental and resource agencies and the ambiguity of their mandates, that the common law—the foundation of our legal culture—never has required that we base regulation on perfect knowledge of the resources themselves. The California Supreme Court, for example, in a 1925 decision upholding the authority of the Fish and Game Commission to set quotas on the production of fishmeal, said only that "experience has proven" that fisheries may be depleted by a very few years of intensive harvesting, and that the state had the power to regulate or prohibit use of the fisheries in any way it chose so long as doing so *tended* to preserve the public's interest in its commonly owned wildlife resources. In that case, industry's claim that there was no apparent limit to the supply of sardines in the California Current and that the state could point to no imminent, objective danger to the stocks from the fishmeal industry was immaterial, though the "contrary was not unsupported by the facts" in the case at hand. The state, moreover, had every right to delegate "a large measure of discretion" to administrative agencies and their scientific advisers to protect that trust.[55] Intelligent eyeballing, as it were, is all that the law requires. That intelligent eyeballing failed to save the sardine fishery in the interwar period was a function of the powerlessness of the scientists who foresaw its doom and the corresponding ability of focused economic and political interests to *keep* the Fish and Game Commission powerless. The common law of wildlife empowers the state to protect its fisheries as it sees fit; however, it was up to the legislature to establish effective means of doing so.

"One might argue," Walker noted, "that in a democracy the necessary role of science is in the formulation of political positions on major issues, not in the provision of technical solutions to those issues."[56] This, in fact, is what scientists and scholars in public service have always done, whether or not they have been explicit about it or even conscious of it. Ultimately, choices and trade-offs are made politically, and the reason we put scientists on the public payroll is to help us make those choices in an informed way. With FCMA and the other now-embattled environmental acts of the late 1960s and 1970s, Congress recognized that resource management is every bit as much a political problem as it is a scientific one. The success of those programs, in turn, will demand that scientists bring to their work a knowledge of history and a willingness to examine critically their own assumptions and ideologies. In proposing and effecting intelligent resource policy, scientists must vigorously exercise their citizenship as well as their expertise on behalf of the whole people, now and in the future.

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The Collapse of the California Sardine Fishery

What Have We Learned?

JOHN RADOVICH

Abstract

For a number of years, Federal scientists, employed by an agency whose primary goal was to assist the development of the U.S. commercial fisheries, looked for causes, other than fishing, for the Pacific sardine's decline, while California State scientists, charged with the role of protector of the State's resources, sought reasons to support the premise that overfishing was having an effect. At the same time, scientists from Scripps Institution of Oceanography looked for fundamental generalizations in theory rather than the activities of man to explain changes in fish populations. For many years, California State personnel struggled without success to gain control over a burgeoning, and later declining sardine fishery.

Faced with the possibility that legislation might be enacted, giving the California Fish and Game Commission control over the sardine fishery, the California fishing industry sponsored the formation of the Marine Research Committee to collect and disburse funds and to coordinate and sponsor more "needed" research, thereby forestalling any action to allow management of the fishery to come under the authority of the California Fish and Game Commission. Subsequently, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) was formed, under which cooperative research proceeded.

Oceanic conditions (temperature) was found to affect profoundly the distribution, year-class production, and yield of sardines. Nonintermingling or only partially intermingling stocks of sardines have been described. Considerable attention has been focused on the complementary role of sardines and anchovies as competing species acting as a single biomass while competing with each other as part of that biomass. Confirmation of this hypothesis was found to have been based on faulty interpretation of basic data. If such a relationship exists, it still needs to be demonstrated. Density-controlling mechanisms, however, which may be of greater importance, include predation, cannibalism, and other behavioral characteristics. Schooling behavior, for instance, which has evolved through natural selection to decrease mortality from predation, may work toward destruction of the prey species when it is confronted by a fishery which evolves more rapidly than does the species defense against it. A model that is consistent with the results of all the previous studies on the sardine must bring one to the conclusion that the present scarcity of sardines off the coast of California, and their absence off the northwest, is an inescapable climax, given the characteristics and magnitude of the fishery and the behavior and life history of the species.

INTRODUCTION

At a symposium of the CalCOFI conference held in La Jolla, California, on December 5, 1975, on "The Anchovy Management Challenge," a paper was presented by W. G. Clark on "The Lessons of the Peruvian Anchoveta Fishery."[1] It is ironic that California's anchovy researchers felt compelled to learn lessons from the collapse of the Peruvian fishery

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which the Pacific sardine's failure could have provided to them as well as to the Peruvian anchoveta researchers. The observations which follow are presented with the hope that a discussion of some of the social, political, and biological factors associated with the decline of the California sardine fishery will have useful applications in interpreting events now taking place in our fisheries.

After 50 years of fishing for the Pacific sardine, *Sardinops sagax* (Jenyns), a moratorium on landings was imposed by the California Legislature in 1967, thus bringing to an end yet another act of one of the more emotionally charged fisheries exploitation-conservation controversies of the 20th century.

By the time the moratorium was imposed, however, the sardine fishery in southern California had already collapsed. The sardine fisheries in the northwest had long since ceased to exist with sardines last landed in British Columbia in the 1947–1948 season, in Oregon and Washington in the 1948–1949 season, and in San Francisco Bay in the 1951–1952 season (Table 1).

Even before the productivity and exploitation of the fishery peaked, researchers from the (then) California Division of Fish and Game issued warnings that the commercial exploitation of the fishery could not increase without limits, and recommended that an annual sardine quota be established to keep the population from being overfished.

Such recommendations were, of course, opposed by the fishing industry which was able to identify scientists who would state, officially or otherwise, that it was virtually impossible to overfish a pelagic species. This debate permeated the philosophies, research activities, and conclusions of the scientists working in this field at that time. The debate conformed to the basic charters (or *raisons d'être*) of each agency involved and persists today, long after the United States Pacific sardine fishery has ceased to exist. As a result of deep-rooted social and political feelings concerning the collapse of the Pacific sardine off California, many conflicting hypotheses have arisen, in spite of the completion of a vast amount of research.

For example, just recently, a prominent representative of a major oceanographic research institution asserted that it was a "false assumption that overfishing killed the former sardine fishery off Northern California. . . . The real cause of the disappearance of the California sardine was a climatic change."[2] The same official, addressing a group of scientists, stated that

> . . . the explanation of the disappearance [of the sardine] seems to be a change of climate that triggered a major biological upheaval. It was very quiet by our standards, we who live in the atmosphere, but it was violent in that several million tons of one species was replaced by another [anchovy].[3]

If this view is valid, one must ask why scientists of the California Department of Fish and Game supported a moratorium on fishing for sardines. Why did they recommend quotas of 250,000 to 300,000 tons of sardines as a measure to forestall the collapse which they had predicted would occur?[4] MacCall recently postulated that a safe estimate of the maximum sustainable yield (MSY) for the Pacific sardine, assuming it were to be rehabilitated, would be about 250,000 metric tons and that if the catch had been held to that limit the fishery would still be viable.[5]

TABLE 1. Seasonal Catch (tons) of Sardines along the Pacific Coast (Each Season Includes June through the Following May[a])

	Pacific Northwest				California							
					Northern California							
Season	British Columbia	Washington	Oregon	Total	Reduction Ships	San Francisco	Monterey	Total	Southern California	Total California	Baja[c] California	Grand Total
1916–1917	—	—	—	—	—	—	7,710	7,710	19,820	27,530	—	27,530
1917–1918	80	—	—	80	—	70	23,810	23,880	48,700	72,580	—	72,660
1918–1919	3,640	—	—	3,640	—	450	35,750	36,200	39,340	75,540	—	79,180
1919–1920	3,280	—	—	3,280	—	1,000	43,040	44,040	22,990	67,030	—	70,310
1920–1921	4,400	—	—	4,400	—	230	24,960	25,190	13,260	38,450	—	42,850
1921–1922	990	—	—	990	—	80	16,290	16,370	20,130	36,500	—	37,490
1922–1923	1,020	—	—	1,020	—	110	29,210	29,320	35,790	65,110	—	66,130
1923–1924	970	—	—	970	—	190	45,920	46,110	37,820	83,930	—	84,900
1924–1925	1,370	—	—	1,370	—	560	67,310	67,870	105,150	173,020	—	174,390
1925–1926	15,950	—	—	15,950	—	560	69,010	69,570	67,700	137,270	—	153,220
1926–1927	48,500	—	—	48,500	—	3,520	81,860	85,380	66,830	152,210	—	200,710
1927–1928	68,430	—	—	68,430	—	16,690	98,020	114,710	72,550	187,260	—	255,690
1928–1929	80,510	—	—	80,510	—	13,520	120,290	133,810	120,670	254,480	—	334,990
1929–1930	86,340	—	—	86,340	—	21,960	160,050	182,010	143,160	325,170	—	411,510
1930–1931	75,070	—	—	75,070	10,960	25,970	109,620	146,550	38,570	185,120	—	260,190
1931–1932	73,600	—	—	73,600	31,040	21,607	69,078	121,725	42,920	164,645	—	238,245
1932–1933	44,350	—	—	44,350	58,790	18,634	89,599	167,023	83,667	250,690	—	295,040
1933–1934	4,050	—	—	4,050	67,820	36,336	152,480	256,636	126,793	383,429	—	387,479
1934–1935	43,000	—	—	43,000	112,040	68,477	230,854	411,371	183,683	595,054	—	638,054
1935–1936	45,320	10	26,230	71,560	150,830	76,147	184,470	411,447	149,051	560,498	—	632,058
1936–1937	44,450	6,560	14,200	65,210	235,610	141,099	206,706	583,415	142,709	726,124	—	791,334
1937–1938	48,080	17,100	16,660	81,840	67,580	133,718	104,936	306,234	110,330	416,564	—	498,404
1938–1939	51,770	26,480	17,020	95,270	43,890	201,200	180,994	426,084	149,203	575,287	—	670,557
1939–1940	5,520	17,760	22,330	45,610	—	212,453	227,874	440,327	96,939	537,266	—	582,876
1940–1941	28,770	810	3.160	32,740	—	118,092	165,698	283,790	176,794	460,584	—	493,324
1941–1942	60,050	17,100	15,850	93,000	—	186,589	250,287	436,876	150,497	587,373	—	680,373
1942–1943	65,880	580	1,950	68,410	—	115,884	184,399	300,283	204,378	504,661	—	573,071
1943–1944	88,740	10,440	1,820	101,000	—	126,512	213,616	340,128	138,001	478,129	—	579,129
1944–1945	59,120	20	—	59,140	—	136,598	237,246	373,844	181,061	554,905	—	614,045
1945–1946	34,300	2,310	90	36,700	—	84,103	145,519	229,622	174,061	403,683	—	440,383
1946–1947	3,990	6,140	3,960	14,090	—	2,869	31,391	34,260	199,542	233,802	—	247,892
1947–1948	490	1,360	6,930	8,780	—	94	17,630	17,724	103,617	121,341	—	130,121
1948–1949	—	50	5,320	5,370	—	112	47,862	47,974	135,752	183,726	—	189,096
1949–1950	—	—	—	—	—	17,442	131,769	149,211	189,714	338,925	—	338,925
1950–1951	—	—	—	—	—	12,727	33,699	46,426	306,662	353,088	—	353,088
1951–1952	—	—	—	—	—	82	15,897	15,979	113,125	129,104	16,184	145,288
1952–1953	—	—	—	—	—	—	49	49	5,662	5,711	9,162	14,873
1953–1954	—	—	—	—	—	—	58	58	4,434	4,492	14,306	18,798
1954–1955	—	—	—	—	—	—	856	856	67,609	68,465	12,440	80,905
1955–1956	—	—	—	—	—	—	518	518	73,943	74,461	4,207	78,668
1956–1957	—	—	—	—	—	—	63	63	33,580	33,643	13,655	47,298
1957–1958	—	—	—	—	—	—	17	17	22,255	22,272	9,924	32,196
1958–1959	—	—	—	—	—	—	24,701	24,701	79,270	103,971	22,334	126,305
1959–1960	—	—	—	—	—	—	16,109	16,109	21,147	37,256	21,446	58,702
1960–1961	—	—	—	—	—	—	2,340	2,340	26,538	28,878	19,899	48,777
1961–1962	—	—	—	—	—	—	2,231	2,231	23,297	25,528	21,270	46,798
1962–1963	—	—	—	—	—	—	1,211	1,211	2,961	4,172	14,620	18,792
1963–1964	—	—	—	—	—	—	1,015	1,015	1,927	2,942	18,384	21,326
1964–1965	—	—	—	—	—	—	308	308	5,795	6,103	27,120	33,223
1965–1966	—	—	—	—	—	—	151	151	568	719	22,247	22,966
1966–1967	—	—	—	—	—	—	23	23	321	344	19,531	19,875
1967–1968	—	—	—	—	—	—	—	—	71	71	27,657	27,728

[a] British Columbia data were supplied by the Canadian Bureau of Statistics and the province of British Columbia; Washington data by the Washington Department of Fisheries; and Oregon data by the Fish Commission of Oregon. Deliveries to reduction ships and data for Baja California were compiled by the United States Fish and Wildlife Service from records of companies receiving fish. California landings were derived from records of the California Department of Fish and Game.

[b] Prior to the 1931–1932 season, fish landed in Santa Barbara and San Luis Obispo Counties are included in southern California. Subsequent landings north of Point Arguello are included in Monterey and those south of Point Arguello are included in southern California.

[c] The amount of sardines landed in Baja California prior to the 1951–1952 season is not known.

Clearly, these views conflict. Why, and to what extent, do these conflicting views persist in scientific circles? Which concepts are in error? What seems to be the truth? The complete answers to these questions, particularly to the last one, are beyond the scope of this paper. However, it is time to recall a few pertinent events which may improve the historical perspective and provide better insights for the interpretation of the mass of ecological data already accumulated.

HISTORICAL REVIEW

Differences in Agency Perspective

The California Fish and Game Commission began with the approval of an act of the California Legislature creating the Commissioners of Fisheries on April 2, 1870, by Governor Haight of California. The principal purpose of the Commission was embodied in the title of the legislation, "An act to provide for the restoration and preservation of fish in the waters of this State." While the objectives of the California Fish and Game Commission and its Department of Fish and Game have expanded since then, their role as protector of the State's fish and wildlife resources has remained paramount.

In 1871 the U.S. Bureau of Commercial Fisheries was created; the primary goal of the new Federal Bureau was to assist in the development and perpetuation of the United States fishing industries. This goal persists today, despite several agency name changes, even though the present National Marine Fisheries Service (NMFS) too has broadened its objectives somewhat in recent years.

For many years, federal personnel from the National Marine Fisheries Service debated vigorously with personnel from the California Department of Fish and Game on what was happening to the Pacific sardine. The Federal scientists, working for an agency whose fundamental charter was to assist the development and maintenance of U.S. commercial fisheries, looked for reasons other than fishing, for the sardine's declining condition, while the scientists employed by the State (whose basic role was protector of the State's resources) supported the premise that overfishing was having a detrimental effect on the standing stock. These were capable, competent scientists using the same data and coming up with different conclusions in part because they were employed by agencies whose fundamental goals were different.

Scientists are directly and indirectly influenced by the values of their society, their institutions, their academic disciplines, as well as by their personal political beliefs. Each scientific discipline is saturated with values imposed by its specific profession, and scientists are influenced by the agencies for which they work and to which they owe some allegiance. Thus, the definition of a problem becomes a biological one, a physical one, an economic one, a psychological one, a sociological one, even a philosophical one, depending on the researcher's discipline.

As another example, oceanographers frequently define their field as encompassing the ocean and all the sciences that are studied in relation to the ocean. This all-inclusive perspective relegates other sciences (biology, chemistry, physics, and geology) to the position of subdisciplines of oceanography. Such a disciplinary perspective tends to focus attention away from the effects of local human activities on various marine resources and to extend efforts, instead, toward the investigation of large-scale processes in search of fundamental generalizations to explain widespread phenomena. One might argue that an elitism tends to develop, where one finds, for the example given, at the top of the scale the physical oceanographer, and at the bottom, the biological oceanographer. Carrying this example one step further, perhaps because marine plankton is more dependent on currents, temperature, and other physical and chemical processes, phytoplanktonologists tend to be more influential than other biological oceanographers. Oceanographic institutions usually have an ichthyologist on their staff who may teach systematics and distribution of fishes, but other fisheries courses are not always taught in the largest oceanographic institutions. From the viewpoint of a school of oceanography, the solution to most fisheries problems invariably involves a large scale, multivesseled, physical and chemical assault on a large part of the world ocean, because that is how the problem is conceived—by definition, of course.

California State Biologists' Struggle for Fishery Control

A belief prevalent early this century was that the oceans were inexhaustible and that man could not affect the species in the sea. These concepts were expounded by McIntosh, who was impressed by the " . . . extraordinary powers of reproduction of animals and plants in the sea . . . and boldly asserted the inability of man to affect the species in the sea."[6] This general belief still exists (with some changes) at the present time. Others, however, felt that human activities could have a profound effect on living marine resources.[6]

Concerned with the protection of California's living marine resources, California state biologists consistently expressed concern about the rapidly growing exploitation of the sardine fishery. For example, as early as 1920, one such biologist, O. E. Sette, wrote about the sardine in Monterey Bay:

> The possibility of depletion cannot be much longer ignored. . . . we have definite clues to the answers . . . and it but remains . . . to . . . substantiate facts which we have concerning the age, rate of growth, migration and spawning. . . . It now remains for continuance of this study to solve all the problems concerned, and insure the perpetuity of our great resource, through the adoption of intelligent conservational measures.[7]

The difficulties and frustrations encountered by the California Fish and Game Commissioners and their staff in attempting to gain control over the burgeoning sardine fishery are well documented in the publications and Biennial Reports of the California Divison of Fish and Game (later called the California Department of Fish and Game). This early history of the sardine industry (its growth, economics, and legal regulation) has been summarized by Schaefer et al.[8]

After the states of Oregon and Washington approved the use of sardines for reduction to fish meal in the 1930s, there were essentially no restrictions on the quantity of landings or the use made of them in the Pacific Northwest. Inasmuch as the California Legislature never delegated full authority for regulating the sardine fishery to the Fish and Game Commission, the Commission was forced to attempt to control the fishery through the exercise of the only authority the Legislature had delegated to it, control over the reduction fishery. Schaefer et al.[8] and

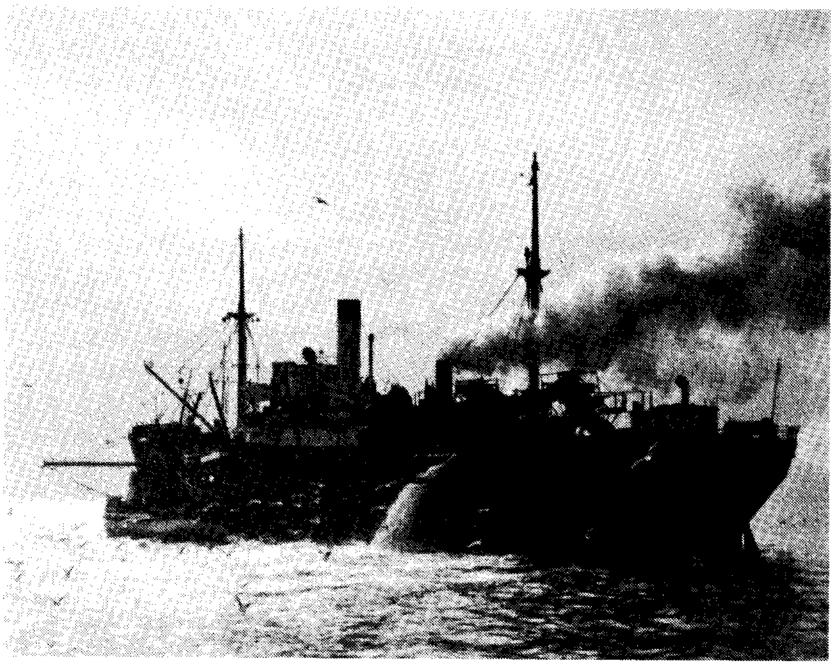

Figure 1 *Lake Miraflores,* the first reduction ship to operate outside the jurisdiction of the State of California, unloading sardines from a purse seiner in the early 1930s.

Ahlstrom and Radovich[9] have summarized the conflicts between canning and reduction interests and the desires of the Commission's biologists to protect the resource from overfishing and depletion.

During the 1930s, straight reductionists* bypassed State control over the reduction fishery by operating reduction ships outside the territorial sea limits, beyond the jurisdiction of the State of California.[9] (See Figures 1 and 2.) To stop the floating reduction plants, an initiative amendment to the California State Constitution was passed in November 1938 that prohibited any fishing vessel from operating in State waters if it delivered fish taken in the Pacific Ocean to points outside the State without authorization from the Commission. The enactment of this law, combined with lower fish oil prices and increased operating costs, ended reduction ship operations after 1938.[8]

As early as 1931, N. B. Scofield, the Chief of the Bureau of Commercial Fisheries of the California Division of Fish and Game, observed that

> the catch has not increased in proportion to the fishing effort expended, and there is every indication that the waters adjacent to the fishing ports have reached their limit of production and are already entering the first stages of depletion. The increase in the amount of sardines caught is the result of fishing farther from port with larger boats and improved fishing gear. . . .
>
> The Fish and Game Commission has consistently endeavored, through legislation and through cooperation with the canners, to restrict the amount of sardines which canners are permitted to use in their reduction plants with the belief that the canning of sardines is the highest use to which they can be put and that the excessive use of these fish in reduction plants would, in time, result in depletion of the source of supply. The majority of the canners, on the other hand, have sought to get quick returns from

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*Straight reductionists were those who reduced all fish received from the fishermen, while canners reduced only a part of the catch consisting mainly of heads and offal.

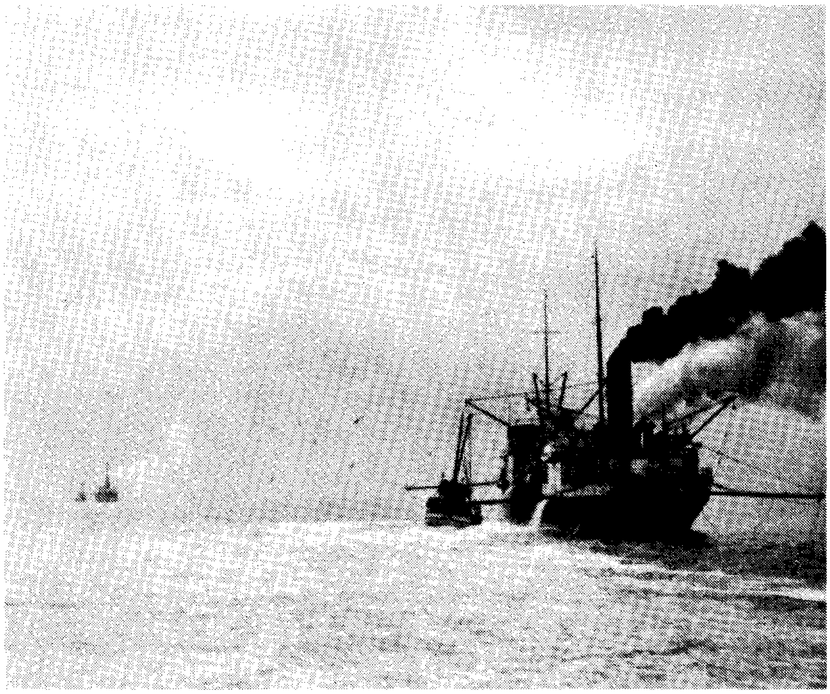

Figure 2 The reduction vessel, *Polarine,* unloading a purse seiner, with two other reduction ships anchored in the distance.

> sardine reduction and have made themselves believe there was no danger of depletion.[10]

In 1931, the State Division of Fish and Game advocated a seasonal limit of 200,000 tons on the amount of sardines that could be landed safely with little effect on the standing stock.[11] In 1934, N. B. Scofield[12] reiterated his view that the catch should be limited to 200,000 tons, indicating that this recommendation had been made 5 years earlier.

In 1938, W. L. Scofield[4] warned that overfishing was causing a collapse in the supply of sardines. He indicated that if the catch were cut to less than the amount replaced annually, the stock could rebuild back to its former productive level. He suggested 250,000 tons as the ideal level of catch. The 250,000 ton limit was also recommended by F. N. Clark,[13,14] who suggested that the limit might be raised somewhat during limited periods of exceptional spawning survival.

Prior to the 1938 initiative amendment to the State Constitution, which happened to coincide with the discontinuance of the reduction ships, an attempt had been made in 1936 to pass federal legislation either making it unlawful to take sardines for reduction on the high seas, or making such operations subject to the laws of the adjacent state. While this legislation was not passed, the attempt to pass it gave impetus to pressures for the establishment of a federal research laboratory on the Pacific Coast. W. L. Scofield[15] wrote:

> The [reduction] ship operators, foreseeing future legislation, resorted to a plan (used before and since) by which anti-reduction legislation could be postponed by asking for a special study of the abundance of sardines and thus disregard the work of the St. F. Lab. [State Fisheries Laboratory] or at least throw doubt upon its findings. The ship operators (mid-1930s) quietly promoted the plan of urging the legislatures of the 3 coastal states

> to ask Congress to have the U.S. Bureau [of Fisheries] make a study of sardine abundance. Wash. and Oregon complied but Calif. legislature refused to ask for Fed. [Federal] help. The U.S. Bur. was anxious to get a foothold in Calif. and sent out O. E. Sette (May 1937). This [was] a shrewd choice because Sette [was] a diplomat and personal friend of Calif. Lab. staff [actually he was a former state fisheries research biologist]. We told Sette he was not wanted in Calif. and asked him to go up to Wash. or Oregon who had asked for help.* Sette answered that he must work in Calif. because most of the sardines were here (not the real reason) and he pointed out that we could not afford to refuse our cooperation in a U.S. Bur. study of sardines. This was true and we had to grin and bear it. Sette started his sardine studies with a staff, housed at Stanford University. By 1938 a plan of cooperative sardine study for each agency was agreed upon.

From this beginning, the two agencies, one state and one federal, expended their efforts in different directions. On the one hand, the State's research biologists, with the responsibility for determining if and when "overfishing" was likely to occur and for making recommendations for appropriate management measures to prevent such overfishing, devoted their energies along those lines, even though their agency had not been delegated the authority to manage fully the commercial fishery. On the other hand, the Federal biologists, with no management responsibilities in (or obligations to) California, maintained a good rapport with the fishing industry, in that they were dedicated to assist the development and maintenance of a viable U.S. fishing industry, and looked for causes, other than fishing pressures, to explain the declines in the sardine fishery. This resulted in numerous debates at meetings and in conflicting scientific viewpoints in technical journals. The debates and conflicts were often based on the same data.

Despite warnings by State biologists that collapse of the sardine fishery was imminent, a large crop of young fish were produced in five successive years, 1936 to 1940 (Clark and Marr[16]). This gave rise to considerable speculation about the effect of environmental conditions on changes in the sardine population and to support for arguments by the fishing industry that nature, not the industry, caused much of the observed sardine population changes. The industry strongly supported the Federal biologists in their search for reasons, other than man, to explain the fluctuations in the sardine population.

The Marine Research Committee

After the large year-classes produced from 1936 through 1940 passed through the fishery, the sardine fishery collapsed to a low point in 1947 (Table 1). The fishing industry, concerned that legislation might be enacted to give the Commission control over the fishery, again resorted to the delaying tactic of advocating or sponsoring more research. In 1947, a meeting was held among representatives of the sardine fishing industry, United States Fish and Wildlife (later renamed U.S. Bureau of Fisheries), Scripps Institution of Oceanography, California Academy of Sciences, and California Division of Fish and Game. This group formu-

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*W. L. Scofield related this incident to me, personally, as follows: "When Sette visited us after first contacting the major local fishing industry leaders, he asked how he could be of help to us. N. B. Scofield told him he could help us best by packing his bags and going back to Washington, D.C." O. E. Sette later personally confirmed this initial dialogue between the representatives of the two agencies.

lated a plan for a Marine Research Committee which would disburse funds collected from a tax on fish landings and would coordinate and sponsor research "to seek out the underlying principles that govern the Pacific sardine's behavior, availability, and total abundance."[17]

The Marine Research Committee was created by an act of the California Legislature in 1947, and was composed of nine members appointed by the Governor. Five members were specified to be selected from persons actively engaged in the canning or reduction industry, one member was the Chairman of the California Fish and Game Commission, one, the Executive Officer of the Division of Fish and Game, an additional member was taken from the Division of Fish and Game, and the ninth member was undesignated; the Director of the California Academy of Sciences was appointed to the undesignated position.

The work was to be carried out largely by Scripps Institution of Oceanography, U.S. Fish and Wildlife Service, California Division of Fish and Game, and the California Academy of Sciences, under the guidance of a technical committee representing the four agencies. Now there were two agencies: the Scripps Institution of Oceanography along with the Federal group, looking for reasons, other than fishing, to explain the sardine's decline; and State biologists also working, with mixed emotions, on a large-scale program. All of the above were somewhat under the auspices of a committee whose vote was controlled by the majority of five members from the sardine fishing industry.

The composition of the Marine Research Committee was changed in 1955 to consist of at least one member representing organized labor, at least one member representing organized sportsmen, two public members, and the same majority of five from the fishing industry.

The difference in perspectives of the biologists of the two fisheries agencies peaked in a joint paper by F. N. Clark (California Department of Fish and Game) and J. C. Marr (U.S. Fish and Wildlife Service)[16] in which the two authors drew different conclusions that were specifically identified from the same data. Also, the authors were careful to point out that the order of authorship was arranged alphabetically.

MORE RECENT RESEARCH EFFORTS

California Cooperative Oceanic Fisheries Investigations (CalCOFI)

Coordination of the efforts of the three principal agencies improved when the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Committee was established in December 1957, with the working head of the unit in each of the three major agencies, Scripps Institution of Oceanography, the U.S. Bureau of Fisheries, and the California Department of Fish and Game, engaged in cooperative work. A fourth member, without voting power, was hired by the Marine Research Committee, and acted as Chairman.

Effects of Temperature on Population Size, Distribution, and Fishing Success

In 1957 dramatic changes in fish distribution revealed the close relationship of fish movements, fishing success, and local abundance of many marine species to seemingly subtle changes in average ocean temperatures.[18] Following these events and the World Sardine Conference that was convened in 1959 in Rome, in which the effects of fishing on the Pacific sardine were debated at length,[19] a change in attitudes of the two government agencies took place. California scientists became more aware of the effects of the environment, and Federal researchers began to appreciate that human activities could in fact adversely affect a pelagic marine resource.

At the 1959 Sardine Conference, Marr pointed out that a relationship existed between the average temperature from April of a given year to March of the following year and the sardine year-class size (Figure 3).[20] He also suggested that the northern anchovy, *Engraulis mordax* Girard, may prefer lower temperature optima than sardines. Radovich showed that up to the collapse of the fishery in the Pacific Northwest, ocean temperature correlated with an index of latitudinal distribution of young sardines (Figure 4) and that year-classes of more northerly originating sardines tended to contribute more heavily to the fishery (Figure 5).[21] Inasmuch as year-class sizes were estimated from the catch, it was not clear, then, to what extent Marr's correlation with temperature was due to year-class size or to effect of temperature on the latitudinal distribution of the origin of the year-class and the effect of its early latitudinal distribution on its subsequent vulnerability to fishing.

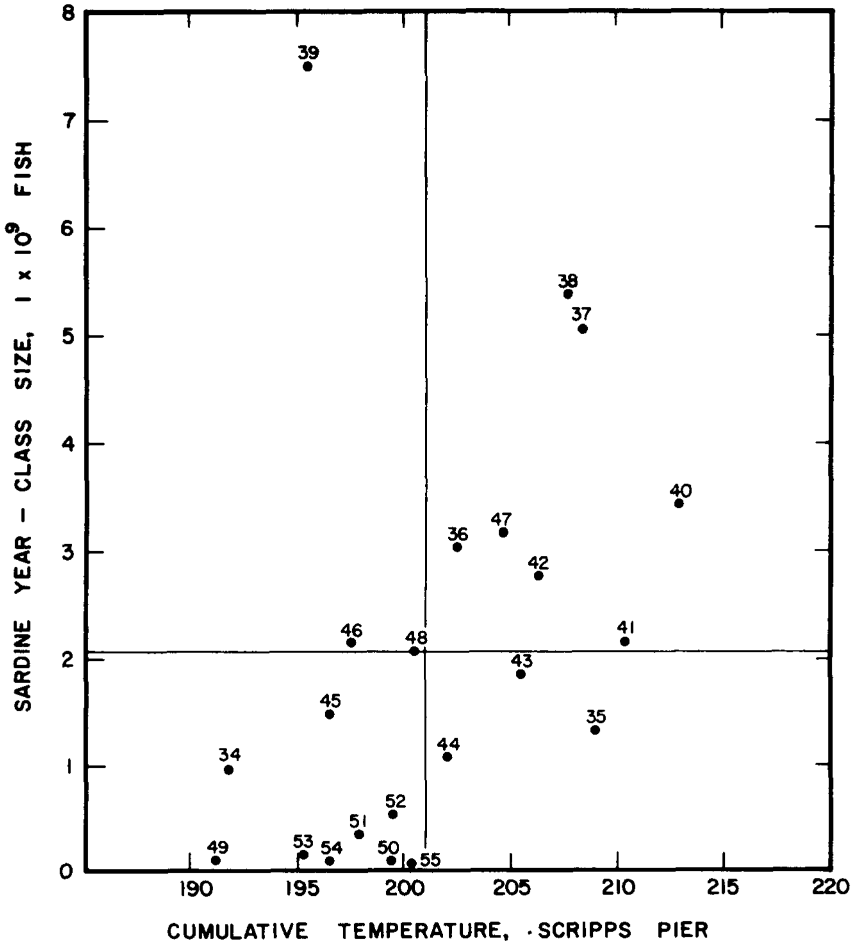

Figure 3 Relationship between year-class size and the sums of monthly mean sea temperature (April through March) at Scripps Pier. After Marr.[20]

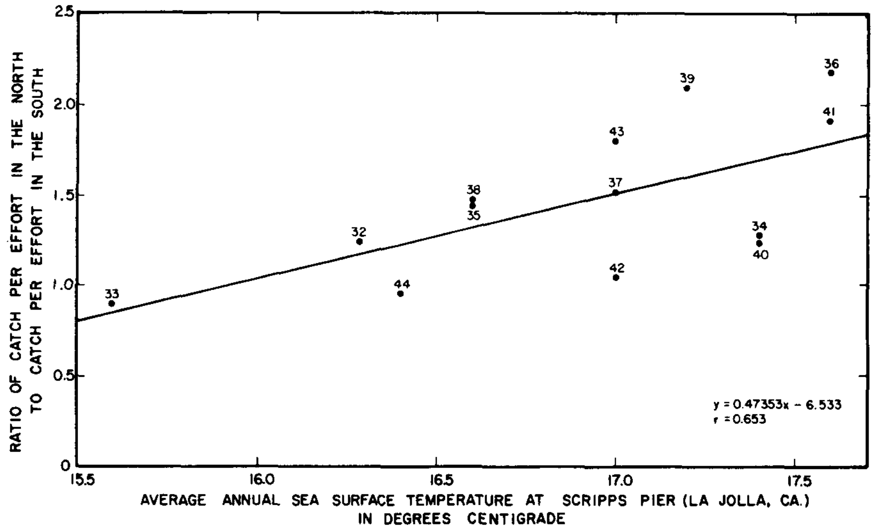

Figure 4 The relationship of sea surface temperatures at Scripps Pier to the index of north-south distribution of the Pacific sardine from the 1932–1933 to the 1944–1945 season. After Radovich.[21]

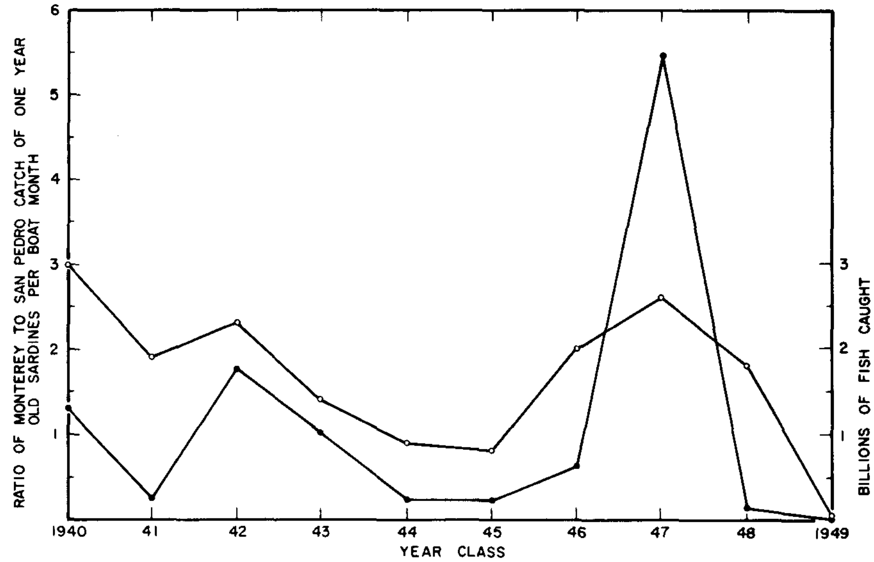

Figure 5 The ratio of the average lunar month catch at Monterey to the average lunar month catch at San Pedro of 1-year-old sardines (filled circles), and the cumulative total of each year-class of sardines taken in the fishery (open circles). After Radovich.[21]

Genetic Subpopulations

Another significant study resulted in delineating genetic strains of sardines by using erythrocyte antigens.[22,23] The studies agreed with Clark's conclusion that the sardine population from the Gulf of California and from the southern portion of Baja California were racially distinct from a single population to the north.[24] Vrooman[23] concluded that sardines from the Gulf of California, southern Baja California, and the northern California populations represented three distinct races, with a poorly defined (and somewhat variable) boundary separating the last two. Unfortunately, by the time that serological techniques had been

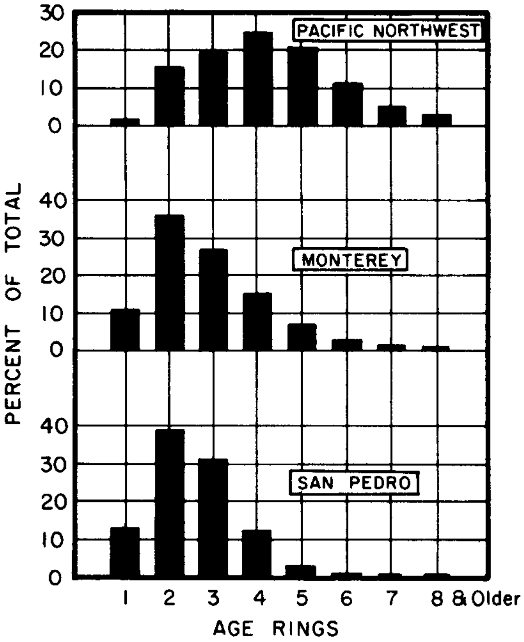

Figure 6 Average age composition of the Pacific sardine in different fishing areas during the 5-year period 1941–1942 through 1945–1946. After Clark and Marr.[16]

developed for separating genetic stocks, sardines had disappeared from the Pacific Northwest.

There were, however, two good lines of evidence to indicate that sardines from the Pacific Northwest and those from southern California did not mix randomly: (1) sardines in the Pacific Northwest were much larger and older than those in California (Figure 6); (2) there was a significant difference in scale types of fish from the two areas.[25] Whereas the northern type had relatively small growth during its first year, but grew more rapidly afterward, the California type scales represented a more rapid growth during the first year and a slower growth thereafter (Figure 7). Also, the northern type scales had well defined annuli (yearly rings) while the southern types had much fainter yearly rings.

Radovich, noting that the sardine temporarily restabilized at a much lower population regime following the decline in the Pacific Northwest (Figure 8), postulated that the stocks off the Pacific Northwest and off southern California were somewhat distinct, either genetically, or due to a strong tendency for fish to favor areas in which they were born (Figure 9).[26] He suggested that the fishery off the Northwest caught fish from the far northern stock during the summer, and that by winter much of this stock had moved off central California, where it was caught by California fishermen. The sizes and scale types of fish caught at these areas and seasons certainly suggested such a migration.[25] Scale types and sizes of fish also suggested that sardines caught in the fall off central California showed up off southern California in the winter the following year. J. L. McHugh (personal communication), in examining sardine samples from the Pacific Northwest and from California concluded, on the basis of meristic and morphometric variations, that fish from the two areas remained somewhat distinct from each other and did not mix to any great degree. The results of this study were never published.

Murphy rejected the existence of a far northern sardine stock by saying " . . . it is not necessary to invoke a third race to explain the

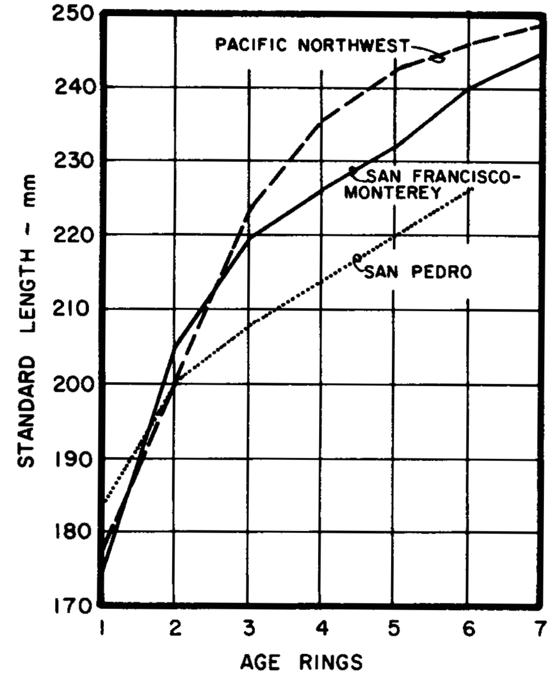

Figure 7 Observed growth curves (size on age) of sardines in several areas. After Clark and Marr.[16]

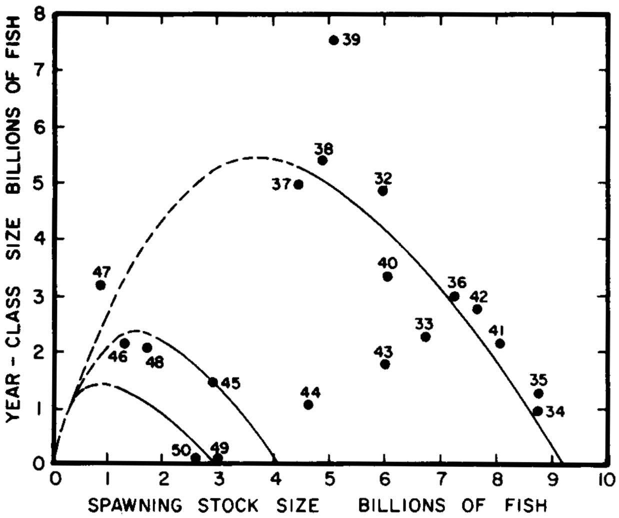

Figure 8 Hypothetical curves representing three probable regimes relating Pacific sardine year-class production to spawning stock size. After Radovich.[26]

collapse of the fishery."[27] He concluded that " . . . the observed quantitative changes in the population offer a sufficient explanation of events without introducing the undocumented qualitative change in the population." In doing so, he ignored the considerable body of evidence that demonstrated the stocks were not uniform or randomly distributed.

Sardine-Anchovy Interspecific Competition

During the period of the CalCOFI expanded program, it had become apparent that the anchovy population was increasing in size,[20] giving cause to speculation that the sardine and the anchovy populations may

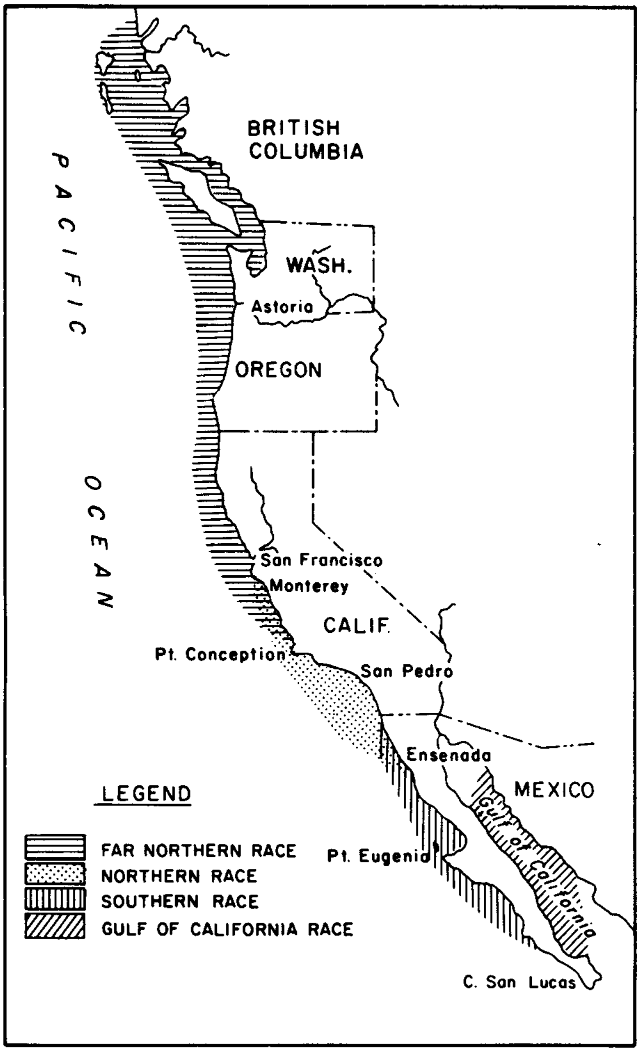

Figure 9 Diagramatic representation of four nonintermingling or partially intermingling stocks of Pacific sardines. The three stocks from the lower latitudes were delineated using arithrocyte antigens (Sprague and Vrooman,[22] Vrooman[23]); the far northern stock is suggested from studies of age and growth (Felin[25]) and population dynamics (Radovich[26]). Although the ranges are shown as overlapping, evidence suggests that the adjacent stocks did not generally occupy the same area at the same time. All stocks tended to range farther south during winters of cold years and farther north during summers of warm years.

be acting complementary to each other.[28] This speculation was based mainly on the increase in anchovy population in the 1950s, the co-occurrences and interrelationships of sardine and anchovy larvae in the California Current Region,[29,30] and the distribution of sardine and anchovy scales in the anaerobic sediments of the Santa Barbara Basin (off Santa Barbara, California).[31]

Murphy and Isaacs in a 1964 report to the Marine Research Committee,[32] estimated the anchovy abundance in southern California at that time at about one-half that of sardines in 1940 and 1941, and 6 times the abundance of sardines in the 1950–1957 period. They suggested that the decrease in sardines between the two periods had been balanced by increases in anchovies. Murphy presented an additional report at that meeting,[33] which also contained a table presenting anchovy and sardine larval catches from 1951 through 1959.

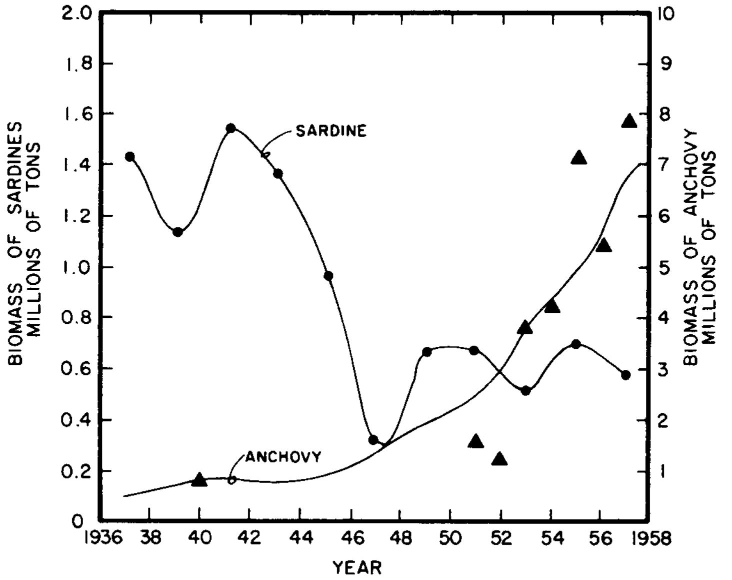

Figure 10 Annual biomass from 1936 to 1958 of the Pacific sardine and northern anchovy. The anchovy curve was generated by analog computer from Volterra competition equations and the sardine biomass was simulated using an analog computer method. After Silliman;[34] data from Murphy[33] and Murphy and Isaacs.[32]

Silliman[34] used data presented at the 1964 Marine Research Committee meeting and an analog computer to generate population curves of sardines and anchovies from Volterra competition equations (Figure 10).* He assumed competition for food to be the limiting factor for the combined biomasses of the two species. Only one point for the anchovy biomass prior to 1951 was used in this simulation, principally because the ichthyoplankton surveys of the CalCOFI program had not been fully implemented until 1951. The earlier point was in 1940 and resulted from the numbers of anchovy larvae taken in surveys made by Department of Fish and Game personnel then. Silliman's simulated curves have been cited in the literature as examples of competition and as substantiation of the Volterra competition equations.[35]

Smith indicated that the early cruises in 1940 and 1941 were conducted during the sardine spawning season and excluded an important portion of the anchovy spawning season.[36] In addition, the cruises only sampled 20% of the area that was later surveyed routinely. He derived total larva estimates for 1940 and 1941 for sardines and anchovies by comparing the 1940 and 1941 values with data obtained from analogous cruises in 1951 to 1960, conducted in the same season and covering the same area. His results (Table 2 and Figure 11) show his anchovy biomass values for 1940 and 1941 to be an order of magnitude higher than the value Silliman used. Smith concluded that both the anchovy and sardine populations declined between 1941 and 1951 and subsequently the anchovy population increased to over 5 million tons between 1962 and 1966. Smith's interpretation is the one commonly held at the present time by scientists working in the CalCOFI program, and is in direct contrast to the interpretation advanced by Silliman.

Murphy attributed the increase in the anchovy population to its use of the void left by the disappearance of the sardine.[27] He hypothesizes that

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*The Volterra competition equations are based on the logistic curve and mathematically describe competition between organisms for food or space.

TABLE 2. Sardine and Anchovy Spawner Biomass Estimates by Ratio and Regression Methods

Year	Murphy Sardine Spawner Biomass (×10^3T)	Regression Sardine Spawner Biomass (×10^3T)	Sardine Larval Estimate (×10^{12})	Anchovy Larval Estimate (×10^{12})	Anchovy Sardine Ratio	Ratio Anchovy Spawner Biomass (×10^3T)	Regression Anchovy Spawner Biomass (×10^3T)
1940	1,296		1,634[a]	5,943[a]	3.64	2,359	
1941	2,001		2,476[a]	7,104[a]	2.87	2,871	
—							
1950	716		3,343	2,602	0.78	279	
1951	570	553	2,685	6,504	2.42	690	637
1952	554	542	2,633	8,132	3.09	856	797
1953	709	450	2,189 (3,442)[b]	13,632	6.23 (3.96)	2,209 (1,404)	1,335
1954	668	658	3,193	18,533	5.80	1,937	1,816
1955	425	404	1,959	17,100	8.73	1,855	1,676
1956	293	351	1,706	15,215	8.92	1,307	1,491
1957	212	234	1,137	20,040	17.63	1,869	1,964
1958	281	299	1,453	28,272	19.46	2,875	2,771
1959	190	117	570 (922)	23,463	41.16 (25.45)	3,910 (2,418)	2,299
1960		201	975	31,414	32.22		3,079
1961		132	642	32,538	50.68		3,189
1962		151	731	63,758	87.22		6,248
1963		78	379	61,533	162.36		6,030
1964		104	505	52,253	103.47		5,121
1965		226	1,098	79,292	72.21		7,771
1966		151	735				
—				52,200	71.02		5,116
1969		27[c]	132[c]	33,623[c]	254.72[c]		3,293[c]

[a] 1940, 1941—larval estimates seasonally adjusted.
[b] Parenthetic numbers for 1953 and 1959 assume larval numbers biased.
[c] 1969—larval counts 75% complete; adjusted for extra retention of small larvae.
After Smith.[36]

food was the major resource for which the two species were competing and, in fact, this assumption was the basis for Silliman's simulation.

It was demonstrated by Soutar and Isaacs that the occurrence of sardine and anchovy scales are aggregated throughout the 1,850 year record in core samples of sediments from the anaerobic Santa Barbara Basin, and that sardine scales have appeared a number of times with a duration of between 20 and 150 years and with periods of absence between occurrences on an average of 80 years.[37] Northern anchovy scales were found to be more abundant throughout the time series. The hypothesis that the Pacific sardine and the northern anchovy are direct competitors is not supported by the less than significant positive correlation between the scale deposition of the two species in the Santa Barbara sediment.[38]

Iles concluded that, because the growth rates of the smaller year-classes were higher, the decline in the sardine population was not due to a reduction in its food supply resulting from environmental changes.[39] He reasoned that the increase in the length of sardines suggests the environment was not saturated with sardines, and hence food was not a limiting factor. He concurred with Murphy,[27] that fishing rates for the sardine population lowered reproduction to an extent that a decline was inevitable and that it was improbable that the population would have declined in the absence of fishing pressures. Iles disagrees with Murphy's contention that the 1949 year-class marked the most significant change in population status. He concurred with Marr[20] that recruitment failure set in during the mid-1940s. Iles also contends that the rise of the anchovy population off California was in response to the environmental

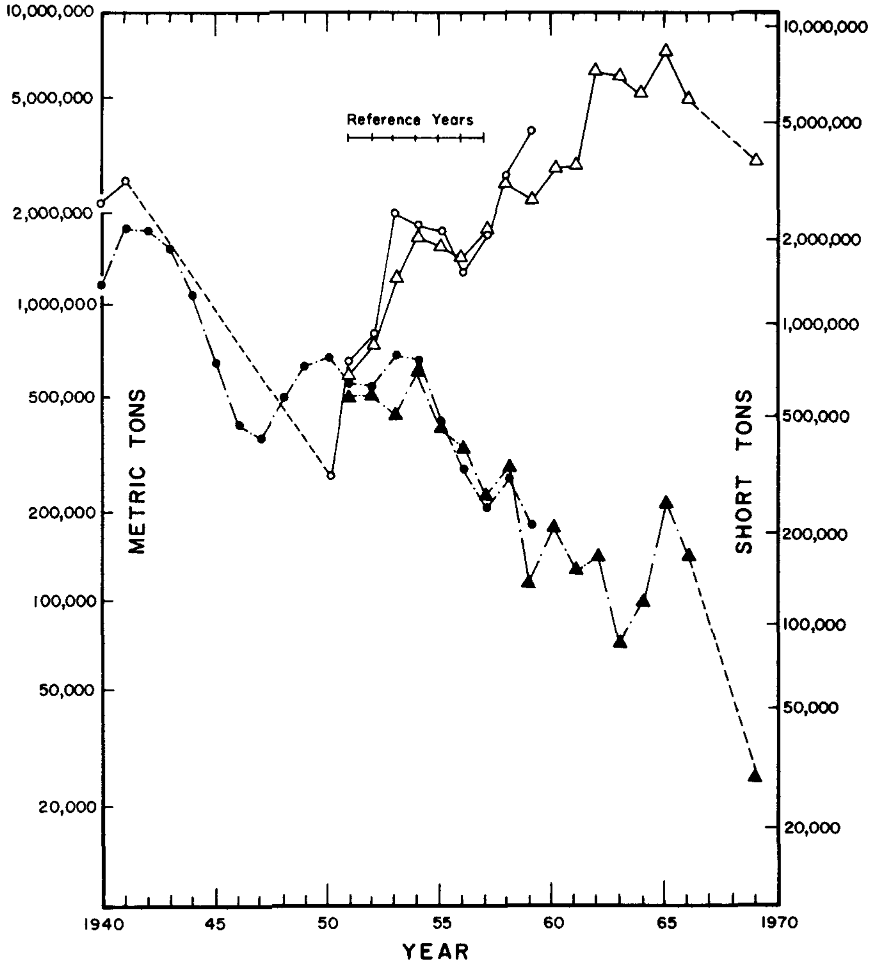

Figure 11 Sardine and anchovy biomass estimates from 1940 through 1969. The solid circle represents sardine biomass calculated from the fishery by Murphy.[27] The solid triangle represents sardine biomass derived from a regression estimate of the relationship between the Murphy biomass estimate and the annual total regional census estimate of sardine larvae during the reference years. The open circle represents the estimates of biomass derived from the ratio of anchovy larvae to sardine larvae and the Murphy sardine biomass estimate from 1940 to 1959. The open triangle represents anchovy biomass derived from a regression estimate of the relationship between the anchovy tonnage calculated from the anchovy to sardine larvae ratio and the annual total regional census estimate of anchovy larvae. Dashed lines represent interpolations between nonadjacent years. After Smith.[36] Compare with Figure 10.

void created by the decline of the sardine and not the cause of the decline.

Lasker has shown that, for the northern anchovy, food may be limiting at the critical time in the larval development when feeding first begins.[40] The presence of the proper food of the right size at the right density in the vicinity of the larva determines whether or not a larval anchovy survives past this critical stage. He has pointed out that extreme patchiness in the distribution of proper food exists in time and space. Upwelling may disperse the food concentrations so that, if it occurred at the critical time, a year-class failure would be a likely possibility. Inasmuch as sardine larvae and anchovy larvae feed on similar food, sardines may be affected similarly at the critical time of first feeding.

MacCall examined anchovy scales from sediments of anaerobic basins and found that the widths of scales during periods of high and low anchovy scale deposition did not differ significantly.[41] This suggested that intraspecific competition for food either did not affect growth rates or was masked by other factors. On the other hand, he found that anchovy scale widths from groups represented by periods of high sardine scale deposition rates were significantly smaller than those from groups based on periods of low sardine scale deposition rates. Anchovies seem to be smaller when sardines are abundant and larger when sardines are scarce. This may be due to interspecific competition for food, although other explanations are also possible. Increased selective predation on anchovies could result in a higher mortality and a smaller average length of the anchovy population. MacCall also pointed out that the record of the past century's abundance of sardine scales does not reveal a period of low abundance comparable to the present one and suggested that the present depletion was, therefore, not a natural one.[41]

Density-Controlling Mechanisms

If food does not appear to be the limiting factor related to poor sardine year-classes, except perhaps at the critical stage of first feeding after the yolk sac has been absorbed, then one should look for other density-controlling mechanisms for sardines and anchovies, such as predation and cannibalism. Hunter has found cannibalism of eggs by anchovies can account for about 50% of the total egg mortality.[42] The percentage would vary depending on the density of anchovies and of other food. Such a relationship would constitute a strong density-limiting force, and may well be the principal interaction between the two species. Sardines eat sardine eggs and larvae and anchovy eggs and larvae.[43]

Radovich suggested that, because man follows aggregations of schools and uses communication techniques to concentrate fishing effort on school groups, each nominal unit of fishing effort expended will take an increasingly larger portion of a declining pelagic fish population.[44–46] The catchability coefficient, then, is a variable function of the population.*

Radovich suggested that behavioral characteristics, such as schooling behavior, which have evolved through natural selection to decrease mortality from predation, may work toward the destruction of the prey

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*MacCall used a power function to approximate the catchability coefficient[47]:

$$Q = \alpha N^{\beta}$$

where Q is analogous to the catchability coefficient, q, N is the mean population size, and α and β are constants.

$$C/f = QN$$

where C is the catch in number and f is the number of nominal effort units. If we assume the two previous equations, it follows that

$$C/f = \alpha N^{\beta+1}$$

At $\beta = 0$, the catchability coefficient is a constant and a linear relationship exists between catch-per-effort and population. At $\beta = -1.0$, C/f is a constant, and at all other values of β, C/f bears a curvilinear relationship to population size.

Fox calculated a β of -0.3 for the Pacific sardine fishery from 1932 to 1954.[48] MacCall estimated a β of -0.724 for the sardine.[47] With a β of these values, if effort is increased beyond a critical point, a population collapse is inevitable (Figure 12) instead of reaching some equilibrium as predicted by Schaefer's model.[49,50]

species when it is suddenly confronted by a fishery which evolves more rapidly than does the fishes' defense against it.[51]

THE END OF THE MARINE RESEARCH COMMITTEE

With the passage of the Fishery Conservation and Management Act of 1976, the United States established a conservation zone between 3 miles and 200 miles off the coast within which the United States has managment authority over fishery resources excepting tuna. The original utility to the fishing industry of the Marine Research Committee, that of forestalling managment of the resources, was somewhat removed.

Therefore, at the request of the California fishing industry, at the end of 1978, the Marine Research Committee was dissolved by an act of the California Legislature; however, by mutual agreement, the University of California, the National Marine Fisheries Service and the California Department of Fish and Game are continuing the California Cooperative Oceanic Fisheries Investigations as a viable cooperative research unit, beginning in 1979.

DISCUSSION

From the foregoing examination of only a small portion of the work which has been done on the Pacific sardine and the northern anchovy, it is apparent that most simplified generalizations are probably incorrect.

Any model attempting to describe these populations must be consistent with the results of all the studies on these species. Following is a brief summary of the major points in this paper, all of which must be considered in any modeling attempt.

A model for sardines must account for a population heterogeneity of sardines that does not randomly mix throughout its geographic range. The evidence suggests the Pacific sardine consists of a clinal distribution of intraspecific populations in which there is limited intermingling and a series of variable overlapping coastal migrations of more than one stock.[25] Sardines in the Pacific Northwest were distributed farther north in the summer months when the fishery in that area operated.[52] During the winter months, many of these fish migrated south and were caught

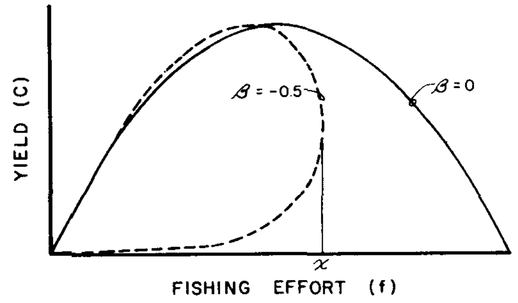

Figure 12 Effect of negative values of β on the equilibrium catch curve. At $\beta = 0$, the catchability coefficient becomes a constant and the usual parabolic relationship depicted by Schaefer[50] holds. If $\beta = -0.5$, as effort is increased above a critical point, x, the yield curve becomes unstable and the population collapses. Such an event appears to have happened with the Pacific sardine. After Fox.[48]

off San Francisco as winter fish.[14] Similarly, sardines located off Monterey in the fall supported the winter fishing off southern California. Following the collapse of the fishery off the Pacific Northwest, the winter fishery failed off central California. With the failure of the central California stocks, the southern California stock migrated into Mexican waters and became unavailable soon after the fall season began.[53]

The model should include the higher vulnerability of the northern stocks and the proper sequence of the stocks' decline, with the northern stocks declining first. Wisner was able to find only the southern (central Baja California) "racial" types in the southern California fishery by the period 1950–1959, as indicated by vertebral number.[54]

The model must be consistent with variable and somewhat independent spawning success for the different areas along the coast,[18,21,25] and with different vulnerability of the different stocks resulting from sardine movements from one fishing area to another during each fishing season.

The model must be able to handle major single-season population shifts such as occurred in 1954 and 1958.[21] It must be consistent with higher average spawning success and less variability in large populations, and with a more concentrated inshore distribution of spawn in lower populations.[21]

The model must consider the intraspecific density-dependent relationship that seems to have existed for the various sardine stocks.[26] It could speculate on the effect of sardine population size on anchovy growth rates, but there is no evidence of the effect of anchovy populations on sardine growth rates. It should include cannibalism, as a population limiting mechanism. It should relate ocean temperature to the distribution of spawn success, and should be able to explain the success of the far northern 1939 year-class and its exceptional contribution to the fishery.

The model must consider the effect of a variable catchability coefficient, which increases as the population declines,[47,48,51] or as a population becomes more available to the fishery.[21] It must also consider the effect on the population of any major change in the abundance of a strong predator.[51] It must consider the variability in the temporal and aerial distribution of proper feed in relation to larvae at the time of first feeding and, finally, it must be consistent with results of all the many studies that have been conducted to date. A detailed model should contain a number of generalizations, many of which complement each other, and some of which do not.

I have presented the beginning of a conceptual framework which, I believe, makes a strong case that the present scarcity of sardines throughout their range and their complete absence off the Northwest is not a natural condition but, instead, is an inescapable climax, given the characteristics and the magnitude of the fishery and the behavior and life history of the species.

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Part III

SCIENTIFIC CONTRIBUTIONS

THE LIFE HISTORY AND FISHERY OF PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*

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ABSTRACT

The Pacific whiting is one of the most abundant and important fishes of the California Current region. This report synthesizes available data, published and unpublished, on the life history and population dynamics of whiting. Aspects of the life history described are distribution, spawning, early life history, feeding, and growth. Information on the population dynamics of the stock is summarized with attention to stock abundance, recruitment variability, and mortality. A synthesis of the fishery, its development and management, is presented.

RESUMEN

Merluccius productus es una de las especies más abundantes e importantes en la región de la Corriente de California. En este trabajo se recopilan los datos publicados e inéditos sobre el ciclo de vida y dinámica de poblaciones de *M. productus*. Los aspectos del ciclo de vida que se discuten incluyen; distribución, puesta, fases larvales y juveniles, alimentación y crecimiento. La información sobre la dinámica de la población se resume en relación con la abundancia de las existencias, variaciones en el reclutamiento y la mortalidad. Se presenta además una síntesis de las pesquerías, su desarrollo y administración.

INTRODUCTION

Commercially and ecologically the Pacific whiting (also called Pacific hake), *Merluccius productus,* is one of the most important fish species on the west coast of North America. It supports a large commercial fishery that has been dominated by foreign nations. In recent years, however, a U.S. fishery has developed through ventures with foreign nations. Besides being an important resource to man, whiting is an important trophic link in the California Current ecosystem. As a large predator, whiting interacts with other fish and shellfish populations, notably the commercially important stocks of Pacific herring, *Clupea harengus pallasi;* northern anchovy, *Engraulis mordax;* and shrimp. Whiting is also important as prey in the diets of marine mammals and large fishes.

The objective of this synopsis is to synthesize available information on the biology and fishery of the coastal stock of Pacific whiting. Since the publication of a similar synopsis in 1970 (U.S. Fish and Wildlife Service 1970), a great deal of new information has become available. Most of this material is unpublished and thus is generally unavailable to scientists, managers, and fishermen. Further goals of this synopsis are to present new information, particularly concerning the migration of whiting, and to suggest areas of needed research.

THE CALIFORNIA CURRENT SYSTEM—THE HABITAT OF PACIFIC WHITING

Pacific whiting ranges from the Gulf of Alaska to the Gulf of California (Hart 1973); however, it is most abundant within the region of the California Current system. The California Current system is the eastern boundary current system of the North Pacific Ocean. It extends from the coastal divergence of the westwind drift at 45°N in winter (and 50° in summer) southward to about 23°N, where California Current water mixes with equatorial water and bends westward to form the North Equatorial Current. The California Current system is composed of (1) an equatorward surface flow—the California Current; (2) a seasonally occurring poleward surface current identified as the Davidson Current north of Pt. Conception, and as the California Countercurrent in southern California; and (3) a poleward subsurface flow—the California Undercurrent. Numerous gyres, including the Southern California Eddy, are semipermanent features of the California Current system. The individual currents are briefly discussed below; a more detailed review can be found in Hickey (1979).

The flow of the California Current is driven by winds and is slow, broad, and shallow. Water of the California Current is subarctic in physical and chemical properties at high latitudes, characterized by low salinity and temperature. As the water flows southward, it becomes more intermediate in nature through mixing with the high-salinity and high-temperature water of the North Pacific Current and the Central Pacific water mass. Eventually, California Current water becomes semitropical off southern Mexico after mixing with equatorial water.

The Davidson Current is the surface poleward flow north of Pt. Conception that develops in winter. The Davidson Current appears in October off Vancouver

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[Manuscript received January 11, 1982.]

Island and develops later farther south. It exists off the Oregon-Washington coast from October until February and off the California coast from November until January.

The California Undercurrent is a northward flow of high-salinity, high-temperature water occurring seaward of the continental shelf and below the main pycnocline. Wooster and Jones (1970) reported that the undercurrent was found 75 km offshore of Cabo Colnett, Baja California, and was centered at 200-500-m depth off the Oregon-Washington coast. A poleward undercurrent develops over the continental shelf in late summer and early fall (Hickey 1979).

LIFE HISTORY

Stocks and Distribution

Stocks. At least four distinct stocks of Pacific whiting may exist. These include (1) a coastal stock ranging from Canada to Baja California, (2) a Puget Sound stock, (3) a Strait of Georgia stock, and (4) a dwarf stock found off Baja California. Two of the stocks, Puget Sound and the coastal stock, have been identified as genetically distinct spawning stocks (Utter and Hodgins 1971).

The separate identities of the dwarf and coastal stocks are at present controversial. Ahlstrom and Counts (1955) examined larvae found off Baja California and were not able to distinguish two separate stocks, thus supporting a concept of one spawning stock. However, MacGregor (1971) and Vrooman and Paloma (1977) discussed several differences in adult dwarf whiting found off Baja California compared with the adult coastal whiting found farther north. Dwarf whiting grow slower from age one onwards, mature earlier, and have several different morphometric and meristic characteristics compared with the coastal whiting. Vrooman and Paloma (1977) believed that these differences indicate separate stocks. However, the differences may not be genetic, and are not inconsistent with changes caused by environmental effects in the different habitats.

The remainder of this report deals with the coastal stock, which is the most abundant and commercially important.

Distribution. As indicated previously, Pacific whiting are found within the coastal region of the California Current system. Normally whiting are not caught seaward of the continental slope, although there are occasional reports of whiting eggs and larvae (as well as of juveniles and adults) far seaward of the slope (Frey 1971). The latitudinal distribution of whiting varies seasonally. In autumn adult whiting make an annual migration from the summertime feeding grounds off the Pacific Northwest coast to spawn in winter off the coasts of southern California and Baja California. In spring and summer, large fish migrate northwards as far as central Vancouver Island, and juveniles remain off the Californias. The migration of whiting is outlined in Figure 1 and is described in detail below.

Spawning

Spawning schools of Pacific whiting have been difficult to locate. Nelson and Larkins (1970), Tillman (1968), Bureau of Commercial Fisheries 1964[1], Erich et al. (1980), and Stepanenko[2] report spawning schools off southern California in midwater at depths of 130-500 m and over bottom depths corresponding to those of the continental slope. (Spawned at these depths, eggs float upwards to the base of the mixed layer.) Ermakov (1974) also reports spawning over the continental slope. However, Erich et al. (1980) report a spawning school some 400 km seaward in the southern part of the Southern California Eddy, and Stepanenko[3] reports a spawning school about 300 km offshore in central California.

The distribution of eggs and small larvae (2-3 mm) indicates that whiting spawn from Cape Mendocino to southern Baja California. Almost all eggs and larvae are located over water depths corresponding to depths of the continental slope, except in the Southern California Eddy, where eggs and larvae are often found over very deep water and far out to sea (400 km). Bailey (1981a) postulated that whiting spawn in the California Undercurrent, which usually occurs over the continetal slope at depths of 200-400 m, but spreads seaward some 200-400 km in the Southern California Eddy and some other locations where eddies occur. Large concentrations of eggs and larvae are found overlying areas of northward geostrophic flow at 200-m depth (Figure 2).

Variation may exist in the latitudinal distribution of spawning. The location of the apparent northern front of spawning is correlated to the sea surface temperature (Table 1). Assuming that temperatues at the sea surface are correlated to those at the depth of spawning, this indicates that in warm years when subtropical water is farther north, spawning occurs at higher latitudes. Alternatively, larvae may be transported by a northward flow.

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[1] Bureau of Commercial Fisheries. 1964. Cruise report: exploratory cruise No. 64. Unpubl. manuscr. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[2] Stepanenko, M.A. 1978. The patterns of the abundance of the California anchovy and Pacific hake, and estimation of their biomass, 1976-1977. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

[3] Stepanenko, M.A. 1980. Reproductive condition and assessment of the spawning stocks of Pacific hake, California anchovy, horse mackerel, and some other fish species in the California Current zone in 1979. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

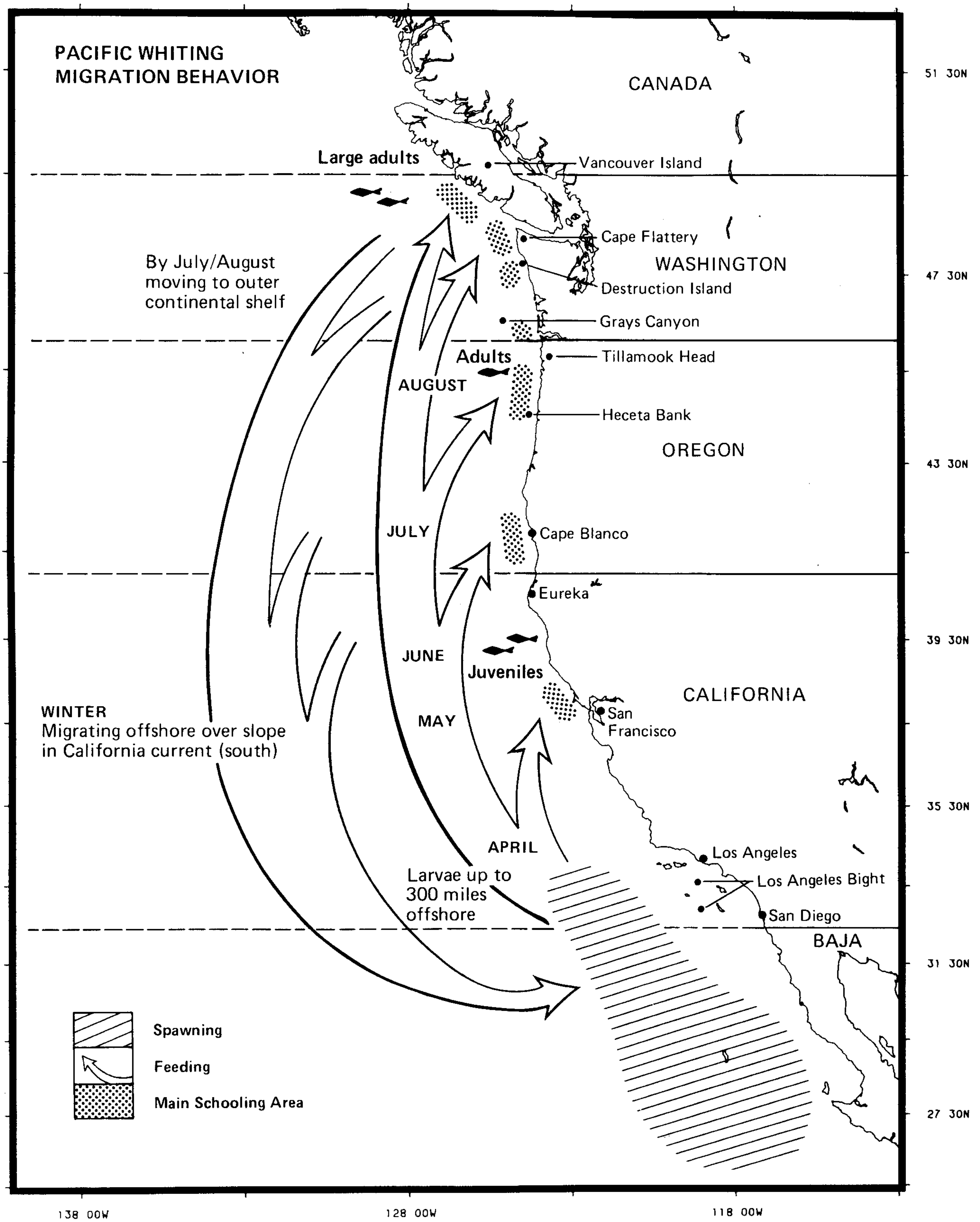

Figure 1. Migratory patterns of Pacific whiting.

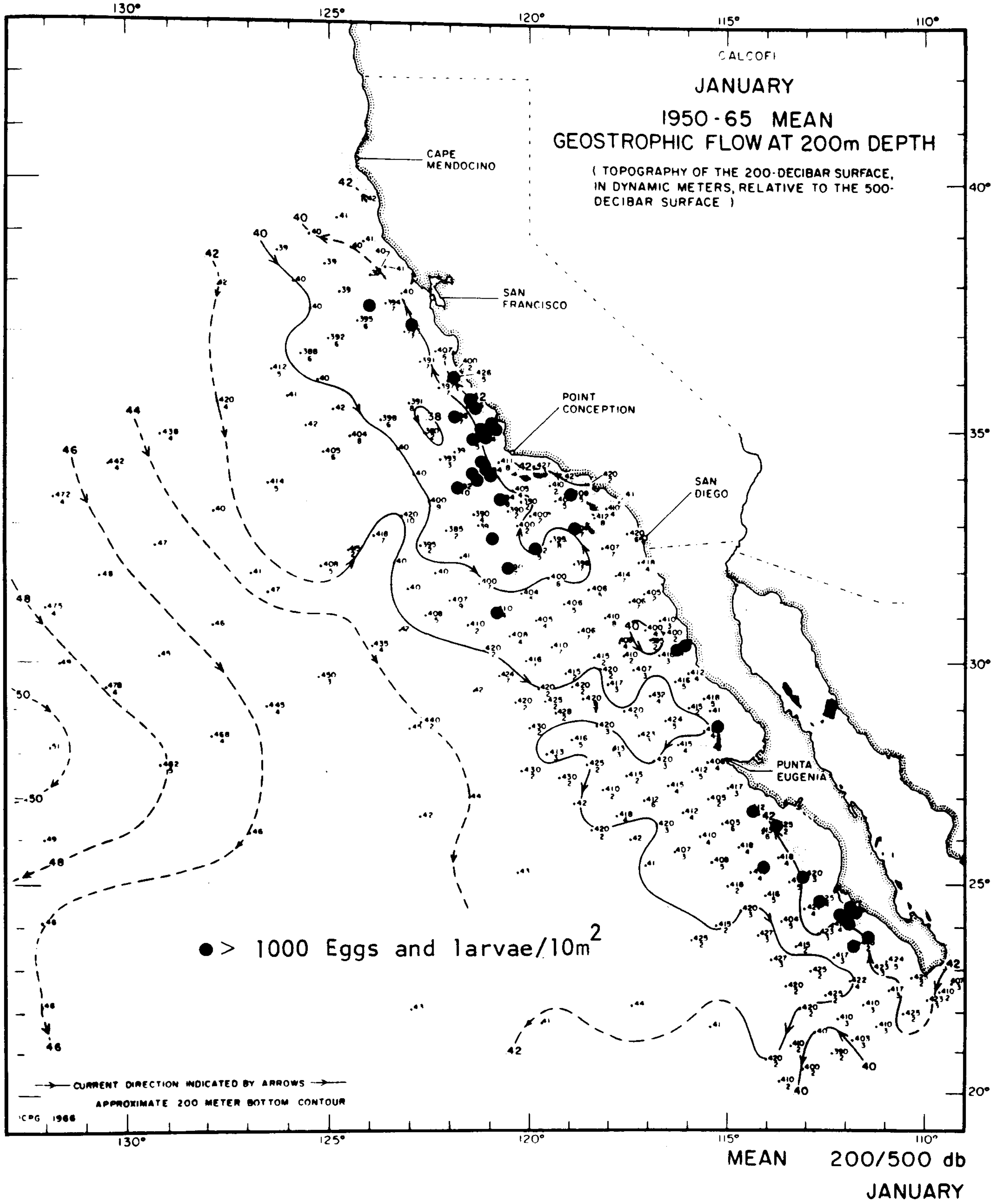

Figure 2. Large catches of Pacific whiting eggs and larvae (all size classes) in January surveys, 1950-79, plotted on a chart showing geostropic flow at 200-m depth (from Wyllie 1967).

TABLE 1

The Northward Extent of 2-3-mm Standard Length Whiting Larvae* during January Surveys, Compared to the Average January 50-Meter Temperature in the Los Angeles Bight

	Temperature		Distance	
Year	°C	Rank	Line	Rank
1963	12.0	9	87	8.5
1964	13.2	4	76	4
1965	12.4	7	80	6
1966	13.5	3	70	2.5
1968	12.8	5	70	2.5
1969	13.6	2	80	6
1972	12.2	8	87	8.5
1975	12.6	6	80	6
1978	13.9	1	63	1

*Measured by the northernmost CalCOFI line where larvae occurred in numbers greater than 100 larvae/10 m^2.

Smaller line numbers are farther north. Temperature and northward extent of larvae are significantly correlated using a Spearman rank correlation statistic ($P<.01$).

Larvae of all size classes occur in significant numbers in the water from December to May (Stauffer and Smith 1977), but some 80% of eggs and small larvae are found in two months, January and February (Figure 3), which indicates a sharp peak in spawning. Most Soviet reports also indicate that January and February are the primary spawning months, but sometimes heavy spawning is reported in March. Spawning is generally completed by late March; in several consecutive years Ermakov (1974) observed schools of postspawning whiting off northern California by early March.

Pacific whiting females mature and spawn at 3 to 4 years of age and at lengths of 34-40 cm (Best 1963; MacGregor 1966, 1971; Ermakov 1974). MacGregor (1971) found some males maturing at 28 cm. Spawning whiting do not appear to migrate vertically, and bilayered schools have been observed on sonar traces. (R. McNeely, Northwest and Alaska Fisheries Center, Seattle, WA 98112, pers. comm.; J. Mason, Pacific Biological Station, Nanaimo, B.C., pers. comm.).

Several modes of eggs appear in whiting ovaries (MacGregor 1966; Ermakov et al.[4]). MacGregor suggests that only one mode develops, because of the poor condition of the females, but he did not examine the ovaries histologically. Foucher and Beamish (1977) reported that only one mode of eggs develops in the Strait of Georgia whiting stock. Ovaries average about 8% of the body weight of spawning females. Ripe ovaries contain 80-600 advanced-mode eggs per gram of ovary wet weight (MacGregor 1966). An equation relating total fecundity to length of the female is $E = 0.00142{*}L^3$ (MacGregor 1966).

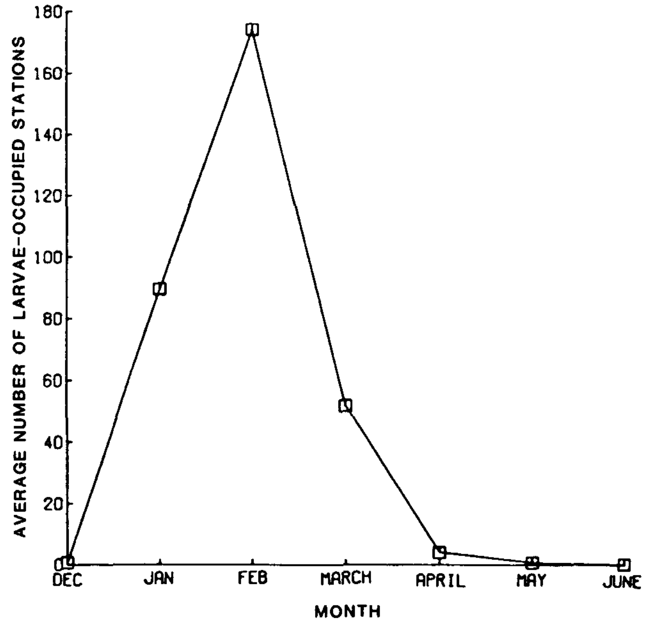

Figure 3. The average monthly number of small whiting larvae per occupied station in the California Cooperative Oceanic Fisheries Investigations survey region, lines 60-120, over the years 1963-79. Small larvae are 2-3 mm-SL.

Early Life History

Egg stage. Ahlstrom and Counts (1955) described the eggs of Pacific whiting. They are smooth spheres, have a single oil droplet, and are 1.14-1.26 mm in diameter (after accounting for 7% shrinkage caused by preservation in Formalin). Egg hatching is temperature dependent (Bailey, in press; Zweifel and Lasker 1976). Whiting eggs may be expected to hatch in 100-120 hr at temperatures found at their habitat depth on the spawning grounds, where temperatures range from 11° to 14°C.

In a laboratory setting, predators capable of eating whiting eggs are numerous and include, among others, medusae, ctenophores, and amphipods (Bailey and Yen, in press). Whiting eggs may be somewhat resistant to tactile and small invertebrate predators because they are motionless and have a very hard cuticle. Fish predation may also be heavy: Ermakov and Kharchenko[5] report finding the stomachs of threadfin bass, *Anthias gordensis,* full of whiting eggs off Baja California. Northern anchovy could also be feeding on whiting eggs, for they consume considerable numbers of their own eggs (Hunter and Kimbrell 1980) and are believed to feed at depths where whiting eggs occur (Holliday and Larsen 1979).

Larval stage. Ahlstrom and Counts (1955) described the larvae of Pacific whiting. They are distinguished by a pigment band around the tail, pigment

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[4] Ermakov, Y., V. Snytko, L. Kodolov, I. Serobaba, L. Borets, and N. Fadeev. (Date unknown). Biological characteristics and the condition of stocks of Pacific hake, rockfish, blackcod, and pollock in 1972. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

[5] Ermakov, Y., and A.M. Kharchenko. 1976. Biological characteristics of Pacific hake and the estimation of its abundance in 1975. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

spots on the dorsal crown of the head, sturdy bodies, and 51-54 myomeres (Figure 4). Preserved yolk-sac larvae are 2.5-3.0 mm standard length. Shrinkage of larvae due to handling is highly variable, from 10-40% depending on the preservative and on the time from death to preservation (Bailey, in press; Theilacker 1981).

Time to absorption of the yolk is temperature dependent (Bailey, in press). At ambient temperatures, absorption of the yolk may take 120-200 hours. A mouth develops before the yolk is fully depleted, and yolk-sac larvae are observed to feed (Sumida and Moser 1980). Larvae take 150-250 hours to starve after yolk depletion (Bailey, in press).

Daily growth of whiting larvae has been described by counting growth increments on their otoliths (Bailey, in press). Growth in length appears to be slow and constant for the first 20 days, after which it rapidly accelerates (Figure 5).

In the laboratory, predators on yolk-sac larvae are more varied than those on eggs and include euphausiids, medusae, ctenophores, amphipods, and carnivorous copepods. Invertebrate predation on whiting larvae is stage- or size-specific; larger larvae are not as vulnerable to predators as yolk-sac larvae (Bailey and Yen, in press).

The diet of larval whiting is composed mostly of copepod eggs, calanoid copepod nauplii, copepodites,and copepod adults (Sumida and Moser 1980). Whiting larvae have relatively large mouths and feed on a broad size range of prey from 50-400 μm in width.

Competitors of whiting larvae in the ichthyoplankton sharing the same temporal and spatial distributions are California smoothtongue, *Bathylagus stilbius*, and snubnose blacksmelt, *Bathylagus wesethi*. Overlap in the vertical and horizontal distribution also occurs with *Vinciguerria lucetia;* rockfish, *Sebastes* spp.; and jack mackerel, *Trachurus symmetricus*. Numerous carnivorous invertebrates are also competitors.

The vertical distribution of whiting eggs and larvae. Eggs are released at 130-500 m in spawning, and most rise upwards to a depth of neutral buoyancy, usually at 40-60-m depth, near the base of the mixed layer (Ahlstrom 1959). If a strong pycnocline does not exist, eggs and larvae may be distributed through the mixed layer. Some evidence exists that larger larvae may be distributed deeper than small larvae (Bailey, in press).

TABLE 2
Percent Biomass of Juvenile Pacific Whiting by Depth Interval and by Age

Depth (fathoms)	Age (yr) 0	1	2	3
0-99	95.4	35.8	14.6	30.7
100-199	4.4	63.4	59.6	41.8
150-199	0.2	0.8	25.8	27.5
	100.0	100.0	100.0	100.0

From the summer 1977 Northwest and Alaska Fisheries Center bottom-trawl survey.

Juvenile stage. Not much is known about juvenile whiting. Juveniles 1-3 years of age are found primarily off central and southern California (Figure 6). Most 0-1 year-olds occur inshore of the 200-fathom (fm) isobath, and older fish are distributed somewhat farther offshore than younger fish (Table 2). The food of juvenile whiting is mainly copepods and euphausiids (P. Livingston "The Feeding Biology of Pacific Whiting," in review).

Adult Life History

Migratory behavior. Tagging of Merluccidae has not proved feasible (Jones 1974); thus the migrations of Pacific whiting are inferred from survey and fisheries data.

Pacific whiting become scarce in survey catches (Table 3) and in the fishery (Table 4) from autumn until early spring (see also Jow 1973; Best 1963; Alton 1972), and whiting eggs and larvae are most abundant in winter off California. These observations have led to a hypothesis that adult whiting leave the coastal waters in autumn to migrate from the shelf and southward for spawning in winter, and then return northward in early spring (Alverson and Larkins 1969). This migratory pattern has been verified from more recent data (Ermakov 1974; Dark et al. 1980).

TABLE 3
Average Trawl Catches (Pound per Hour) of Pacific Whiting by Month and Year

Year	Jan.	Mar.	May	July	Aug.	Sept.	Nov.	Dec.
1961	—	—	—	2,403	—	9,784	—	97
1962	—	45	71	—	11,131	—	425	—
1963	100	—	175	—	4,315	—	450	—
Mean	100	45	123	2,403	7,723	9,784	438	97

From Alton 1972.

Speeds of migration may be estimated from the sequential appearance of fish up the coast after spawning. Postspawning accumulations of whiting normally

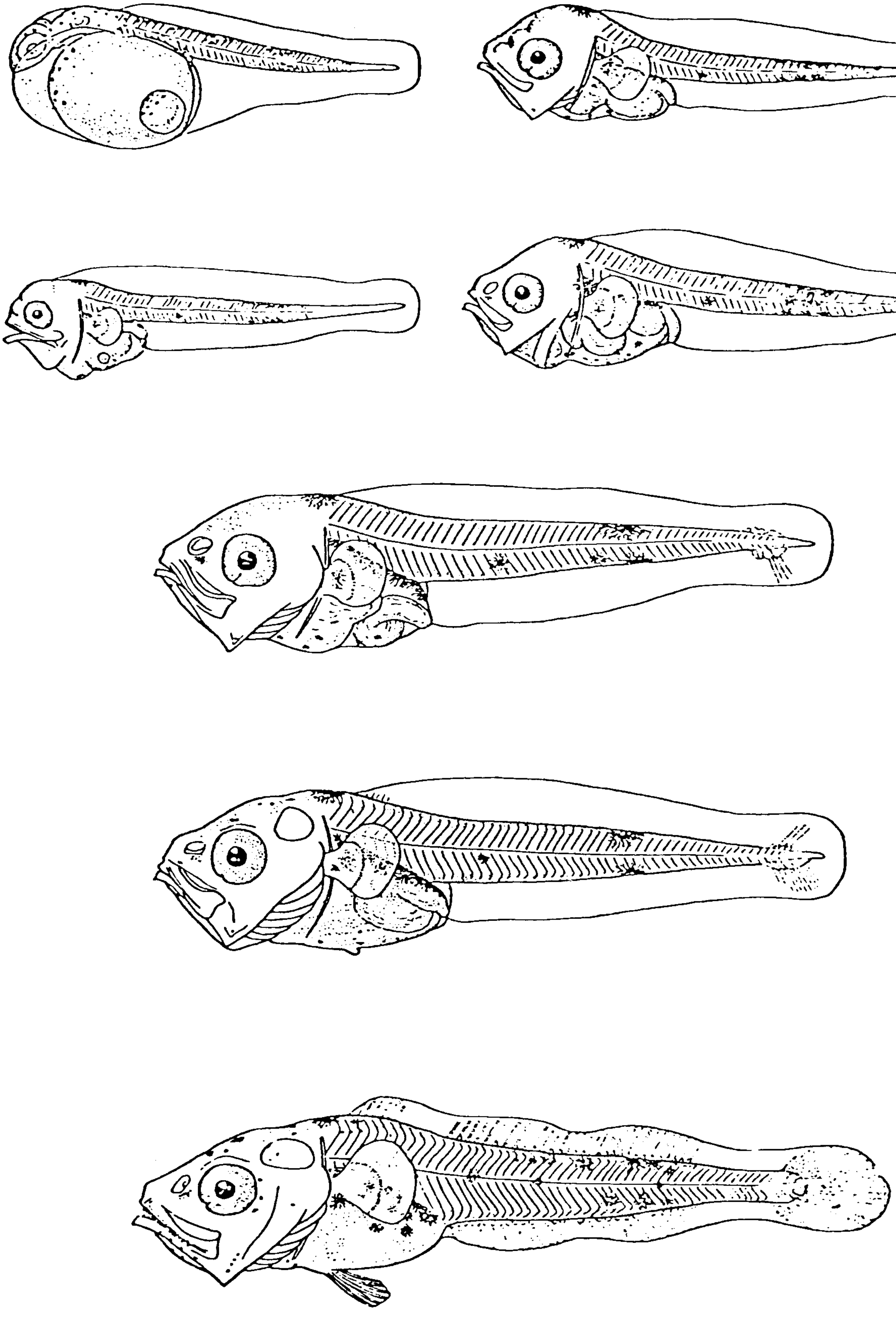

Figure 4. Stages of Pacific whiting larvae (from Ahlstrom and Counts 1955).

TABLE 4
The Proportion of Soviet Catches in the INPFC Vancouver-Columbia Area by Month, 1973-76

Month	1973	1974	1975	1976	x
1	—	—	—	—	—
2	—	—	—	—	—
3	—	.012	—	—	.003
4	.032	.073	—	—	.026
5	.008	.085	.026	.122	.060
6	.106	.049	.163	.207	.131
7	.305	.212	.406	.202	.281
8	.296	.116	.167	.261	.210
9	.158	.453	.136	.188	.234
10	.094	—	.086	.017	.049
11	—	—	.016	—	.004
12	—	—	—	.002	—

have appeared around San Francisco (38°N) in early March (Ermakov 1974; Erich et al. 1980) and have been later observed off southern Oregon (42°N) in the third week of April for five consecutive years from 1966 to 1971 (Ermakov 1974). A population traveling on this schedule would move, on the average, about 10 km/d. By May, concentrations appear off Vancouver Island. These estimated mean population speeds compare favorably to speeds obtained from direct observation of individual schools. Ermakov (1974) concluded from direct observation of a lead school that the northward migration is at speeds of 5-11 km/d.

Ermakov (1974) hypothesized that the timing of the spawning migration was linked to the seasonal appearance of the Davidson Current off the Oregon-Washington coast. Analysis of the movement of the Soviet fishing fleet in relation to Bakun's (1973, 1975) indices of wind stress tends to support this hypothesis. Adult whiting generally begin to disappear from the Pacific Northwest in autumn when the wind direction shifts and the Davidson Current appears.

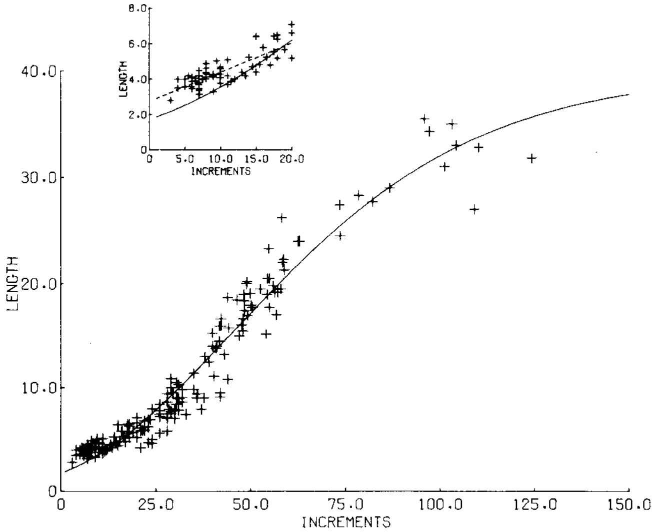

Figure 5. The growth of larvae caught off southern California determined from otolith increments. A Gompertz curve was fitted to the data, $Y = 1.72 * \exp[3.15 * (l - \exp[-0.02624 * X])]$. *Insert:* daily growth for the first 20 days was better fitted with a straight line ($Y = 2.75 + 0.16X$) (from Bailey, in press).

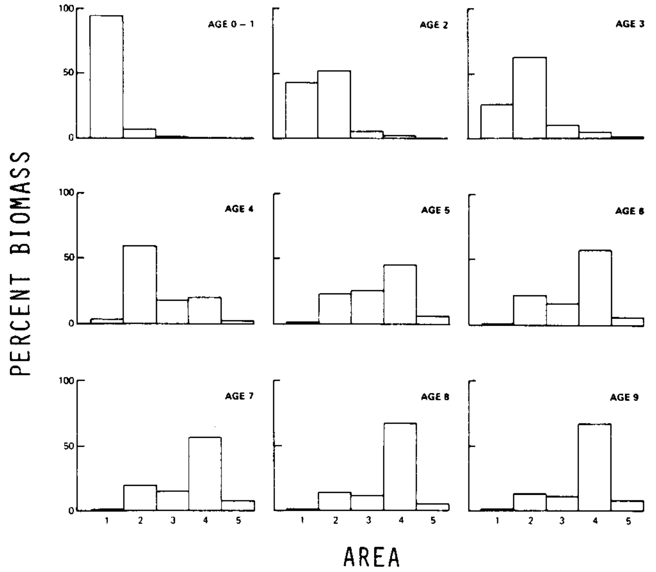

Figure 6. The distribution of biomass by International North Pacific Fisheries Commission area for each age class in the 1977 Northwest and Alaska Fisheries Center trawl survey: Area 1, Conception; Area 2, Monterey; Area 3, Eureka; Area 4, Columbia; Area 5, Vancouver (from Bailey and Ainley, in press).

Adult whiting also make seasonal inshore-offshore migrations. Ermakov (1974) reports that in spring and early summer whiting schools concentrate over the continental slope. By mid-June, a large portion of the stock moves inshore to depths less than 100 m. Later, in early August, whiting move offshore, and by mid-October they begin to migrate southward for spawning. These observations of bathymetric migrations are supported by data in Alton (1972) showing that the average depth of catches in bottom trawls decreased in early summer and increased in autumn (Figure 7). These movements are similar to the dynamics of the California Undercurrent, which is located over the continental slope in spring and spreads over the shelf in early summer (Huyer et al. 1975; Huyer and Smith 1976). Further research on the migration of whiting in relation to ocean currents is needed and would be of value to stock assessment and management efforts.

Adult whiting also migrate on a diurnal schedule. Fish are dispersed from near surface to 20-m depth at night (10 p.m. to 3 a.m.). They descend quickly at dawn and form schools. At night they rise to the surface again in 30-40 min (Nelson and Larkins 1970; Ermakov 1974). These diurnal migrations have been compared to the migrations of their primary prey, euphausiids, as a causal mechanism (Alton and Nelson 1970). As noted previously, spawning whiting do not appear to migrate vertically.

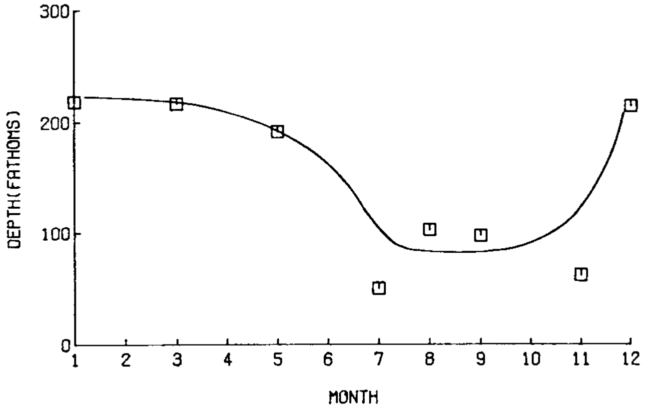

Figure 7. The average depth of Pacific whiting bottom-trawl catches by month, plotted from data in Alton (1972).

Schooling. Pacific whiting form schools in daytime near the bottom. Schools are sometimes shaped in bands composed of distinct clusters (T. Dark, Northwest and Alaska Fisheries Center, Seattle, WA 98112, pers. comm.) whose long axes are often parallel to isobaths (Nelson and Larkins 1970). Soviets reported that schools may be from less than 0.5 km up to 20 km in length and 0.25 to 3.2 km in width. Above the shelf, schools are, in general, within 20 meters of the bottom and are 6-12 m thick. Often the underside of a school is 2 m off bottom. Quite a bit of variability in school size, depth, and structure is observed (M. Nelson, Northwest and Alaska Fisheries Center, Seattle, WA 98112, pers. comm.), and school characteristics are more variable and less oriented over the continental slope than over the shelf (Nelson and Larkins 1970).

Ermakov (1974) concluded that schools are formed of similar-sized fish. He reports densities of 15-19 fish/1000 m^3 in daytime and less than 1 fish/1000 m^3 at night. Spawning schools of whiting form dense aggregations in the pelagic layer, ranging in depth from 100 to 500 m (Stepanenko[6]; Ermakov 1974; Nelson and Larkins 1970). Stepanenko[7] reported one school of spawning whiting that was 4.2 miles long and had a biomass of 81 thousand MT.

Age and growth. Age compositions of commercial catches are determined from annual growth patterns observed from otoliths. The primary source of data on Pacific whiting age and growth comes from the analysis of commercial age compositions (Dark 1975; Francis 1982). Growth in length is rapid during the first 3 years, then it slows and approaches an asymptote in the oldest ages (10-13 yr). At about 4 years of age, females grow noticeably faster, and by age 11 may average 32 cm larger than males (Dark 1975).

TABLE 5

Parameters of the von Bertalanffy Growth Equation

Source and sex classification	l_∞	k	t_o
Dark (1975)			
Male	56.29	0.39	0.20
Female	61.23	0.30	0.01
Male, female combined	60.85	0.30	0.03
Francis (1982)			
Male, female combined	55.40	0.26	−1.61

Individual males may reach 66 cm, and some females may reach 80 cm in length. Growth in length was analytically described by the von Bertalanffy growth equation:

$$l_t = l_\infty\,(l-e^{-k(t-to)})$$

where

l_t = body length at age t

and l_∞, k, and t_o are parameters of the curve.

Table 5 gives values of these parameters estimated for Pacific whiting. Francis (1982) found that between ages 3 and 7 growth in length is not uniform throughout the main feeding season (April-October) and that it appears to reach a maximum during midsummer (June-August).

The length-weight relation empirically fits the following equation:

$$W = a\,l^b$$

where

W = weight in grams, and
l = length in centimeters.

Table 6 gives estimates of a and b for Pacific whiting. By age 3, males have grown to between 50 and 60% of their total weight at age 11, and females to between 40 and 50% of their total weight at age 11. Males attain an average weight of between 900 and 1000 g by age 11 and females between 1100 and 1200 g. Francis (1982) found that growth in weight is markedly seasonal. During the winter spawning season (November-March), adults between ages 4 and 11 lose a minimum of between 5 and 10% of their total body weight, and during the feeding season (April-October) adults between ages 4 and 11 gain a minimum of between 11 and 30% of their initial body weight. Francis (1982)

TABLE 6

Parameters of the Weight-Length Equation $w = a\,l^b$

Source and sex classification	a	b
Dark (1975)		
Male	.034682	2.55618
Female	.020444	2.69509
Francis (1982)		
Male, female combined	.001815	2.73343

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[6] See footnote 2 on page 82.

[7] See footnote 3 on page 82.

TABLE 7

The Percent Occurrence of Food Types in the Diet of Pacific Whiting Determined by Soviet Scientists*

	Washington-Oregon Month				California Month				
Food type	5	6	9	10	3	4	5	6	11
Euphausiids	81.6	99.6	1.2	40.2	83.3	83.1	99.8	84.0	93.5
Shrimp	4.9	0.4	17.3	1.3	—	—	—	—	15.2
Squid	—	—	—	1.3	—	—	—	—	—
Fish	14.3	—	12.4	37.7	5.6	0.9	1.4	1.4	10.9

*Ermakov, Y., and A.M. Kharchenko. 1976. Biological characteristics of Pacific hake and the estimation of its abundance in 1975. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

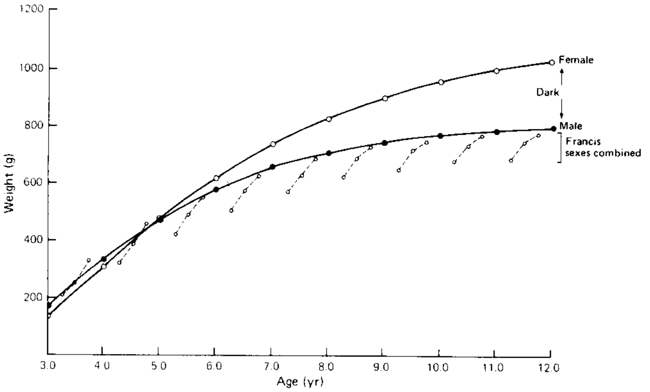

Figure 8. The annual growth in weight of Pacific whiting (from Dark 1975, solid lines) compared to seasonal estimates of growth by age class (from Francis, unpubl. manuscr., dotted lines).

also found that to accurately represent the seasonal dynamics of growth a separate weight-length equation was needed for each age. Figure 8 gives a comparison of the weight-age relationships arrived at by Dark (1975) for 1964-69 and Francis (1982) for 1976-80.

Feeding. The feeding behavior of Pacific whiting has been studied by several investigators, but a comprehensive seasonal and geographic examination of feeding is lacking.

Adult whiting probably do not feed on the spawning grounds (Tillman 1968) but begin to feed "ravenously" during the postspawning migration north (Ermakov 1974). In summer, whiting are observed to feed at night towards the surface (Alton and Nelson 1970); however, if patches of prey are abundant near bottom, whiting may remain there at night to feed (Ermakov 1974).

There are apparent geographic, seasonal, annual, and size-specific differences in feeding behavior. The most frequently occurring prey items in the summer diet are euphausiids and Pacific sand lance, *Ammodytes hexapterus*, off Vancouver Island (Outram and Haegele 1972) and euphausiids and shrimps from California to Washington (Alton and Nelson 1970; Gotshall 1969a). Ermakov and Kharchenko[8] found that off Washington and Oregon euphausiids decrease in frequency of occurrence in the diet in autumn compared to summer (Table 7). Shrimp and fish sometimes occur frequently. Jackowski[9] found that in summer off Vancouver Island, Pacific herring were important in the diet of whiting (Table 8); and in northern California waters where adult and juvenile distributions overlap, cannibalism is often observed (T. Dark, pers. comm.).

TABLE 8

The Percent by Weight of Food Types in the Diet of Pacific Whiting Determined by Polish Scientists* in Summer 1979

	Region		
Food type	Eureka	Columbia	Vancouver
Euphausiids	94.2	94.0	85.6
Juv. rockfish	1.0	1.6	—
Pacific herring	—	—	5.9
Juv. Pacific herring	—	—	6.6
Osmerids	—	0.4	—
Pacific whiting	0.5	—	—
Sablefish	—	2.0	0.1
Flatfish	—	0.4	—
Squid	0.7	—	—
Shrimp	—	1.6	—
Other fish	3.2	—	1.7
Other	0.4	—	0.1

*Jackowski, E. 1980. Biological characteristics of Pacific whiting from Polish surveys of the west coast of the U.S.A. and Canada in 1979. Unpubl. manuscr., presented at the U.S.-Poland bilateral meetings, 1980.

Livingston ("The Feeding Biology of Pacific Whiting," in review) found that Pacific herring were an important component in the diet of whiting off Oregon-Washington in 1980, composing almost 70% of the diet (by weight) of whiting greater than 55 cm, and 50% of the diet of whiting less than 55 cm. Alton and Nelson (1970) found that in the spring and summer of 1965 and 1966, euphausiids, mostly *Thysanoessa spinifera*, composed 57% of the biomass of whiting stomach contents. Fish, mostly deepsea smelts or Osmeridae spp., composed another 34% of stomach contents.

Gotshall's (1969a) study demonstrated considerable seasonality in the diet of whiting off northern California. Crustaceans, which are the major food in spring

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[8] See footnote 5 on page 85.

[9] Jackowski, E. 1980. Biological characteristics of Pacific whiting from Polish surveys of the west coast of the U.S.A. and Canada in 1979. Unpubl. manuscr., presented at the U.S.-Poland bilateral meetings, 1980.

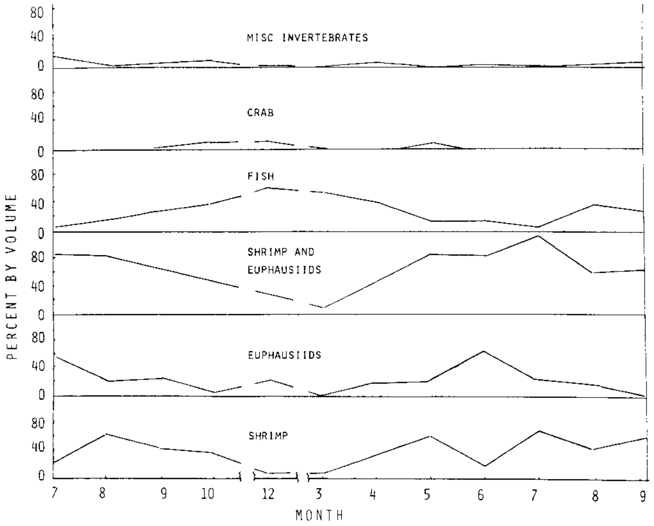

Figure 9. The percentage (by volume) of different food types in the diet of Pacific whiting by month (data from Gotshall 1969a).

and summer, decline in the diet in winter, and are replaced by fish as the dominant food (Figure 9). In spring and summer an average of 50-60% of the stomach contents of whiting was ocean shrimp; however, these results should be viewed conservatively because the sample size was small.

Larger whiting more frequently eat fish and less frequently eat euphausiids compared to smaller whiting (Figure 10). Larger whiting also appear to consistently eat more shrimp than smaller whiting (Figure 11).

The question of whether whiting's feeding on ocean shrimp is a significant factor in shrimp abundance has provoked some controversy. Catches of shrimp off the Oregon-Washington coast have increased significantly since the late 1960s, and this increase appears correlated to the harvest of whiting (Figure 12). It has been hypothesized that removing large whiting by fishing has reduced predation pressure on the shrimp population. This same trend has occurred off the California coast. However, other factors, such as increasing fishing effort or normal changes in abundance, cannot be ruled out as responsible for the increase in shrimp catches, and the question of a whiting-shrimp interaction deserves more rigorous examination. Francis (1982) briefly addresses this issue.

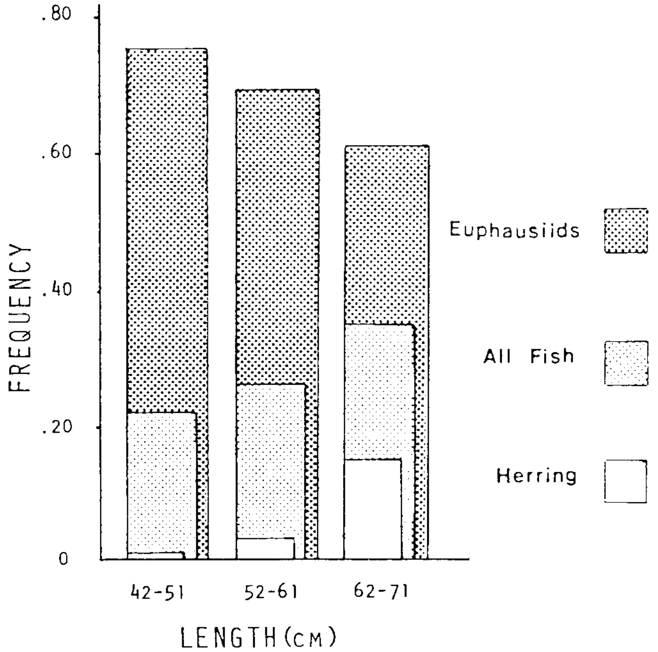

Figure 10. Frequency of occurrence of prey types in different Pacific whiting size classes off Vancouver Island (data from Outram and Haegele 1972).

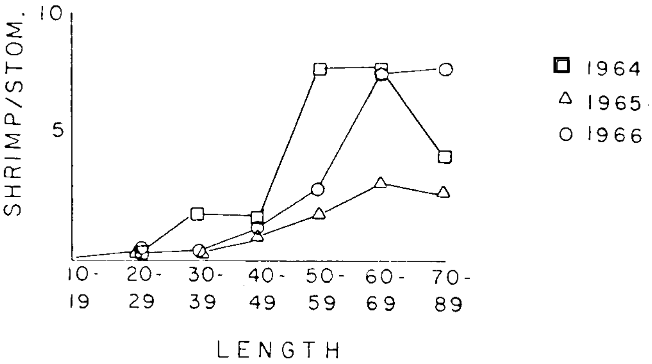

Figure 11. The number of ocean shrimp per stomach of Pacific whiting off Vancouver Island (data from Gotshall 1969b).

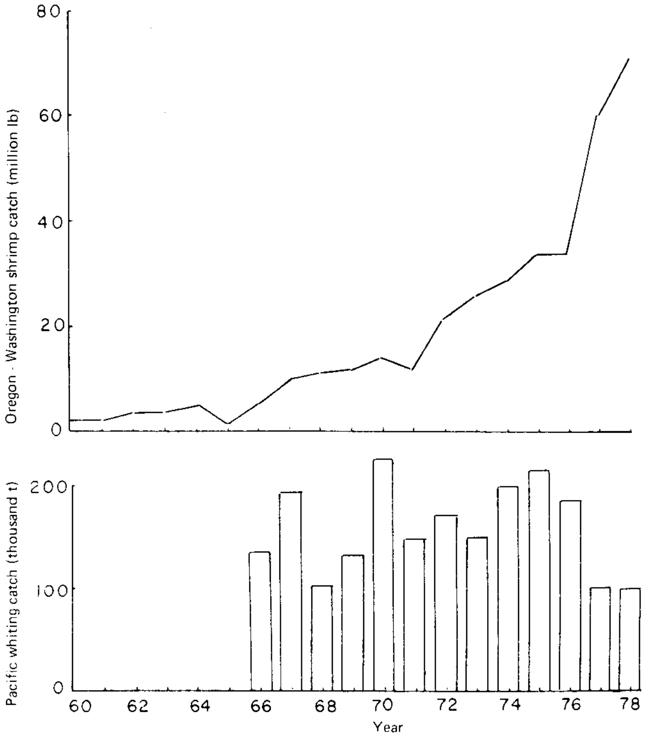

Figure 12. Shrimp catches off the Oregon-Washington coast and catches of Pacific whiting.

TABLE 9

Distribution of Pacific Whiting Biomass by INPFC Area from Three Northwest and Alaska Fisheries Center Surveys

Year	Source	Vancouver	Columbia	Eureka	Monterey and Conception	Total
				Metric tons		
1975*	Midwater	3,791	165,941	25,596	42,020	237,348
	Percentage	2	70	11	18	
	Bottom	667	189,630	7,222	10,107	207,626
	Percentage	—	91	3	5	
	Total	4,458	355,571	32,818	52,127	444,974
	Percentage	1	80	7	12	
1977	Midwater	343,821	316,440	360,944	108,087	1,129,292
	Percentage	30	28	32	10	
	Bottom	6,560	32,917	9,501	20,662	69,640
	Percentage	9	47	14	26	
	Total	350,381	349,357	370,445	128,749	1,198,932
	Percentage	29	29	31	11	
1980	Midwater	322,335	260,476	182,783	578,841	1,344,435
	Percentage	24	19	14	43	
	Bottom	16,678	16,938	13,579	127,647	174,832
	Percentage	10	10	8	73	
	Total	339,013	277,404	196,362	706,488	1,519,267
	Percentage	22	18	13	47	

*1975 areas do not correspond to 1977 and 1980 survey areas.

Competitors. Competitors with Pacific whiting for food resources are numerous. Among competitive fishes are other Gadidae; flatfish, Pleuronectidae; soles, Bothidae; smelts, Osmeridae; Cottidae; Pacific herring; albacore, *Thunnus alalunga;* Hexagrammidae; lingcod, *Ophiodon elongatus;* Myctophidae; rockfish, Scorpaenidae; sablefish, *Anoplopoma fimbria;* and Salmonidae. Numerous marine mammals may also be competitors, including the rough-toothed dolphin, *Steno bredanensis;* gray whale, *Eschrichtius robustus;* minke whale, *Balaenoptera acutorostrata;* Bryde's whale, *B. edeni;* sei whale, *B. borealis;* fin whale, *B. physalus;*blue whale, *B. musculus;* humpback whale, *Megaptera novaeangliae;* and right whale, *Balaena glacialis* (Fiscus 1979).

Predators. Predators of Pacific whiting reported in the literature include the great white shark, *Carcharodon carcharias;* soupfin shark, *Galeorhinus zyopterus;* Pacific electric ray, *Tetranarce californica;* bonito, *Sarda chiliensis;* albacore; bluefin tuna, *Thunnus thynnus;* rockfish; sablefish; lingcod; dogfish, *Squalus acanthias;* and arrowtooth flounder, *Atheresthes stomias* (Best 1963; Nelson and Larkins 1970; Pinkas et al. 1971). Marine mammals that feed on whiting include the California sea lion, *Zalophus californianus;* northern elephant seal, *Mirounga angustirostris;* Pacific whiteside dolphin, *Lagenorhynchus obliquidens;* killer whale, *Oreinus orca;* Dall porpoise, *Phocoenoides dalli;* sperm whale, *Physeter macrocephalus;* northern sea lion, *Eumetopias jubatus;* and northern fur seal, *Callorhinus ursinus* (Fiscus 1979).

Bailey and Ainley (1982) analyzed otoliths collected from California sea lion scats at the Farallon Islands for 4 yrs, 1974-78, and describe the seasonal and annual dynamics of sea lion feeding on Pacific whiting. Sea lions fed most heavily on whiting, primarily juveniles, in spring and summer and may consume about 185 thousand tons each year.

POPULATION DYNAMICS

Size of Stocks

The abundance of the Pacific whiting stock has been assessed from trawl-hydroacoustic surveys. In 1980 the abundance of whiting from central California to southern Vancouver Island over the continental shelf was estimated by scientists of the Northwest and Alaska Fisheries Center to be 1.52 million metric tons (MT). Most of this biomass was composed of juveniles off the coast of central California. From similar surveys in 1975 and 1977, the stock biomass was estimated at 0.44 million and 1.20 million MT (Table 9). Based on earlier surveys by the U.S. Bureau of Commercial Fisheries, Alverson (cited in Tillman 1968) calculated about 0.68 million MT of whiting. Estimates of whiting abundance based on hydroacoustic methods (Kramer and Smith 1970; Dark et al. 1980), however, have limitations. Critical problems include (1) the difficulty in calibrating target strength, (2) the failure to identify species by acoustic signals, and (3) the detection of whiting near the bottom (Thorne[10]). Regardless of these problems,

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[10] Thorne, R.E. Assessment of population abundance by echo integration. SCOR, Working Group No. 52. Symposium on assessment of micronekton, April 27-30, 1980.

whiting offer one of the more optimum circumstances for hydroacoustic assessment compared with many other species.

Soviet scientists have determined that the average biomass of whiting from 1967-73 was 1.36 million MT (Efimov[11], Ermakov and Kharchenko[12], Vologdin[13]). They estimated 1.40 and 1.86 million MT of whiting in 1974 and 1975, respectively. The Soviets conducted two surveys in 1979 with resulting estimates of 1.20 and 2.88 million MT.

Estimates of spawning biomass of whiting determined from egg and larval surveys are considerably higher than those stated above. Ahlstrom (1968) calculated that the spawning biomass of whiting was 1.8 to 3.6 million MT. Stepanenko[14] estimated that the spawning biomass of whiting was 2.4 million MT in 1977 and 2.65 million MT in 1979.

Estimates of spawning biomass from egg and larval surveys are extremely crude in the case of whiting because: the size composition and fecundity of the spawners is relatively unknown; the stage duration of eggs and larvae was not used for these approximations; fecundity schedules of adults are based on very little data; and it is unknown whether whiting are multiple spawners. Estimates are further confounded by the extreme patchiness of eggs and larvae. In spite of these problems, ichthyoplankton surveys are useful for assessing the relative abundance of the stock, and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton surveys conducted since 1950 have been useful in monitoring changes in the spawning potential of the population. The spawning stock appears to have decreased in the late 1960s and early 1970s compared with earlier years, but has recently increased to previous levels (Stauffer and Smith 1977).

Recruitment

Because of the spatial distribution of age classes, recruitment of the exploited stock occurs at 3-6 years of age depending on the location of fishing. Interannual variations in recruitment are great, as exemplified by the dominance of the age composition of the stock by strong year classes for several consecutive years (Figure 13).

The factors most often considered to affect reproductive success of marine fishes are cannibalism, food supply, predation, and larval transport. Although cannibalism is sometimes observed, it is probably fairly low because the majority of adult whiting spend a limited time in the spawning area (1-3 mo). However, Sumida and Moser (1980) found that some large larvae eat smaller larvae, and there are a few reports of adult predation on juveniles.

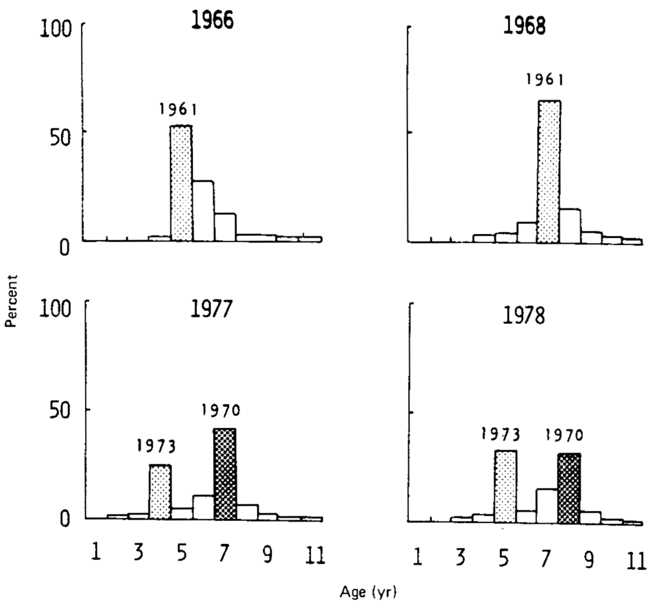

Figure 13. Age compositions of Pacific whiting caught off Oregon and Washington from research surveys (1966 and 1968) and from U.S. observer fishery data (1977 and 1978) (from Bailey 1981a,b).

Bailey (in press) found that the food requirement of whiting larvae is low because of relatively low growth and metabolic rates. The large mouth size of larvae enables first-feeding larvae to ingest a wide spectrum of food particles, including juvenile and adult copepods (Sumida and Moser 1980). Bailey (in press) calculated that a first-feeding whiting larva can satisfy growth and metabolic requirements by ingesting 31 copepod nauplii, 6 small calanoid adult copepods, or 0.6 *Calanus* copepodites per day. By comparison, a first-feeding northern anchovy larva, with its small mouth, must capture at least 200 *Gymnodinium* cells per day to satisfy metabolic (excluding growth) requirements alone (Hunter 1977). It was concluded that starvation from first-feeding failure is probably not as variable for whiting larvae as it appears to be for northern anchovy and that whiting may not be as dependent on finding patches of prey as are northern anchovy (Lasker 1975).

Predation on eggs and larvae is a difficult problem to assess and is poorly understood. A wide variety of invertebrate organisms are capable of feeding on whiting eggs and larvae. Yolk-sac stages are most vulnerable to predation by invertebrates (Bailey and Yen, in press). Predation by invertebrates may be

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[11] Efimov, Y.N. 1974. The size of stocks and status of fishery of Pacific hake. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

[12] See footnote 5 on page 85.

[13] Vologdin, V. 1980. Results of the hydroacoustic surveys with trawlings off the Pacific coast of North America in 1979. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

[14] See footnotes 2 and 3 on page 82.

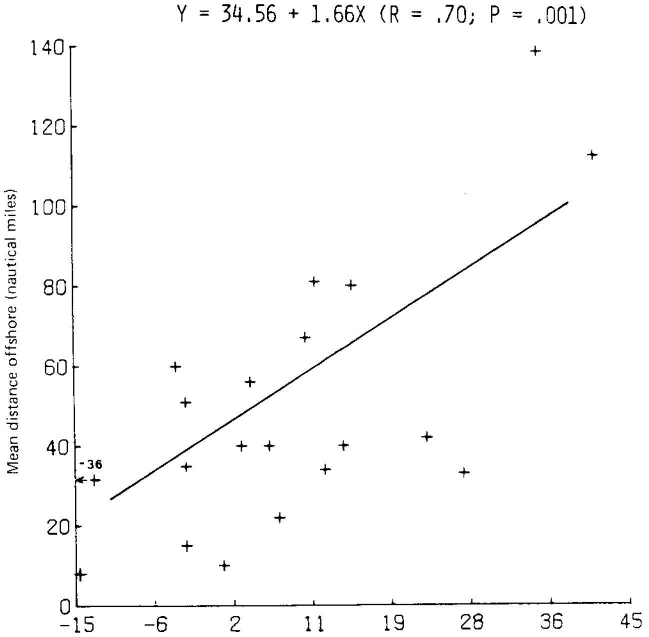

Figure 14. The distribution of larvae offshore in January-February surveys versus the January upwelling index, 1950-79 (linear correlation coefficient, R = 0.70, P = 0.001) (from Bailey 1981 a,b).

important in cold years when development is slow through the stages most vulnerable to predation.

Oceanographic conditions appear to play a major role in the recruitment of Pacific whiting (Bailey 1981 a,b). The offshore distance of larvae is apparently positively correlated to indices of wind-driven Ekman transport (Figure 14). Although there is a good deal of variability in this relationship, it is statistically significant and indicates that larvae may be transported offshore in years of high upwelling. Since the juvenile nursery is inshore over the continental shelf, advection of larvae offshore is expected to be detrimental to survival. In fact, Ekman transport during the spawning months is negatively correlated to year-class strength (Figure 15). Further work must be done on the survival of larvae swept offshore to test this hypothesis.

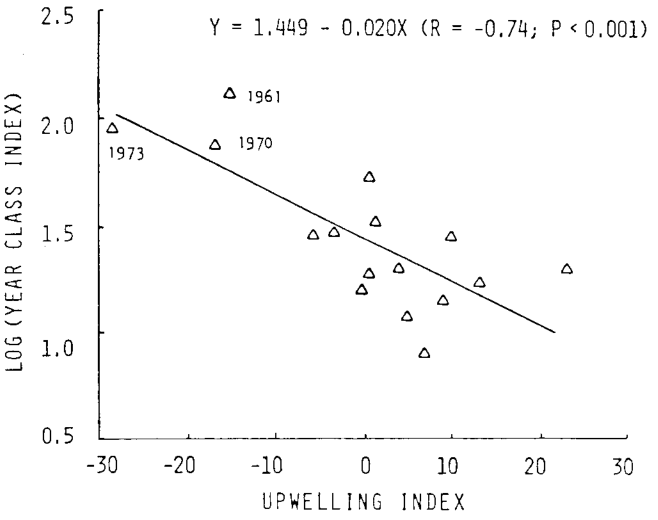

Figure 15. Log of the year-class index against the January upwelling index (from Bailey 1981a,b).

Temperature may also influence recruitment, possibly by the predation-temperature interactions noted above and the previously described influence of temperature on the location of spawning. The average winter temperature and Ekman transport in a multiple regression model account for 68% of the observed variation in an index of year-class strength (Bailey 1981 a,b). There is no apparent relationship between spawning biomass of the population and recruitment.

Mortality

Estimates of annual instantaneous natural mortality rates range widely. These estimates, as well as several estimates for fishing and total mortality rates are presented in Table 10. A cohort analysis performed by Francis (1982) on the 1973-80 catch-by-age data gives estimates of age-specific fishery mortality (catchability) as well as recruitment of the exploited stock at age 3.

TABLE 10

Estimates of Annual Instantaneous Mortality Rates of Pacific Whiting

Investigators	Males	Females	Both Sexes
M: natural mortality			
Tillman (1968)	0.72	0.62	x=0.67
Nelson and Larkins (1970)			0.56
Efimov (1974)[1]			0.35
PFMC[2]			0.30-0.60
Jackowski (1980)[3]			0.30
Ehrich, et al. (1980)			0.56
Low (1978)[4]			0.50
Francis (in prep.)			0.19-0.86 (variable age-specific natural mortality)
F: fishing mortality			
Efimov (1974)[1]			0.30
Ehrich, et al. (1980)			0.67
Z: total mortality			
Efimov (1974)[1]			0.65
Ehrich et al. (1980)			1.23

[1] Efimov Y.N. 1974. The size of stocks and status of fishery of Pacific hake. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

[2] Pacific Fishery Management Council. 1980. Pacific coast groundfish plan. Draft report. Pacific Fishery Management Council, 526 S.W. Mill St., Portland, OR 97201.

[3] Jackowski, E. 1980. Biological characteristics of Pacific whiting from Polish surveys of the west coast of the U.S.A. and Canada in 1979. Unpubl. manuscr., presented at the U.S.-Poland bilateral meetings, 1980.

[4] Low, L.L. 1978. Hake natural mortality and yield potential. Unpubl. manuscr. Northwest and Alaska Fish. Cent. Natl. Mar. Fish. Serv. NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

Dynamics of the Population

Over the past 200 years the Pacific whiting population has experienced some major changes in abundance (Soutar and Isaacs 1974).Based on an analysis of fish scales deposited in sediments, at the turn of the last century the population was almost an order of magnitude larger than recent abundance levels. These changes in abundance have been correlated to changes in abundance of the northern anchovy (Soutar and Isaacs 1974) and are inversely correlated to offshore Ekman transport (Bailey 1981a,b).

Several mathematical models have been constructed that simulate changes in the whiting population. These include models by Francis (1982), Francis et al. (1982), Bernard (Oregon State University, Newport, OR), Stevens and Goodman (Scripps Institution of Oceanography, La Jolla, CA), Tillman (1968), and Riffenburgh (1969).

THE PACIFIC WHITING FISHERY

Historical Catches and Effort

Pacific whiting has been the target of a large foreign fishery off the west coast of the United States and Canada (Table 11). A Soviet fishery for whiting began in 1966 with a catch of 137 thousand MT. From 1973-76 Poland, West Germany, East Germany, and Bulgaria joined fishing operations for Pacific whiting. Reported catches peaked in 1976 at 237 thousand MT. The average annual all-nation reported catch from 1966 to 1980 was 162 thousand MT. (These catches were compiled from data at the Northwest and Alaska Fisheries Center.)

A small domestic fishery for whiting, used in the manufacture of pet food, has existed since at least 1879 (Jow 1973). This fishery has been rather insignificant, with catches in the range of 200-500 MT/yr. However, in recent years the domestic fishery has become important: U.S.-foreign joint-venture fishing caught 9 thousand MT and 28 thousand MT in 1979 and 1980, respectively.

Historical effort statistics for the fishery, excluding Canadian waters, were calculated from weekly aerial surveillance data from the NMFS Enforcement Division (supplied by Bill Dickenson, NMFS, Northwest Regional Office, Seattle, WA). Effort for two classes of vessels—large Soviet BMRT stern trawlers and smaller Soviet SRT side trawlers (see "Technical Aspects" below)—were calculated in vessel-days on the fishing grounds. Effort by the SRT trawlers was greatest in 1966 and declined steadily (Table 12). Effort by the BMRT trawlers was greatest in 1975 and 1976.

To obtain a rough estimate of overall catch per unit of effort (CPUE) for the foreign fishery in U.S. waters, SRT effort was converted to effective BMRT effort by assuming a relative fishing power of P_{SRT} = 0.31 from the ratio of average horsepower of SRT vessels to BMRT vessels (1150 HP).

Catch/standard BMRT day indicates that the highest rates occured in 1967 and from 1977 to 1980. Since the latter period coincides conspicuously with passage of the Magnuson Fishery Conservation Management Act of 1976 (MFCMA) and the onset of intense observer coverage, these statistics indicate that actual catches were possibly underreported from 1968 to 1976.

TABLE 11

Annual All-Nation Catches of Pacific Whiting (x 10^3 MT) in U.S. and Canadian* Waters.

Year	U.S.S.R.	Poland	Domestic/ joint venture	Other	Total
1966	137.0	—	—	—	137.0
1967	206.1	—	—	—	206.1
1968	103.8	—	—	—	103.8
1969	161.8	—	—	0.12	161.9
1970	226.2	—	—	2.3	228.5
1971	151.8	—	—	1.4	153.2
1972	150.8	—	—	0.4	151.2
1973	143.8	2.0	—	5.1	150.8
1974	173.7	44.3	—	8.4	226.5
1975	155.4	57.2	—	5.1	217.7
1976	158.0	25.7	—	53.0	236.8
1977	111.0	19.5	—	1.9	132.4
1978	70.9	27.3	2.7	3.4	104.2
1979	96.8	22.3	13.1	3.6	135.9
1980	0.1	49.0	40.8	0.8	90.7

*Zyblut, E. 1981. Dept. of Fisheries and Oceans, Govt. of Canada, Vancouver, B.C. Personal communication.

TABLE 12

Historcial Effort Statistics for the U.S.S.R.-Poland Foreign Pacific Whiting Fishery (Solely) in U.S. Waters

Year	BMRT vessel days	RST vessel days	Standard BMRT days P_{ST}=0.31	Catch (1000 MT)	CPUE (MT/BMRT day)
1966	2,670	14,490	7,128	137.0	19.2
1967	2,730	10,350	5,915	195.1	33.0
1968	5,677	2,079	6,317	68.0	10.8
1969	5,607	1,589	6,096	109.0	17.9
1970	7,847	658	8,049	200.8	24.9
1971	7,245	651	7,445	146.7	19.7
1972	5,131	518	5,290	111.3	21.0
1973	5,904	—	5,904	141.1	23.9
1974	7,717	—	7,717	201.1	26.1
1975	10,401	—	10,401	196.9	18.9
1976	6,917	—	6,917	177.8	25.7
1977	4,076	—	4,076	127.2	31.2
1978	2,779	—	2,779	96.9	34.9
1979	4,452	—	4,452	114.9	25.8
1980	1,553	—	1,553	44.0	28.3

Assumptions – P_{ST}=0.31
P_{BMRT}(Poland)=1.00
CPUE = catch per unit effort

Technical Aspects

As the major country fishing for whiting, the Soviet Union has improved its whiting fleet considerably. In 1966 the fleet was mainly medium-sized side trawlers (SRTs) of about 500 gross tons. The proportion of large stern trawlers with freezing capacity (BMRTs) has gradually increased to replace the side trawlers. The typical BMRT is 3170 gross tons, has a crew of 22-26, and uses a midwater trawl with a headrope length of 97 m. The daily production capacity is 30-50 MT of frozen fish and 20-35 MT of meal and oil. Support vessels in the fishery include factory ships, refrigerated transports, oil tankers, personnel carriers, tugs, and patrols.

The Soviet fishery is a well-coordinated expedition, and acoustics are used to guide the net over fish concentrations. Prior to 1976, about 100 BMRTs would typically participate in the fishery (Pruter 1976), but lately the fleet has been reduced to about 39 large stern trawlers. In early years of the fishery most whiting were filleted, and small fish were reduced to meal. Recently the average size of hake has become considerably smaller, and an increasing proportion of the catch is frozen whole.

The foreign fishery is closely tied to the migratory movements of the whiting population. Historically, the fishery began in waters off Oregon in April and moved northward as schools made their way up the coast in summer. This was documented from aerial sightings of the Soviet fishery (Figure 16). In autumn, as fishing activity halted, whiting began to migrate offshore and southward for spawning. More recently, fishing has been restricted by treaty to the period from June until October. Based on aerial surveillance records and Ermakov's (1974) analysis of the fishery, rich fishing grounds appear to be associated with prominent geographical sites such as banks, sharp "curves" in the continental slope, and canyons. Especially productive grounds are found near the Heceta Banks, Yaquina Head, Cape Flattery, Cape Blanco, and Destruction Island. Most fish are caught in depths of 100-199 m (Table 13).

Management

Prior to implementation of the MFCMA in 1977, the foreign fishery was managed by bilateral agreement. Since 1977 management has been directed by a Preliminary Management Plan (PMP)[15] for groundfish prepared by the Department of Commerce. Subsequently, the Pacific Fishery Management Council has prepared a fisheries management plan (FMP) for groundfish, including whiting, which is currently under review. A conservative estimate of maximum sustained yield in the plan is 175.5 thousand MT. The FMP specifies geographic and seasonal restrictions, mesh size, incidental catch levels, and an optimal yield (in the form of quotas). Under the MFCMA only the Soviets and Poles have been granted licenses as the major foreign interests that may fish for Pacific whiting. Recently. U.S. fishermen have become involved in the whiting fishery through joint ventures in which U.S. trawlers harvest whiting for delivery to foreign processing vessels.

TABLE 13
Catch (Percentage) by Depth Strata of Pacific Whiting Taken by Foreign Trawlers in 1979

Depth (m)	0-99	100-199	200-299	300-399	400-499	>500
Percentage	15.7	47.7	26.2	6.9	2.3	1.2

From: French, R., R. Nelson Jr., and J. Wall. 1980. Observations of foreign and joint venture fishing fleets off the coast of Washington, Oregon, and California, 1979. Unpubl. rep. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

Francis et al. (1982) present a management analysis of the Pacific whiting fishery in which a policy algorithm is developed that aims to use strong year classes in a practical and efficient manner while protecting the stock when it is in poor condition and environmental conditions do not appear conducive to immediate improvement.

Effects of the Fishery on the Population

Commercial fisheries may affect the abundance and recruitment of marine fish populations in several ways. Besides reducing the total spawning biomass of the population, removing a stock's largest and oldest fish also (1) lowers the quality of the spawning product if offspring from smaller fish are less fit (Hempel 1979); (2) reduces the number of age classes that contribute to spawning; thus the maintenance of healthy levels of spawning stock depends on successful re-

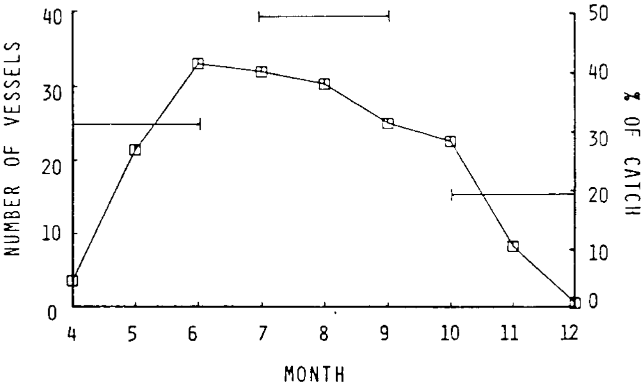

Figure 16. The average monthly number of foreign vessels fishing Pacific whiting sighted in aerial surveys, 1967-72 (squares) and the average percentage of the catch in 3-mo periods for the same years.

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[15] Pacific Fishery Management Council. 1980. Pacific coast groundfish plan. Draft report. Pacific Fishery Management Council, 526 S.W. Mill St., Portland, OR 97201.

cruitment from fewer age classes (Smith 1978); and (3) changes the distribution of spawning if the population stratifies by size or age on the spawning ground.

The spawning potential of the whiting population has had no discernible effect on recruitment from 1960-75 (Bailey 1981a,b), partly because of the overwhelming effects of environmental factors. For example, the strong 1961 year class arose from an extremely low spawning stock, but under favorable environmental conditions it became a very strong year class. Similar situations gave rise to the strong 1970 and 1973 year classes.

The long life of *Merluccius* spp., as well as of other gadids, is probably an adaptation to stabilize the stock from the effects of extreme recruitment variability, and reduction in the number of spawning age classes by heavy fishing must be a destabilizing influence. In a population with fewer age classes, the probability of a stock collapse would increase if recruitment failure occurred in a succession of years. This type of interaction appears to have influenced the recruitment of other stocks. In an analysis of the population dynamics of the Pacific sardine, *Sardinops sagax,* Murphy (1968) concluded that after the number of spawning age classes was reduced by fishing, several years of recruitment failure caused catastrophic population declines.

Since the mid-1960s, a change in the spawning grounds of Pacific whiting has occurred. Larvae have become much less abundant off Baja California and more abundant off central California compared with earlier years (Bailey 1980). In addition, the deposition of scales from young whiting markedly declined off Baja California from 1965-69 compared with earlier prefishing periods (Soutar and Isaacs 1974). Smith (1975) first suggested that this change was related to the beginning of an intensive fishery for adults in 1966. He suggested that large adults spawn farther south and that harvesting this component of the population has caused the spawning decrease in the southern end of the range. Further analysis supports an interaction between the spawning distribution and the fishery (Bailey 1980, 1981a,b). Although the spawning location of whiting is related to temperature, the recent change in the distribution of larvae is independent of temperature changes. An analysis of covariance indicated significantly different slopes and intercepts for pre- and post-spawning periods (Figure 17).

ACKNOWLEDGMENTS

Numerous scientists at the Northwest and Alaska and Southwest Fisheries Centers freely made data available. T. Laevastu, R. Schwartzlose, T. Dark, and R. Lasker reviewed earlier versions of the manuscript and made helpful comments. We also appreciate the encouragement of W. Wooster and R. Marasco.

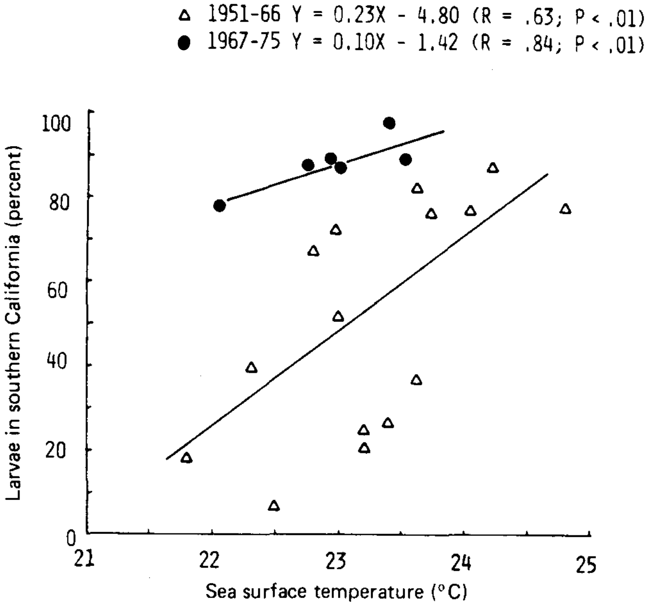

Figure 17. Regressions of the percentage of Pacific Whiting larvae off southern California compared to Baja California against the mean January-March sea surface temperature off Baja California for the pre- and postfishing periods, 1951-66 and 1967-75.

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TURBULENCE, TRANSPORT, AND PELAGIC FISH IN THE CALIFORNIA AND PERU CURRENT SYSTEMS

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ABSTRACT

The California and Peru Current systems are compared in terms of three environmental processes thought to be likely regulators of reproductive success of pelagic fishes: (1) turbulent mixing, leading to destruction of fine-scale food strata required for successful first feeding of larvae, (2) offshore transport, resulting in loss of reproductive products, and (3) upwelling intensity, as it relates to total productivity of the system. Newly generated climatological distributions of coastal-oceanic temperature contrast, wind-generated turbulent energy production, sea surface wind stress, and surface Ekman transport are presented. A consistent pattern of avoidance of centers of maximum upwelling, which are characterized by intense turbulent mixing and offshore transport, is noted in the reproductive strategies of anchovies. Large stocks tend to occur in regions of low turbulent mixing, downstream of upwelling maxima.

RESUMEN

Se comparan los sistemas de corrientes de California y Perú en relación con los procesos ambientales estimados como reguladores del éxito en la reproducción de los peces pelágicos: (1) la mezcla turbulenta que elimina los estratos conteniendo organismos de talla pequeña, necesarios para un umbral óptimo en la alimentación de las larvas; (2) flujo mar afuera que ocasiona pérdida de gametos y productos de la reproducción; y (3) la intensidad del afloramiento y su relación con la productividad total del sistema. Se discuten las características climatológicas en relación con el contraste en la distribución de la temperatura en la zona oceánica y costera, la turbulencia generada por el viento, la acción del viento sobre la superficie del mar, y el transporte Ekman en aguas de superficie. La estrategia de las anchovetas durante su época de reproducción muestra una caracteristica constante. Así, evitan los centros de afloramiento máximo donde se produce una acción de mezcla intensa y turbulenta, y las zonas de corrientes mar afuera. Las poblaciones tienden a concentrarse en regiones donde la acción de mezcla y turbulencia es de intensidad baja, en la corriente procedente de las zonas de máxima surgencia.

INTRODUCTION

The four major eastern boundary current systems of the world—the California, Peru, Canary, and Benguela—appear to have similar environmental dynamics and are dominated, in terms of exploitable biomass, by very similar assemblages of pelagic fish species (Table 1). Bakun and Parrish (1980) presented a rationale for interregional comparative studies as a means for developing insights to enhance effectiveness in managing fishery impacts in the face of fluctuating environmental conditions.

The economic importance of the stocks of pelagic fishes in the four principal eastern boundary currents and their apparent tendency to collapse under heavy exploitation make it of great interest to know to what extent we can transfer experience from one system to another, i.e. whether to expect similar outcomes from similar actions. For example, in the Peru Current system a massive anchovy-dominated system has, under heavy exploitation, recently shifted to a sardine-dominated system. The presently expanding exploitation of the central stock of California Current anchovy invites comparison of the two situations. Conversely, extremely heavy exploitation of sardine, jack mackerel, and mackerel resources off Peru and Chile is reminiscent of the heavy exploitation of similar California Current stocks, followed by collapse and subsequent shifting of the system to anchovy dominance several decades ago.

Deducing the environmental factors controlling reproductive success through pattern recognition of environmental-reproductive relationships derived from different eastern boundary current systems is one method to integrate the oceanographic and fishery research that has been carried out in the different regions. Reproduction is singled out as the most significant life-history feature because recruitment variability is considered to be the principal factor responsible for pelagic fish population fluctuations in upwelling regions (Troadec et al. 1980; Csirke 1980; Lasker 1981). Natural selection implies that observed reproductive

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[Manuscript received February 8, 1982.]

TABLE 1
Dominant Anchovy, Pilchard, Horse Mackerel, Hake, Mackerel, and Bonito in the Four Major Eastern Boundary Currents

California Current	Peru Current	Canary Current	Benguela Current
Engraulis mordax	*Engraulis ringens*	*Engraulis encrasicholus*	*Engraulis capensis*
Sardinops sagax	*Sardinops sagax*	*Sardina pilchardus*	*Sardinops ocellatus*
Trachurus symmetricus	*Trachurus symmetricus*	*Trachurus trachurus*	*Trachurus trachurus*
Marluccius productus	*Merluccius gayi*	*Merluccius merluccius*	*Merluccius capensis*
Scomber japonicus	*Scomber japonicus*	*Scomber japonicus*	*Scomber japonicus*
Sarda chiliensis	*Sarda chiliensis*	*Sarda sarda*	*Sarda sarda*

After Bakun and Parrish 1980.

strategies represent successful accommodation to the most crucial environmental factors. Thus, compelling patterns in seasonal and geographical relationships of reproductive and environmental characteristics suggest important causal linkages over the period during which the reproductive characteristics were generated. The assumption that these same linkages continue to affect reproductive success on a year-to-year basis provides a rational basis for including these factors in empirical modeling efforts.

Recent studies have directed attention toward three classes of environmental processes considered to be likely regulators of pelagic fish reproductive success.

1. Destruction of fine-scale food particle concentrations by wind-generated turbulent mixing has been found detrimental to larval anchovy survival by a series of laboratory and seagoing experiments (Lasker 1975, 1978; Lasker and Smith 1977). Comparative studies of anchovy reproduction in the California Current system versus turbulence and water column stability (Husby and Nelson, this volume) have added corroborative evidence.
2. A comparative study of seasonality and geography of ocean transport and fish reproductive strategies in the California Current (Parrish et al. 1981) has indicated a general pattern of avoidance of intense offshore flow conditions in the reproductive habits of a wide variety of coastal fish stocks. The suggestion is that offshore loss of reproductive products may exert an important control on reproductive success.
3. The major upwelling regions of the oceans are notable for high levels of primary organic production and for particularly massive fish stocks (e.g., Cushing 1969). Recognition of this pattern has led to the widespread belief that fish abundance in these regions is dependent on maintenance of organic production by the upwelling processes, and that long time-scale variations in upwelling intensity may induce fish stock fluctuations. Bakun and Parrish (1980) reviewed a number of recent studies in which estimates of variations in upwelling intensity in the California Current system have been related to fish stock variations.

In this paper we focus primarily on the first two hypotheses. The third is considered in terms of the linkage between offshore surface transport and coastal upwelling, the differing effects being distinguished according to the time and space scales on which they operate; for example offshore transport previous to and upstream of spawning activity might enhance larval survival by ensuring adequate food particle concentrations, whereas the same level of offshore transport right at the spawning site could result in offshore loss of eggs and larvae.

Offshore surface transport is adequately represented as Ekman transport (Parrish et al. 1981), except in the immediate vicinity of the equator. Actual transport is the sum of the Ekman and geostrophic components; however, we have not specifically addressed the

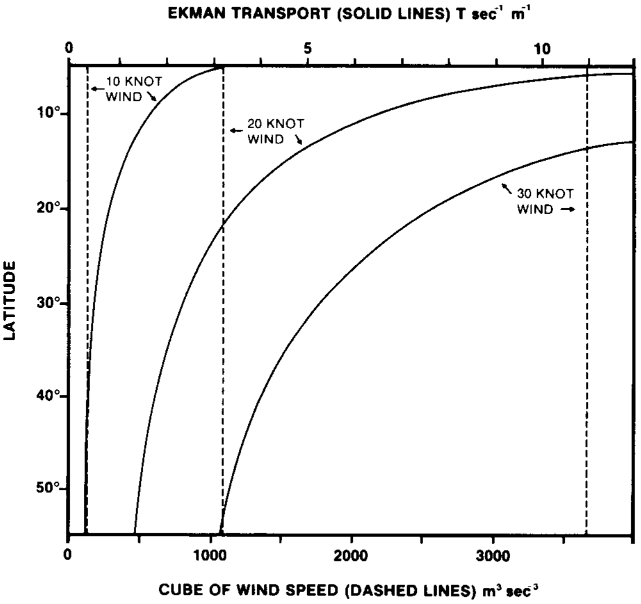

Figure 1. Turbulent mixing energy production (proportional to the third power of the wind speed) vs Ekman transport, for several values of wind speed.

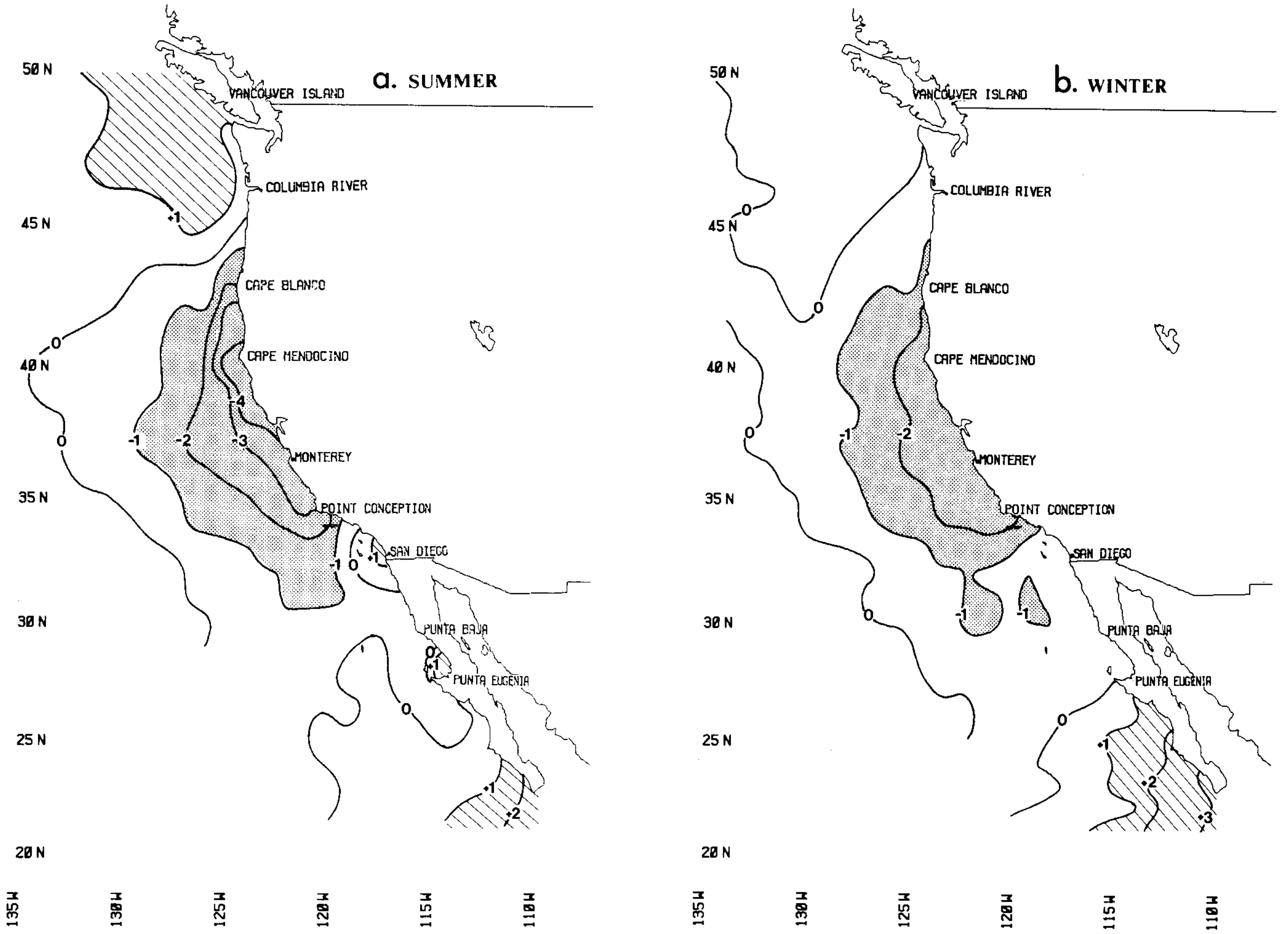

Figure 2. Coastal temperature anomaly (degrees Celsuis) computed as the difference between the temperature at each location and a smoothed reference temperature considered to be characteristic of offshore conditions at the same latitude (see text). *(a)* Summer (May, June, July, Aug.). *(b)* Winter (Nov., Dec., Jan., Feb.).

geostrophic component because Peru Current flow fields are not yet available on the proper scale. The rate of production of wind-generated turbulent mixing energy varies as the third power, or "cube," of the wind speed (Niiler 1975). Thus for a given wind speed, turbulent mixing energy production is not dependent on latitude, whereas Ekman transport has a strong latitude dependence (Figure 1). This difference is basic to our interregional comparison; for example, a given level of offshore transport would be accompanied by a much lower level of turbulent mixing off Chimbote at 10°S than in the Southern California Bight at 33°N.

SEA SURFACE CLIMATOLOGY

California Current Coastal Temperature Anomaly

Summer and winter distributions of coastal temperature anomaly for the California Current region (Figure 2) were constructed as follows. All the sea surface temperature observations available in the Fleet Numerical Oceanography Center's version of the National Climatic Centers' File of Marine Surface Observations (TDF-11) for each group of months were averaged by 1-degree latitude and longitude quadrangles. A smoothed offshore temperature reference was constructed by successively applying, at each 1-degree latitude increment, a 5-degree latitude by 3-degree longitude moving-average filter centered at the eleventh 1-degree quadrangular sample westward from the coast. To further minimize sampling irregularities, the three highest and three lowest of the fifteen sample averages covered by the filter at each step were discarded and the remaining nine averaged together; the result is a smoothly varying function of latitude, which we chose as a reference of the offshore oceanic temperature conditions. Finally, the value of this reference at the proper latitude was subtracted

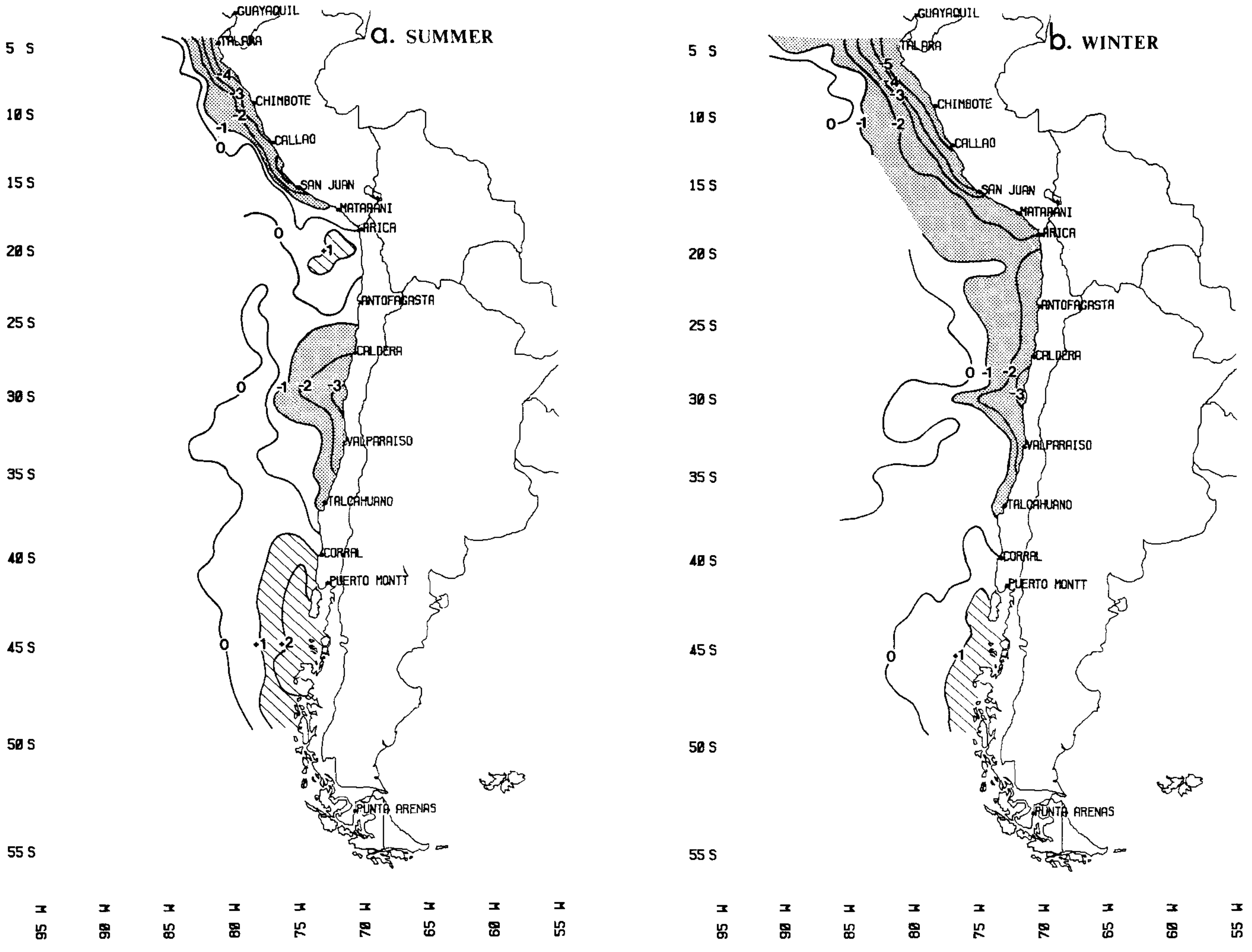

Figure 3. Coastal temperature anomaly (degrees Celsius) computed as the difference between the temperature at each location and a smoothed reference temperature considered to be characteristic of offshore conditions at the same latitude (see text). *(a)* Summer (Nov., Dec., Jan., Feb.). *(b)* Winter (May, June, July, Aug.).

from each 1-degree averaged temperature. Coastal temperature anomaly as used herein is therefore the difference between the temperature at each location and the large-scale temperature offshore; it thus filters the global scale equatorward temperature gradient, thereby highlighting local effects.

The area of negative anomaly greater than 1°C (shaded in Figure 2) delineates the area of maximum upwelling that is centered off northern California. The lobe of negative anomaly extending southward from Point Conception appears to be advective in origin, although local Ekman pumping (oceanic upwelling) associated with the strong positive wind stress curl in this location (Nelson 1977) may be a factor. During the summer, positive anomalies greater than 1°C appear in the interior of the Southern California Bight and within Sebastian Vizcaino Bay, north of Punta Eugenia (Figure 2a). Positive anomalies off the Pacific Northwest appear to be continuous with generalized warm advection into the Gulf of Alaska region. The area off Punta Baja has negative anomalies consistent with an upwelling region, but their magnitude is very low compared to the region north of Point Conception. The winter distribution (Figure 2b) is grossly similar to that for summer, but with a general lessening of gradients.

Peru Current Coastal Temperature Anomaly

The coastal temperature anomaly distribution for southern hemisphere summer (Figure 3a) off Peru and Chile indicates two distinctly separate upwelling maximum regions, one off Peru and the other off north-central Chile centered at about 30°S. These are separated by a region of warm anomaly near Arica.

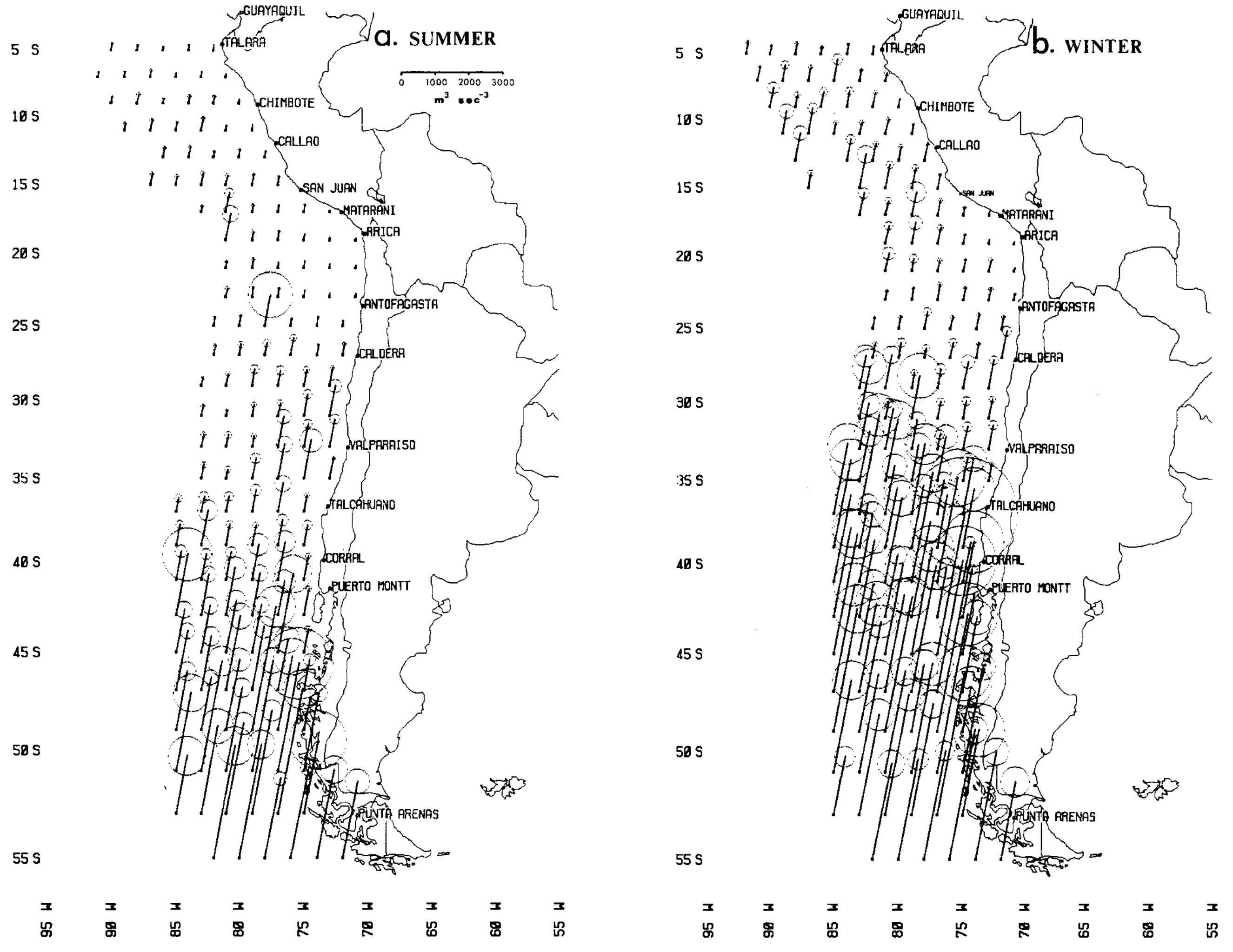

Figure 4. Cube of wind speed (m^3sec^{-3}) indicating rate of turbulent mixing energy production by the wind. Mean magnitude is indicated by length of each symbol; the standard error of each mean magnitude is indicated by the radius of the circle plotted at the top of each symbol (see scale on figure). *(a)* Summer (Nov., Dec., Jan., Feb.). *(b)* Winter (May, June, July, Aug.).

Water mass analysis (Cañon 1978) indicates distinctly different source waters for the upwelling occurring in the two regions. South of 40°S latitude, coastal warming is associated with warm poleward advection resulting from bifurcation of the mid-latitude west wind drift.

During the winter (Figure 3b) the coastal temperature anomaly off Peru is somewhat more intense than in the summer. The area of near-coastal warming off Arica disappears, but a definite minimum in the coastal temperature deficit continues to separate the two upwelling maxima. The negative temperature anomaly in the Chilean upwelling maximum appears to be slightly less intense in winter, as is the coastal warming south of 40°S. This smoothing of gradients in the coastal temperature anomaly distribution during winter relative to those in the summer distribution is similar to the situation noted for the California Current region (Figure 2).

Peru Current Turbulent Mixing Energy Production

One-degree summaries of wind reports were constructed from the same TDF-11 data file. In order to clarify the presentations in this paper, symbols are plotted only for alternate 1-degree quadrangles in both latitude and longitude coordinates. Thus only one-fourth of the total number of independent samples are shown. The South American coast is too large an area to indicate all the samples on a figure. The complete data set has been examined, and the reduced set shown illustrates the characteristic features. Where a particular sample contains fewer than ten observations, no symbol is plotted.

The distributions of the cube of the wind speed

(Figure 4) show much higher values in the south than in the north, with the region of extremely high values extending farther north in the Southern Hemisphere winter than in the summer. The regions near the coast are generally less turbulent than offshore; a notable exception is the Chilean upwelling maximum region near 30°S during summer. Low turbulence production is characteristic of the coastal region of Peru and of the extreme northern part of Chile, with summer being the least turbulent period. A spatial minimum of wind-generated turbulence is located within the coastal bight near Arica throughout the year.

Peru Current Wind Stress

The resultant stress of the wind on the sea surface is directed equatorward during summer (Figure 5a) along the coasts of Peru and Chile to 40°S. Moderate magnitudes characterize most of the coast of Peru; very low values occur within the coastal bight near Arica. Strong equatorward stress overlies the region of negative coastal temperature anomaly centered near 30°S (Figure 3), which is identified as the Chilean upwelling maximum. South of 40°S strong coastward stress is associated with large-scale westerly airflow.

During winter (Figure 5b) the equatorward stress off Peru strengthens substantially. The bight off Arica continues as a definite minimum in the distribution. The strong resultant stress found in summer near 30°S has disappeared; the offshore region at this latitude is under the influence of the westerly airflow, which has expanded northward. The "roaring forties" (the area south of 40°S) show magnitudes of resultant coastward stress similar to those in summer; however, relatively large standard error ellipses demonstrate stormy, highly variable winter conditions.

Peru Current Ekman Transport

The latitudinal variation in the Coriolis effect (Figure 1) modifies the distributional patterns when the stress distributions (Figure 5) are converted to Ekman Transport (Figure 6). Strong offshore transport is indicated off Peru, particularly in winter. Numerical magnitudes in this case should be viewed with caution because the Ekman transport relationship breaks down at the equator; it is presently unclear how close to the equator Ekman transport continues to acceptably approximate actual transport conditions.

The Chilean upwelling maximum near 30°S is associated with strong offshore-directed Ekman transport during summer (Figure 6a), which relaxes in winter (Figure 6b). Thus the seasonal Ekman transport cycle is similar to that in the Californian upwelling maximum (Parrish et al. 1981), but opposite in phase to that off Peru. The coastal bight near Arica appears as a region of minimal offshore transport, separating the two upwelling maximum regions and their associated intense offshore transport conditions. South of 40°S the Ekman transport is generally parallel to the coast and equatorward, with a definite onshore component south of about 48°S latitude.

ANCHOVY AND SARDINE STOCKS OF THE CALIFORNIA CURRENT AND PERU CURRENT SYSTEMS

Anchovy

Anchovies are among the most abundant fishes in eastern boundary current regions. In the Peru Current region the dominant anchovy is *Engraulis ringens;* a closely related species, the northern anchovy *(Engraulis mordax),* dominates in the California Current region. Both species are widely distributed; according to Cañon (1978) *E. ringens* ranges from 4°30′S to 42°30′S, and according to Miller and Lea (1972) *E. mordax* extends from 23°N to 53°N. Both species have extended spawning seasons, with some eggs and larvae being taken all year. Eggs and larvae occur over nearly the entire range of both species; however, they are heavily concentrated in distinct spawning grounds.

Meristic, morphometric, and tagging studies suggest that there are at least two major stocks of *E. ringens* (Tsukayama 1966; Rojas de Mendiola 1971; Jordán and Malaga 1972; Serra and Gil 1975). The bulk of the Peruvian fishery was based on a stock centered off northern and central Peru. A smaller stock centered off southern Peru and northern Chile was the basis of the Chilean fishery. Both of these stocks are currently greatly depleted. There is meristic and spawning-pattern evidence for a third stock near Talcahuano (36°S) in central Chile (Brandhorst, et al. 1965; Jordán 1980). A separate fishery has existed on this apparent stock and another pelagic species, *Clupea bentincki* (Serra 1978).

The Peruvian stock has its major spawning grounds located in northern and central Peru from 6°-14°S, and the highest concentrations of eggs occur near Chimbote at about 9°S (Santander 1980). Santander (1981) suggests that the areas and time of maximum spawning do not co-occur with the areas and periods of maximum upwelling; spawning is greatly reduced in the core of maximum upwelling (14°-16°S).

Cañon (1978) found several centers of spawning for the Peru-Chilean stock in northern Chile, especially near Arica (18-19°S) and Mejillones (22-23°S). However, the available literature does not indicate how far the spawning grounds extend into southern Peru. Anchoveta eggs have been found as far south as 40°S (Cañon 1978), and it is reported (Serra et al. 1979) that the spawning grounds of the potential central

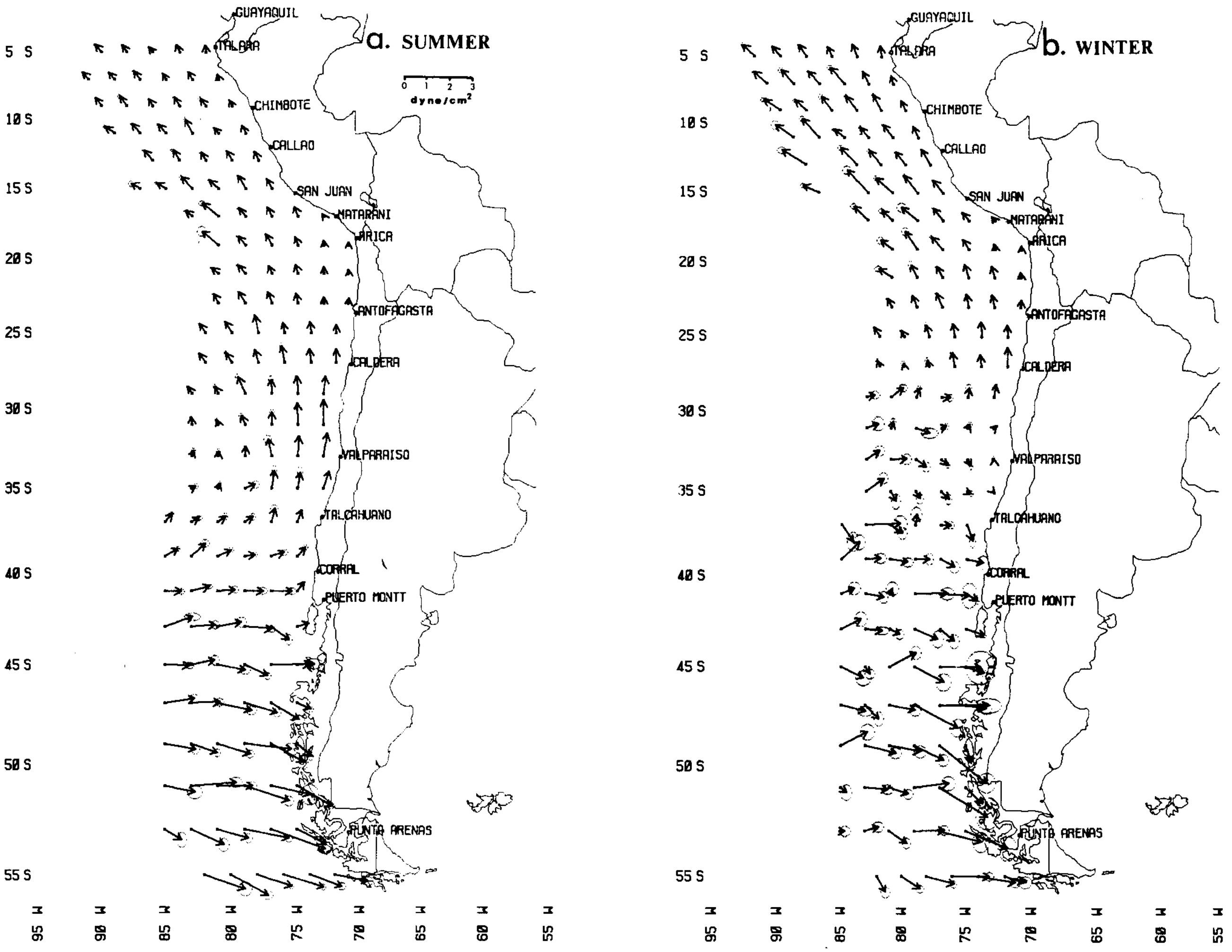

Figure 5. Wind stress on the sea surface (dynes cm^{-2}). Magnitude is indicated by length of symbol (see scale on figure); direction is indicated by orientation of symbol. Standard errors of the means of the meridional and zonal components are indicated by the vertical and horizontal axes of the elipses plotted at the head of each symbol. Computation of stress is as described by Bakun et al. 1974. *(a)* Summer (Nov., Dec., Jan., Feb.). *(b)* Winter (May, June, July, Aug.).

Chilean stock are in the vicinity of the fishery at Talcahuano (36°S).

Meristic, morphometric, electrophoretic, and tagging studies with *E. mordax* suggest that there are at least three stocks in the California Current region (McHugh 1951; Vrooman et al. 1981; Haugen et al. 1969). According to Richardson (1980) the spawning grounds of the northern stock are centered at about 44°-46°N in the Columbia River plume; spawning occurs in summer, and is highly concentrated in July. The central stock's spawning grounds are principally in the Southern California Bight (30°-34°N); spawning occurs throughout the year, with a distinct maximum from February to April and a minimum from August to October (Lasker and Smith 1977). Both the Californian and Mexican anchovy fisheries are based on the central stock, which in recent years has been the largest of the three. The spawning grounds of the southern stock are centered in southern Baja California (25°-28°N); the peak spawning season is similar to that of the central stock, but slightly earlier in the year. Peak larval abundance occurs from January to March (Smith 1972).

The Peruvian anchoveta stock was by far the largest of the Engraulid stocks of the Peru and California Current regions, and it has supported fisheries at least one order of magnitude greater than any of the other stocks. Landings for the period just before its collapse averaged about 10 million metric tons (MT) per year (Valdivia 1980), and virtual population estimates show that the spawning biomass averaged about 20 MT during the early years of the fishery (Csirke 1980). It is difficult to determine the catches or population size of the Peru-Chilean stock, for it was a minor but undetermined proportion of the Peruvian landings and a major proportion of the Chilean land-

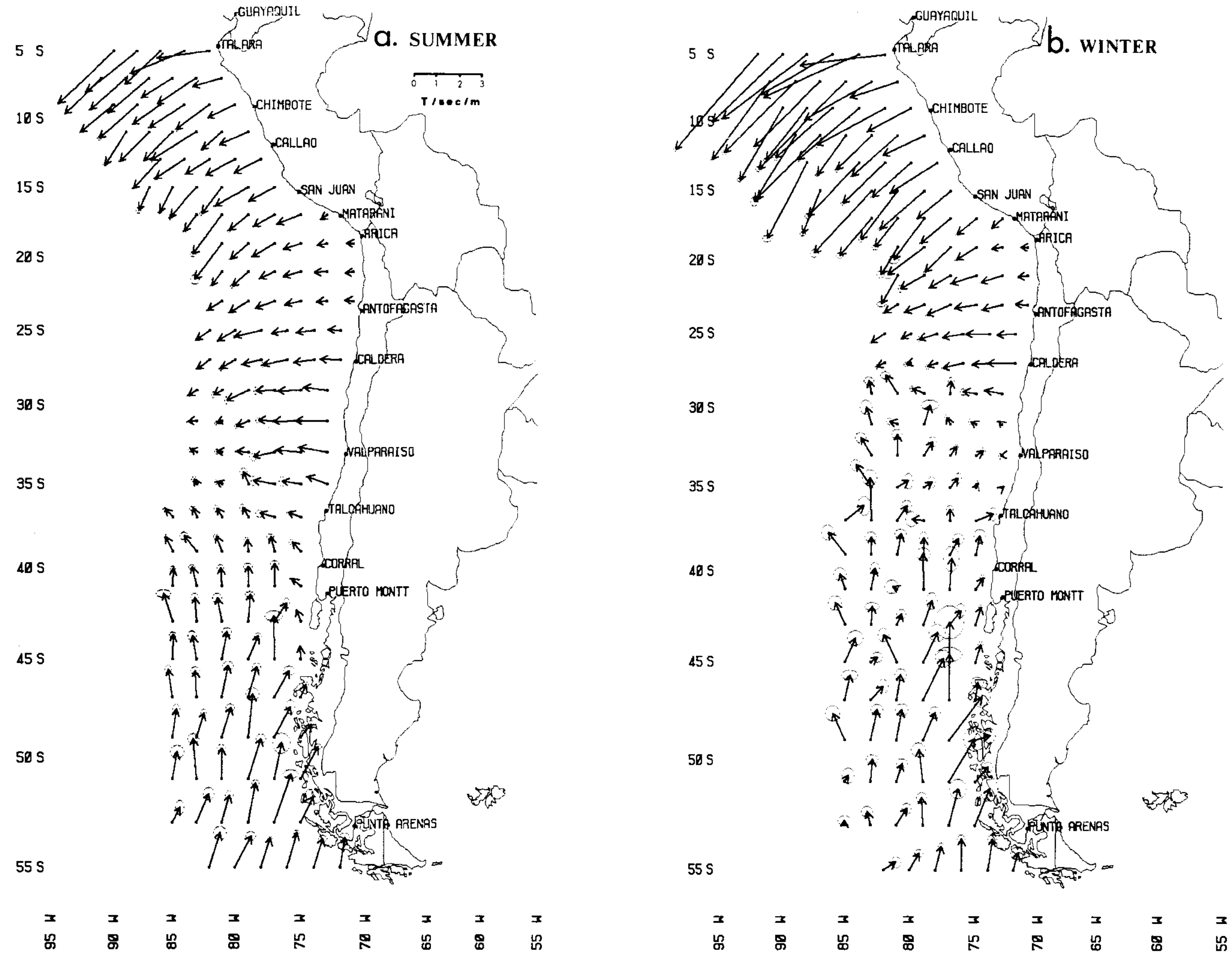

Figure 6. Surface Ekman transport (metric tons per second per meter) computed from the wind stress vectors shown in Figure 5. *(a)* Summer (Nov., Dec., Jan., Feb.). *(b)* Winter (May, June, July, Aug.).

ings. The peak Chilean landings of anchoveta were just under 1 MT (Boré and Martínez 1981), the great majority of which was apparently from the Peru-Chilean stock, since the landings from the Talcahuano region, which did not separate *Clupea* and *Engraulis,* had a maximum of just less than 0.2 MT.

The central stock is the only one of the three California Current stocks that has been extensively fished. Combined catches of the Mexican and Californian fisheries on this stock have recently reached 0.3 MT. Peak landings would have undoubtedly been larger than this if the California fishery had not commenced under intense regulation. Spawning biomass estimates based on larval surveys are available for the three California Current stocks. Estimates for the northern stock, based on two years of surveys and several different methods of calculating spawning biomass, vary between 0.14 MT and 1.0 MT (Richardson 1980). Larval surveys during the 1960s suggested that the spawning biomass of the central stock was from 3 to 4 MT, and the southern stock averaged about 1 MT (Vrooman and Smith 1972). Recent spawning biomass estimates based on egg surveys and Hunter and Goldberg's (1980) and Hunter and Macewicz's (1980) recent findings on the reproductive physiology of the northern anchovy suggest that the biomass estimates based on larval surveys were too large (Stauffer and Piquelle 1981).

The available evidence suggests that the virgin biomass of the Peruvian *Engraulis* stock was about 20 MT; the Peru-Chilean and Southern California Bight stocks were about 1-4 MT, with the Peru-Chilean stock probably the larger of the two. The stocks spawning near Talcahuano, in the Columbia River plume, and off of southern Baja California were both probably less than 0.5 MT.

Sardine

Radovich (1981) reviewed the available information on the sardine *Sardinops sagax* in the California Current region and concluded that there was good evidence for three stocks and sufficient evidence to hypothesize a fourth stock. Two of the stocks occurred together with the southern and central stocks of anchovy, respectively. The Gulf of California stock has no anchovy counterpart, and the hypothesized fourth stock would be a counterpart to the northern stock of anchovy. During the peak of the sardine fishery, landings varied from about 0.5 MT to 0.8 MT. Landings from the Southern California Bight were only 0.1 to 0.2 MT, with the rest coming from central California, which was the major fishing area, and from the Oregon to British Columbia region. Landings in central California and possibly those in the Oregon to British Columbia areas, were derived from sardines that used the upwelling region as feeding grounds and that migrated to the Southern California Bight for spawning.

The fishery for the sardine *Sardinops sagax* in the Peru Current system is quite recent, and therefore there is little published information on the population structure. The information presented below is primarily from Santander (1981) in the case of Peru and from the Chilean Fisheries Resource Catalogue (Boré and Martínez 1981) in the case of Chile. In Peru the area in which eggs and larvae of sardine were found has expanded considerably since 1972, when eggs were largely limited to northern Peru and were primarily located farther offshore than the anchoveta eggs and larvae. Since 1972 the co-occurence of anchoveta and sardine eggs and larvae has increased, and sardine eggs and larvae are common all along the Peruvian coast; however, the area of most intense spawning is still in northern Peru (i.e., 5°-11°S). In Chile there is extensive spawning in the area between Arica and Antofagasta (18°-23°S), and eggs have been found as far south as Isla Mocha (38°S. B.J.R. Serra, pers. comm.). The fishery is the most intense in the Arica to Coquimbo area (18°-30°S); however, since 1978 there have been substantial catches in the Talcahuano area (37°S). Chilean sardine landings reached 1.6 MT in 1979.

TRANSPORT, TURBULENCE, AND REPRODUCTION

The same data used to produce the 4-month seasonal distributions (Figures 4, 5, 6) were subdivided into 2-month sets in order to plot the seasonal progression of turbulent mixing and offshore transport conditions (Figure 7) and of turbulence and alongshore stress conditions (Figure 8) for the spawning centers and other significant areas. Characteristic 2-month values of the cube of wind speed for selected locations in the California Current region were assembled from the distributions presented by Husby and Nelson (this volume); corresponding estimates of alongshore stress and offshore Ekman transport were assembled from Nelson's (1977) charts.

The area off Chimbote, which is the spawning center of the major anchoveta stock, is low in average wind-generated turbulence throughout the year. However, offshore Ekman transport is large (Figure 7), particularly during the winter, when it is the maximum plotted for all areas. Because of Chimbote's proximity to the equator it is possible that Ekman transport overestimates the actual transport; when plotted in terms of alongshore stress (Figure 8), which avoids addressing the effect of rapid decrease of Coriolis near the equator, the cycle at Chimbote shifts toward the origin. One might hypothesize that the spawning of anchoveta during the season of largest alongshore stress (offshore transport) may be related to avoidance of detrimental effects of intermittent El Niño events, which occur most intensely during the Southern Hemisphere summer.

The seasonal pattern in the Southern California Bight, which is the principal spawning ground for the pelagic fishes of the California Current, including the central subpopulation of northern anchovy, is near the origin in both diagrams (Figures 7 and 8). However, it may be noted that the lowest average turbulence is encountered in the summer and fall, whereas spawning is most common in the spring and also in the winter in the case of anchovy. One may hypothesize that the relationship to the upwelling cycle may be the factor that determines spawning seasonality given the low turbulence and offshore transport conditions within the bight throughout the year.

The area off Arica near 18°S is consistently very low in both wind-generated turbulence and offshore transport. This area resembles the Southern California Bight in this and in several other respects, including warm coastal temperature anomalies during summer and location directly downstream from maximum upwelling regions. We need more information about the extent of spawning to properly evaluate its comparative significance.

In comparison to the three largest anchovy stocks of the eastern Pacific, the three smaller stocks appear to spawn in regions of somewhat higher turbulence. The southern Baja California stock spawns in an area where turbulence and offshore transport are moderate throughout the year, with values somewhat higher in the winter-spring transition than during the rest of the year. The high-latitude stocks (the northern stock of

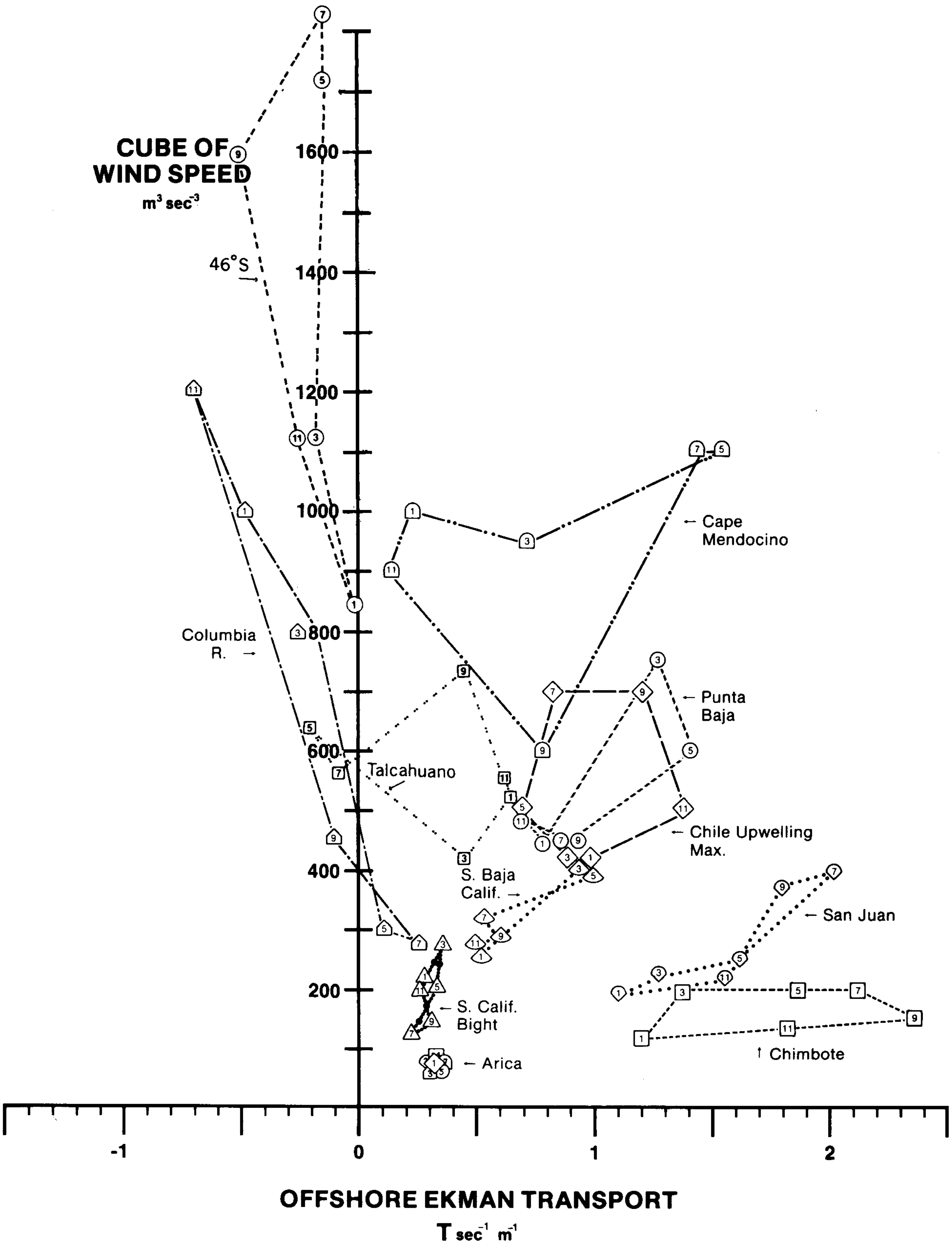

Figure 7. Characteristic seasonal relationships of turbulent mixing energy production (proportional to cube of wind speed) and offshore-directed Ekman transport for various locations off the west coasts of North and South America. Each numbered symbol represents a 2-month sample, with the number corresponding to the first month of the two (e.g., 1 represents Jan.-Feb., 3 represents Mar.-Apr., etc.).

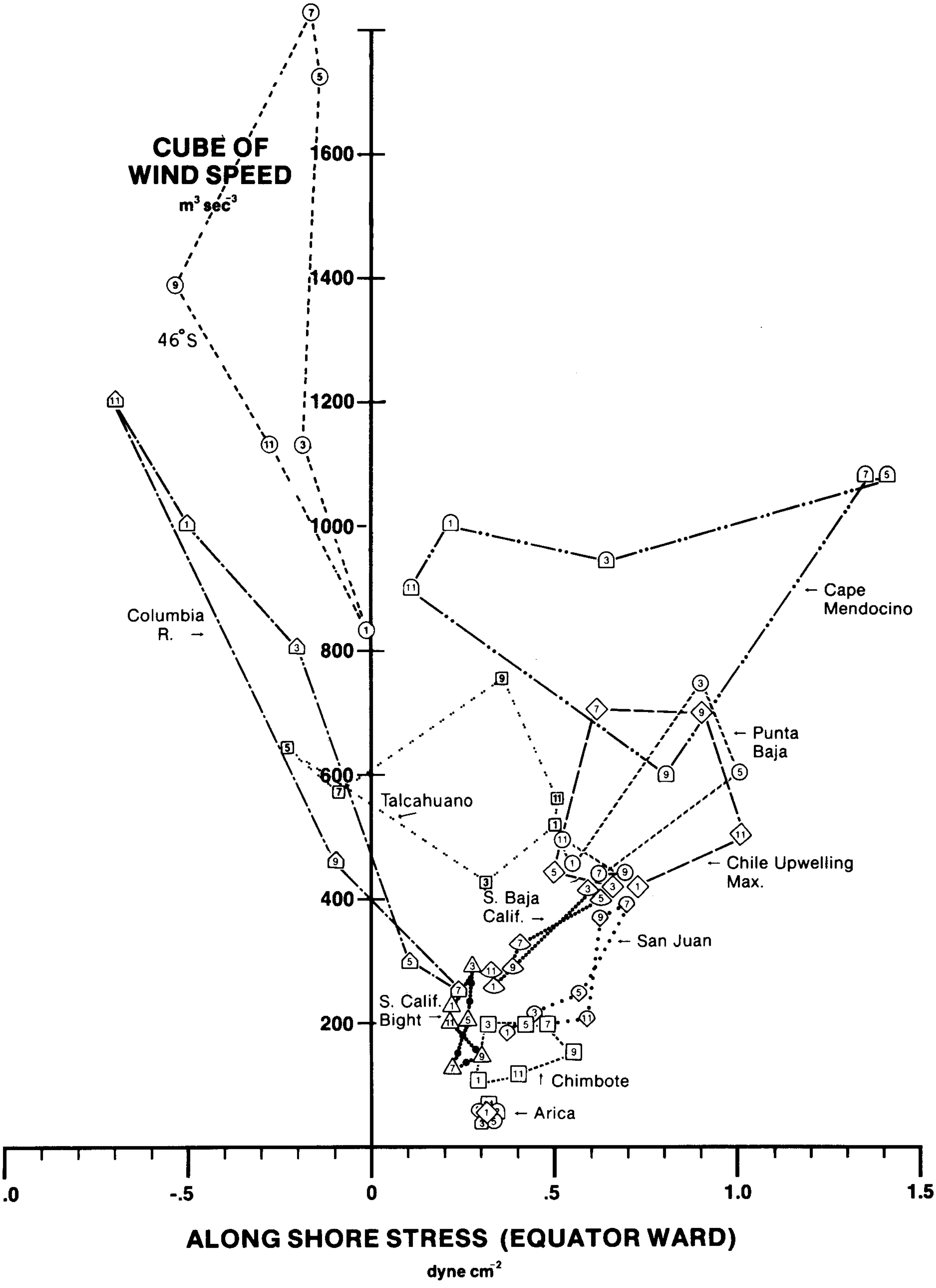

Figure 8. Characteristic seasonal relationships of turbulent mixing energy production (proportional to cube of wind speed) and alongshore wind stress (positive equatorward) for various locations off the west coasts of North and South America. Each numbered symbol represents a 2-month sample, with the number corresponding to the first month of the two (e.g., 1 represents Jan.-Feb., 3 represents Mar.-Apr., etc.).

anchovy, which spawns in the Columbia River plume, and the Talcahuano anchoveta stock) spawn in areas where turbulence is considerably higher than in the other spawning centers and where Ekman transport varies seasonally from onshore to offshore. The stock spawning in the Columbia River plume does so only in the summer, when the seasonal progression enters the space in the diagrams where the other stocks spawn. The Talcahuano stock (if it is a separate stock) is reported as spawning mainly in embayments protected from the higher levels of turbulence occurring off the coast (F.L.E. Robles, pers. comm.).

In the diagrams, the space occupied by the upwelling centers within the regions of maximum upwelling tends to be displaced toward the upper right of the space occupied by the spawning areas: e.g., Cape Mendocino (39°N), San Juan (15°S), and the Chilean upwelling maximum (30°S). This is also the case for the Punta Baja (30°N) area, which is a secondary upwelling region. The seasonal progression at 46°S latitude has a similar shape and orientation to that off the Columbia River at 46°N but is situated at a substantially higher turbulence level, never entering the areas in the diagrams occupied by the spawning regions. We would therefore not expect an extreme southern stock to be able to reproduce successfully enough to maintain a significant population at this latitude in the South American system.

In this connection, it is recognized that the meteorological and oceanographic "equators" are located to the north of the geographical equator, and thus a strict correspondence in latitude might not be expected; i.e., analogous features might be closer to the equator in the Southern Hemisphere than in the Northern Hemisphere. However, note that very much the same space is occupied in the diagrams by the Chilean upwelling maximum at 30°S and by the upwelling center at Punta Baja at 30°N; even the march through the annual cycle is in the same sense, although of course 6 months out of phase.

In concluding our discussion of the diagrams (Figures 7 and 8), we must comment on the precision of the displayed estimates. Available marine surface data are particularly sparse in certain coastal regions off South America, so sampling variability is a problem. Also, gradients in real distributions occur on small scales, which are not well resolved by our summaries. Thus, while we are confident in the general relationships of the spaces displayed, certain smaller details are less certain. For example, the indication of stronger offshore transport off Chimbote during September-October than during July-August may not be reliable; note that because of Chimbote's proximity to the equator the horizontal axis of its seasonal pattern in the transport diagram (Figure 7) is greatly expanded relative to that in the stress diagram (Figure 8).

CONCLUDING REMARKS

This paper represents only a "first cut" through the information available in the collected marine observations and accumulated knowledge of spawning habits. We are convinced that comparative studies are (1) useful for understanding linkages between fish stocks and environmental processes that are often extremely difficult to investigate experimentally, and (2) very cost-effective when making use of data for which the investment has already been made.

Figures 7 and 8 represent two potential dimensions of a multivariate "reproductive habitat space." To the extent that the other crucial dimensions can be isolated and the favorable intervals defined, the excursions by various spawning sites into and out of the favorable space can perhaps be monitored, providing a basis for formulating empirical models that could be used to predict and simulate effects of management actions.

In adopting this view it is important to recognize the differences in scale, both of time and space, on which the various environmental processes affect eventual recruitment. For example, the critical time scale for turbulence to induce mortality by dissipating food concentrations may be several days at most. The effects of transport of larvae are expected to act on scales of a month or more, with consequences extending into the juvenile stage. Upwelling variations on seasonal and interannual time scales may affect the average background concentration of food organisms, which underlies the patterns altered by the short-scale turbulence mechanism. Likewise, upwelling and its associated offshore transport may be a favorable factor on long time scales and broad space scales, i.e. previous to the spawning season and upstream of spawning grounds, and an unfavorable factor when acting at the precise time and location that larvae may be present. We have noted a pattern of avoidance of upwelling maximum regions and areas of high turbulence in the spawning strategy of engraulids. An exception is the situation off north-central Peru, where an enormous engraulid population has existed in what we are calling an upwelling maximum region. In this case the steadiness of the upwelling process and the low turbulent mixing, which is unique to this region, could be a factor. Smaller-scale upwelling centers, e.g., the area near San Juan, which exist within the larger-scale upwelling maximum region, appear to be avoided in spawning habits (Santander 1981).

One preliminary comparative result with direct management implications is worth noting. The recent alternations between anchovy domination and sardine-mackerel domination in the two systems have yielded the consistent experience that the exploitable biomass in a sardine- and mackerel-dominated system is located poleward compared to that in an anchovy-dominated system. Thus the shifts in species composition have resulted in a spatial shift of the patterns of exploitation across national boundaries, where they appear to have a tendency to remain. The possibility of shifting the exploitable component of the organic production of a shared system to another nation's waters presents a particularly strong argument to a self-interested nation against overexploitation of the resources off its own coast.

ACKNOWLEDGMENTS

We are grateful for the reviews and editorial comments provided by Haydeé Santander, Rodolfo Serra, and Fernando Robles.

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TURBULENCE AND VERTICAL STABILITY IN THE CALIFORNIA CURRENT

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ABSTRACT

Summaries of historical surface marine wind observations and subsurface temperature data are used to examine the seasonal and spatial characteristics of wind-generated turbulent energy production and of stability of the upper water column over the California Current region. A recent hypothesis suggests that survival of first-feeding larval anchovies, *Engraulis mordax,* depends on the aggregation of properly sized food organisms in a stable water column in the absence of strong wind-induced turbulence. A comparison of wind mixing and stability indices for regions encompassing the principal spawning grounds of the three subpopulations of northern anchovy demonstrates that peak spawning occurs during seasons and in locations associated with stable stratification, relatively low rates of turbulent energy production, and weak offshore transport (upwelling).

The average intensity of wind-generated turbulent energy production is similar during peak spawning periods in all three regions. This suggests optimum levels of turbulence and stability in the upper water column—levels that favor survival of first-feeding larvae. Although examination of mean conditions is useful in a comparative study, the average intensity of turbulent wind mixing over a spawning season is not likely to be well correlated with interannual variability in recruitment. Rather, the existence of sufficient time-space windows within which turbulence does not exceed critical values may be the relevant factor. To investigate this possibility, time series of wind-generated turbulent energy production are presented for recent periods associated with large variations in year-class strength.

RESUMEN

Para estudiar las características estacionales y espaciales de la producción de energía eólica turbulenta y la estabilidad de la columna superior de agua en la región de la Corriente de California, se emplean observaciones del viento en la superficie del mar y de temperatura subsuperficial. Ultimamente se ha planteado una hipótesis que propone que la supervivencia de las larvas de anchoveta, *Engraulis mordax,* al iniciar su alimentación, depende del conjunto de organismos alimenticios de medida apropiada presentes en una columna de agua estable donde no existe fuerte turbulencia eólica. Una comparación de los índices de mezcla eólica y los de estabilidad de las regiones que abarcan las principales áreas de desove de las tres subpoblaciones de anchoveta del norte, muestra que el período de máximo desove ocurre en estaciones y lugares en donde la estratificación es estable, los índices de producción de energía eólica turbulenta son relativamente bajos, y la surgencia de aguas es débil.

La intensidad media de la producción de energía eólica turbulenta es igual en las tres regiones durante los períodos de máximo desove. Esto implica que existen niveles óptimos de turbulencia y estabilidad en la parte superior de la columna de agua, los cuales son propicios para la supervivencia de las larvas. Si bien un examen de las condiciones medias es útil en un estudio comparativo y es improbable que la intensidad media de la mezcla eólica turbulenta durante la estación de desove esté bien correlacionada con la variabilidad interanual en el reclutamiento. Más bien parece que el factor determinante podría ser la existencia de suficientes intervalos de tiempo y espacio, donde la turbulencia no excede valores críticos. Para investigar esta posibilidad se presentan series de tiempo de la producción de energía eólica turbulenta de etapas recientes vinculadas con importantes variaciones en la cantidad de anchoveta para cada generación.

INTRODUCTION

The concept of a "critical period" in the early life history of fishes was formulated in Hjort's pioneering studies (1914, 1926) on the year-class strength of Norwegian herring and cod stocks. The critical-period hypothesis suggests that survival of larval fish might be affected by (1) a lack of food at the time of first feeding, and (2) currents that transport larvae to areas unfavorable to further growth. The relationships of nonseasonal fluctuations in surface transport to larval survival and year-class strength have been investigated in recent correlative studies on Pacific mackerel, *Scomber japonicus,* (Parrish and MacCall 1978) and Atlantic menhaden, *Brevoortia tyrannus,* (Nelson et al. 1977). Parrish et al. (1981) have discussed the

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[Manuscript received February 22, 1982.]

general relationship of surface transport mechanisms to reproductive success of pelagic fishes in the California Current system. However, even where apparent linkages between surface drift conditions and stock variations have been demonstrated, larval survival is still critically dependent on food availability. Hjort emphasized the first of these two critical-period mechanisms in determining year-class strength (May 1974).

Recent laboratory and field studies by Lasker et al. (1970) and Lasker (1975, 1978) indicate that survival of first-feeding larval northern anchovies, *Engraulis mordax,* may depend on several related factors: (1) the existence of fine-scale food strata containing high concentrations of properly sized food particles, (2) the coincidence of patches of larvae with adequate patches of food, and (3) the absence of predator populations sufficient to destroy the larval patches (Lasker and Smith 1977). On the principal anchovy spawning grounds off southern California, Lasker (1978) found that stability of the water column in the upper 30 m appeared to be a necessary condition for these fine-scale food strata. From additional survey data, Lasker (1981b) concluded that stability in the upper layers of the ocean during the anchovy spawning season is prerequisite to a successful year class. Wind-generated turbulent mixing associated with storms or strong coastal upwelling events destroys the required vertical stratification and patchiness, thereby contributing to increased larval mortality, which may result in a poor year class.

The purpose of this study is to describe the spatial patterns and annual cycles of climatological indices of wind-generated turbulent energy production and vertical stability in the California Current region. Bakun and Parrish (1980) suggested that information on the normal requirements for reproductive success of pelagic fishes might be obtained by comparing environmental conditions in the spawning areas with the conditions in regions where spawning does not usually occur. In this study, we compare monthly and seasonal indices of wind-generated turbulent mixing and upper ocean stability in the principal northern anchovy spawning areas to further explore the relationship of a stable ocean to larval survival, as described by Lasker (1981a). We will examine these indices in relation to the timing and locations of spawning of the three subpopulations of northern anchovy (Figure 1). To the extent that the mechanisms in Lasker's hypothesis exert a strong control on spawning success in the three subpopulations, there should be marked similarities among the wind-mixing and stability indices in all three spawning regions along the west coast of North America.

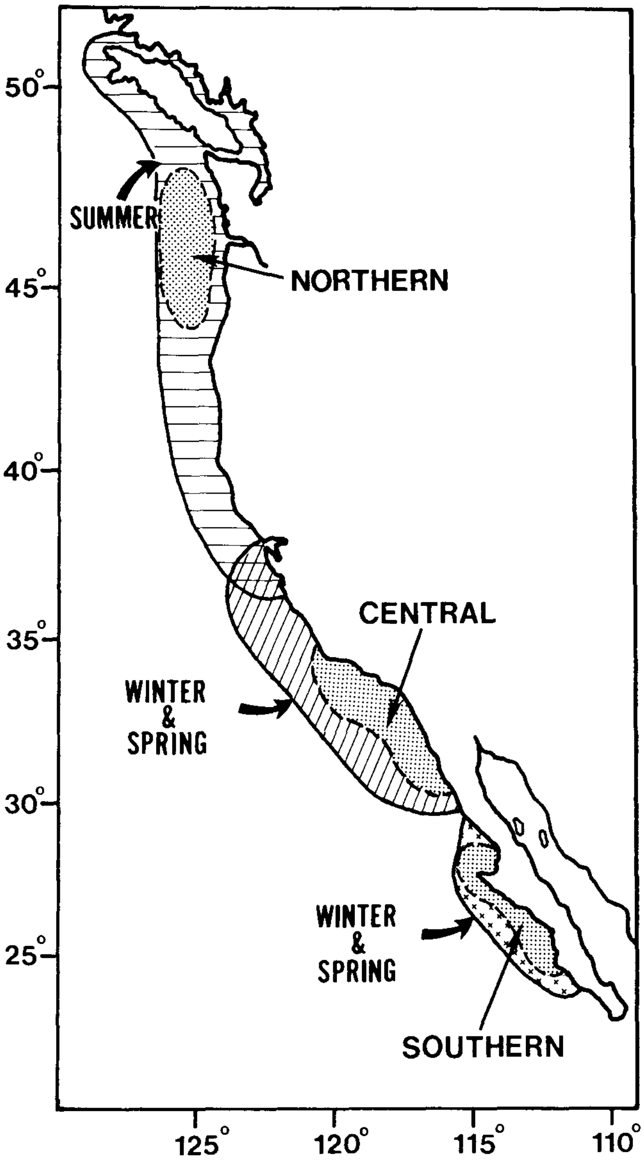

Figure 1. Geographic ranges (hatched), principal spawning areas (shaded), and seasons of the three subpopulations of northern anchovy, *Engraulis mordax.* Geographic ranges are modified from Smith and Lasker (1978) and Vrooman et al. (1981). Spawning areas have been inferred from egg and larvae distributions during the peak spawning months (Kramer and Ahlstrom 1968; Hewitt 1980; Richardson 1980).

DATA DESCRIPTION

Stability within the upper layers of the ocean is primarily determined by a balance between the net downward heat flux across the air-sea interface and turbulent mixing processes associated with wind-stirring and convective cooling. The evolution of transient and seasonal thermoclines can be predicted on the basis of the imbalance between the heat input from the atmosphere to the ocean and the intensity of turbulent wind mixing, which redistributes heat throughout the mixed layer. Strong surface heating during extended periods of light winds can produce strong stratification and rapid transitions to shallow mixed layers (Elsberry and Garwood 1978). Atmospheric forcing associated with winter storms or strong coastal upwelling "events" can destroy the stratification in the upper layers of the water column and rapidly deepen the "well-mixed" layer. Nelson (1977) and Nelson and Husby (in press) described the climatological distributions of surface wind stress and surface heat flux over the California Current region. This study extends the previous work to include summaries of an index of wind-generated turbulent energy production associated with redistribution of heat in the upper layers of the ocean and an index of upper-layer vertical stability resulting from surface heat flux and turbulent mixing processes.

Wind Mixing

The rate at which turbulent kinetic energy of the wind is added to the upper ocean and becomes available to mix the stable thermocline layers is proportional to the third power, or "cube," of the wind speed (Niiler and Kraus 1977). The proportionality factor is not well established and must be determined empirically from laboratory measurements and field calibrations. Because our main purpose is to make intraregional and seasonal comparisons, a sufficiently accurate index of the rate of turbulent energy production can be computed from the cube of the surface wind speed. Estimated and measured surface wind speeds were obtained from the historical surface marine weather observations archived in the National Climatic Center's (NCC) Tape Data Family-11 (TDF-11). This is the same set of data used by Nelson (1977) to compute surface wind stress and wind stress curl over the California Current.

Long-term monthly and quarterly means of the cube of the scalar wind speed were computed from all available surface marine reports from 1850 to 1972 for each 1-degree square area within a geographical region extending from 20°N to 50°N and from the west coast of North America to 10 degrees of longitude offshore. The same summary grid and editing procedures described by Nelson (1977) were adopted. Winter and summer quarters were chosen to approximately coincide with the peak spawning seasons for the southern, central, and northern subpopulations of the northern anchovy, respectively. Because we are interested in characterizing wind-generated turbulence in the important nearshore spawning habitats (Brewer and Smith 1982), long-term means were also computed for several partial 1-degree coastal squares that were not included in Nelson's (1977) wind stress distributions.

The principal sources of error in climatological means based on surface wind data are associated with imprecise Beaufort wind force estimates and nonuniform distributions of data in time and space (see Nelson 1977 for a discussion of errors). These errors are accentuated by computing the cube of a scalar variable. Sampling bias is even more critical to the stability index calculations (described in the next section) for which the available data are at least one order of magnitude less than the surface weather reports. Although each of the long-term monthly 1-degree square means is independent of all other months and squares, statistical independence is less important than the ability to present characteristic spatial and temporal distributions of wind speed cubed and vertical stability in the California Current. Therefore, when contoured fields have been used to display the results, the mean distributions were machine contoured, subjectively smoothed, and recontoured to remove "bull's-eyes" associated with extreme variability and inadequate sampling. Because most of the sampling error occurs offshore, this procedure should not substantially affect the conclusions for the nearshore regions.

Vertical Stability

Vertical stability of an oceanic water column depends on the vertical distribution of density, which is a function of temperature, salinity, and pressure. A water column is stably stratified if the density increases with depth. A commonly used index of the static stability of the water column, suggested by Hesselberg and Sverdrup (1915; cited in Sverdrup et al. 1942), is proportional to the vertical gradient of sigma-t, σ_t, (the density at atmospheric pressure):

$$E' = 10^{-3}\, d\sigma_t/dz \qquad (1)$$

The total expression for stability contains additional small terms related to the vertical gradients of temperature and salinity and the adiabatic temperature change due to compressibility. However, Hesselberg and Sverdrup (1915) have shown that stability in the upper 100 m is accurately expressed by Equation (1).

The computation of sigma-t requires values of temperature and salinity as a function of depth. The numbers of hydrographic stations that include vertical profiles of both temperature and salinity, over the entire California Current region, are rather small in terms of spatial and temporal coverage. For this reason, the more extensive set of mechanical bathythermograph (MBT) observations, which provide profiles of temperature versus depth, was used to compute an index of the vertical stability of the upper water column. The use of the vertical temperature structure to approximate the stability of the upper layer is valid if density depends primarily on temperature (i.e., little error will result in using only vertical temperature gradients to compute stability if the salinity is constant with depth or if the salinity gradients are small).

The waters flowing southward in the California Current are characterized by a shallow salinity minimum, which is due to the cool, low-salinity subarctic water mass being overrun from the west by the warmer, high-salinity subtropical water of the central Pacific anticyclonic gyre (Reid 1973). Figure 2 displays the January and June mean temperature-salinity (T-S) curves at standard depths to 500 m for three lines of 1-degree squares at 46°N, 33°N, and 27°N, respectively. The rightmost curves in each panel represent the 1-degree squares adjacent to the coast. These curves were derived from the National Oceanographic Data Center's (NODC) Station Data II file (SDII), including data to 1973.

The eastern North Pacific Ocean north of 40°N is influenced strongly by an annual excess of precipitation over evaporation, and the vertical salinity structure is characterized by a permanent halocline between 100 and 200 m (Tully 1964). Figure 2A shows this subarctic structure, particularly for the T-S curves 3 to 4 degrees of longitude offshore, where the upper 50-100 m is characterized by relatively uniform and low salinity values (32.5^0/oo), below which there is an increase in salinity to a value of 33.8^0/oo at 200 m. The nearshore coastal waters off the Pacific Northwest are strongly influenced by the seasonal discharge of the Columbia River drainage basin. Peak discharges during May and June produce a large plume of low-salinity water (<32.0^0/oo) in the upper 30 m; the plume extends toward the southwest from the mouth of the Columbia River (46°N) and can be distinguished as far as 500 km from shore (Barnes et al. 1972). Although the Columbia River plume is identified by low salinities in the surface layer, the distribution of the plume has been observed to be closely approximated by the 20-m isopleth of the thermal mixed layer depth during July (Owen 1968). During winter the region of diluted surface waters extends seaward about 50 to 100 km and from about 100 km south of the mouth of the Columbia River to the Strait of Juan de Fuca.

The cool subarctic waters in the California Current are modified by lateral mixing with the subtropical water mass to the west and by upwelling along the coastal margin (Tibby 1941). The first two 1-degree squares adjacent to the coast at 33°N (Figure 2B) are representative of conditions within the Southern California Bight. The seasonal changes in the upper 75 m of the water column are primarily due to the increase in solar insolation that contributes to the for-

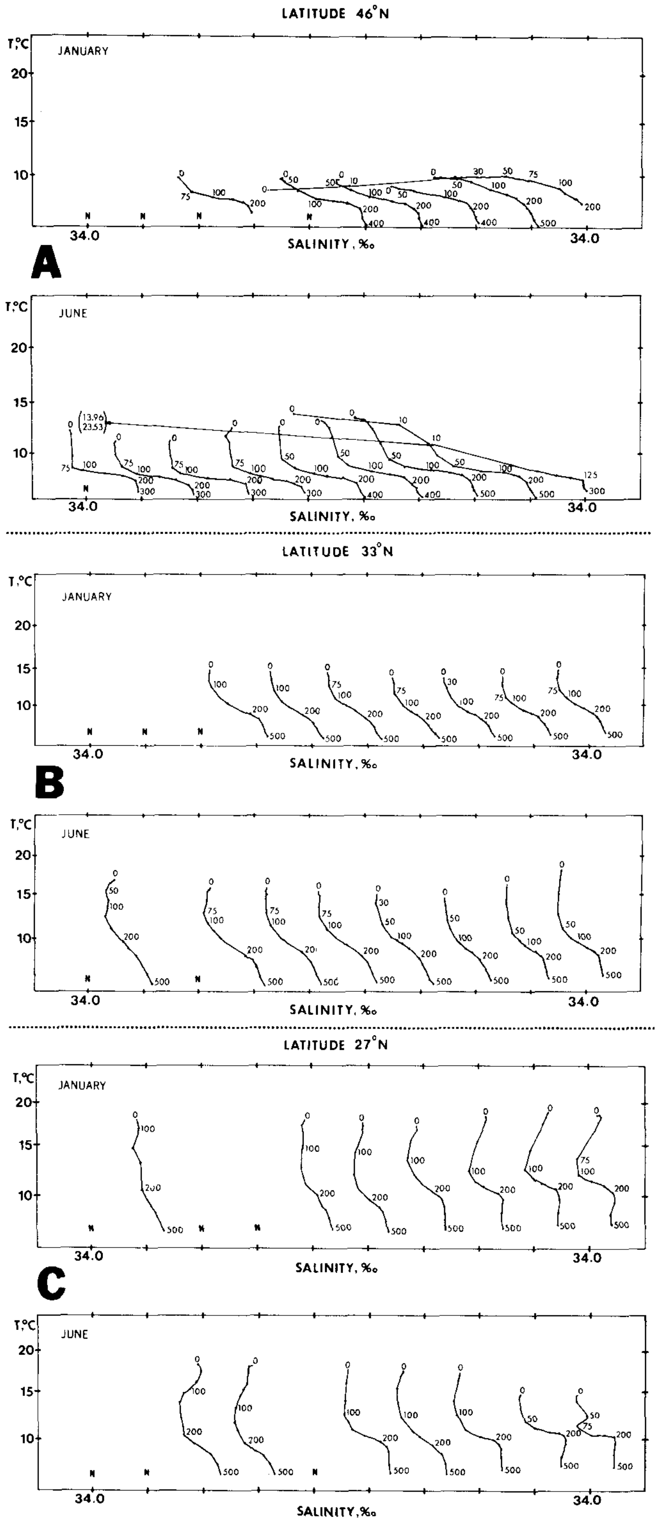

Figure 2. Mean temperature-salinity (T-S) curves for January and June for adjacent 1-degree squares from 10 degrees of longitude offshore to the coast at *(A)* 46°N; *(B)* 33°N; and *(C)* 27°N. In each diagram, the leftmost T-S curve corresponds to the 1-degree square located farthest offshore. The rightmost T-S curve corresponds to the 1-degree square closest to the coast. Each T-S curve is plotted relative to a salinity of 34^0/oo at each tick mark, and tick marks are spaced at intervals of 1^0/oo. The depth in meters of particular T-S pairs is identified on each curve. The letter N denotes that no data were available to compute a mean T-S curve at that location.

mation of a strong near-surface thermocline. The salinity profile is relatively constant, with a slight decrease with depth down to 50-75 m. The effects of coastal upwelling are evident in the T-S curves 3 to 4 degrees of longitude offshore, where there is relatively little seasonal change in the T-S structure between January and June. The cool water upwelled farther north at Point Conception during early summer is advected toward the south; seasonal warming is suppressed. The T-S curves farther offshore reveal the effects of lateral mixing (between the subarctic water mass flowing south and the subtropical water mass to the west) in the increased salinities (33.0-33.5$^0/_{00}$) in the upper layers.

Farther south near Punta Eugenia (Figure 2C) the influence of an equatorial water mass is noted in the warmer, more saline (~34.5$^0/_{00}$) water in the 200-500-m depth range in the first four 1-degree squares adjacent to the coast. This water mass indicates the poleward flow of Equatorial Pacific water beneath the equatorward surface flow of the California Current (Reid et al. 1958). This warm, saline countercurrent has been traced as far north as the coast of Washington (Cannon et al. 1975; Reed and Halpern 1976). The effects of coastal upwelling are again evident in the much colder surface waters during June at the two squares adjacent to the coast. Excluding these coastal squares during the months of maximum upwelling (upwelling-favorable winds occur during the entire year off Baja California, and maximum upwelling occurs in April and May; Bakun and Nelson 1977), the T-S structure in the upper 100 m is characterized by relatively constant salinity or a decrease in salinity with depth to a minimum value at 75-100 m, and is associated with a strongly stratified temperature profile. The well-defined January subsurface salinity minima in the three squares adjacent to the coast may result from anomalous northward surface flow, which transports southern, high-salinity water into the region.

These seasonal mean T-S curves (Figures 2A, B, and C) do not completely describe the total range of temperature-salinity structures along the entire coast and particularly not in the offshore squares, where some T-S curves are based on data from only three hydrographic stations. However, these data adequately represent the modification of the subarctic water mass in the trajectory of the California Current from north to south, and the mixing of the shallow salinity minimum—which is found at a depth of 50 m near its source region at 47°N (Reid 1973)—with higher salinity water to the west and below the minimum.

The T-S curves reveal that in the vicinity of the central and southern subpopulations of the northern anchovy (Figure 2B, C), vertical stability in the upper 100 m can be closely approximated by the vertical distribution of temperature (i.e., salinity is nearly constant with depth). However, north of about 40°N, vertical stability in the near-surface layers is strongly influenced by a large increase in salinity with depth. The influence of excess precipitation over evaporation and freshwater discharge from the Columbia River is evident in winter. More marked effects are apparent during summer (Figure 2A), when the plume structure contributes to strong thermal stratification in the upper 20-30 m of the water column within 300-500 km of the coast. In this case, upper-layer temperatures increase while salinity decreases; both effects contribute to less dense water at the surface and stronger vertical density gradients in the upper water column. Although an index of stability computed just from temperature data underestimates the correct magnitude, our analyses of the mean T-S relationships suggest that temperature data alone can also be used to compute qualitative indices of vertical stability in the principal spawning area for the northern subpopulation of the northern anchovy.

The index of vertical stability was computed from the file of MBT profiles archived in the Master Oceanographic Observation Data Set (MOODS) at the U.S. Navy's Fleet Numerical Oceanography Center (FNOC), Monterey, California. Our extract of this file contains a rather complete set of approximately 131,000 MBT casts taken in the California Current between 1931 and 1975. However, a substantial number of the profiles are serial or near-replicate casts taken at the locations of weather ships, coastal lightships, and U.S. Navy radar picket ships, which operated in the eastern North Pacific Ocean from 1960 to 1965. To eliminate some of this station-specific sampling bias, we subsampled the data set by removing profiles obtained within 56 km (30 n mi) and 24 h of each other. This editing reduced the extract file to approximately 74,000 profiles. Over 90 percent of these profiles extended to at least 137 m (450 ft). The reduced data set contains between two and three times the numbers of profiles as the NODC SDII file. In addition, the MBT data provide better vertical resolution for the stability calculations than can be achieved from the standard-depth hydrocast data.

Two parameters were computed for each MBT profile extending deeper than 50 m: (1) the mixed layer depth (MLD) and (2) the strength of the first significant stratification, which we have termed "thermocline strength." The majority of the MBT profiles were digitized at intervals of 5 m. Mixed layer depth was defined as the upper limit of the first 5-m interval in which the temperature gradient ($\Delta T/\Delta Z$, Z positive downward) exceeded −0.3°C per 5 m (−0.06°C m^{-1}). The layer of first significant stratification was identified as the first depth interval below the mixed layer where the vertical temperature gradient exceeded −0.06°C m^{-1}. The bottom of the thermocline was chosen to coincide with the upper depth of two successive 5-m intervals within which temperature gradients did not exceed −0.06°C m^{-1}. The index of thermocline strength was then calculated as the temperature difference between the MLD temperature and the temperature at the bottom of the thermocline. The relationships among MLD, bottom of the thermocline, and thermocline strength are shown schematically in Figure 3, which also depicts summer and winter thermal structure typical of the eastern North Pacific Ocean (Tully 1964).

Thermocline strength and mixed layer depth were summarized by 1-degree square areas and long-term months and quarters within the same 1-degree latitude-longitude grid used to compile the mean distributions of wind speed cubed. Because the numbers of subsurface data are an order of magnitude less than the observations of surface wind, the mean distributions of the two stability indices are substantially "noisier" than the distributions of wind speed cubed, particularly in the offshore areas. Some of the sampling "noise" in the contoured fields has been removed by subjective smoothing. Within the region most intensively studied by the CalCOFI surveys during the last 30 years, the subsurface data are adequate to define coherent spatial patterns of the stability indices.

DISTRIBUTIONS OF WIND-MIXING AND STABILITY INDICES

The three indices that have been summarized are bulk estimates of the intensity of wind-generated turbulence production and the strength of upper-layer stratification. The thermal MLD approximates the depth to which turbulent processes (expressed as wind speed cubed) dominate. Thermocline strength measures the magnitude of the density gradient (vertical stability) beneath the mixed layer, that is, in the seasonal (summer) and permanent (winter) thermocline (Figure 3). A possible linkage between these environmental conditions and successful year classes of the northern anchovy has been related to the existence of chlorophyll maximum layers (Lasker 1975, 1978), which are found in the thermocline and in the upper nutricline. Chlorophyll maxima lie somewhat deeper off Washington and Oregon (Anderson 1972) than off southern California (Reid et al. 1978; Cullen 1981). Low mean turbulence production and relatively high stability over a spawning season might favor persistent chlorophyll maxima; high turbulence production and low stability would not.

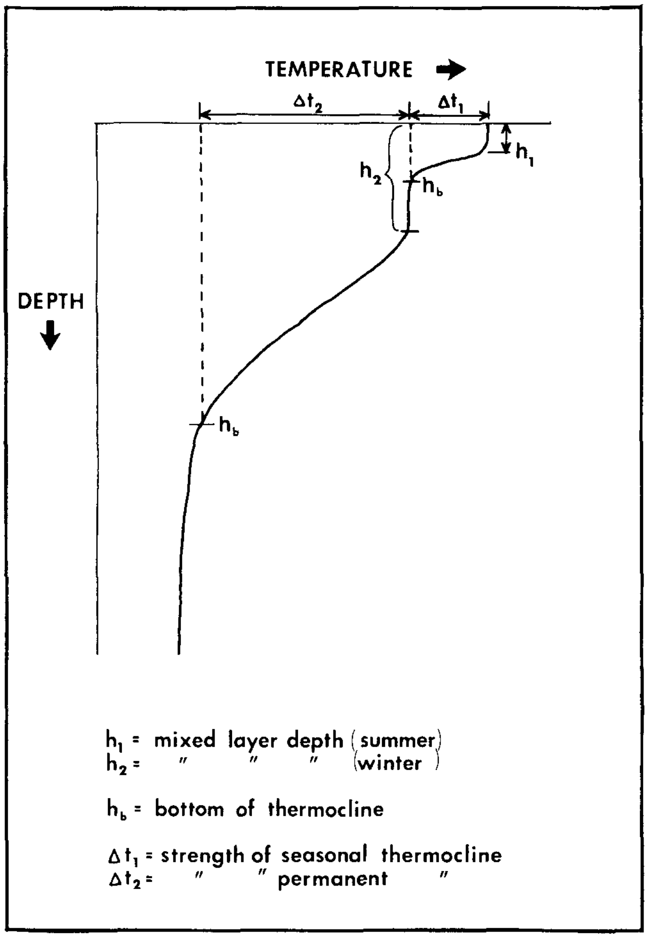

Figure 3. Schematic profile of temperature versus depth depicting typical summer and winter mixed layer and thermocline structure.

Spatial Patterns

Distributions of wind speed cubed, thermocline strength, and mixed layer depth for winter (December-February, Figure 4A) and summer (June-August, Figure 4B) illustrate characteristic features of the locations and peak spawning periods for the central and southern subpopulations (winter-spring spawners) of northern anchovy and for the northern subpopulation (summer spawners). During winter (Figure 4A) low turbulence production, moderate to strong upper-layer thermal stratification, and relatively shallow mixed layer depths characterize (1) the nearshore region (from the coast to 100 km offshore) in the Southern California Bight and (2) a broad area extending toward the southwest from southern Baja California. Both regions correspond to the general spawning areas for the central and southern stocks (Figure 1), although the spawning grounds for the southern stock have not been

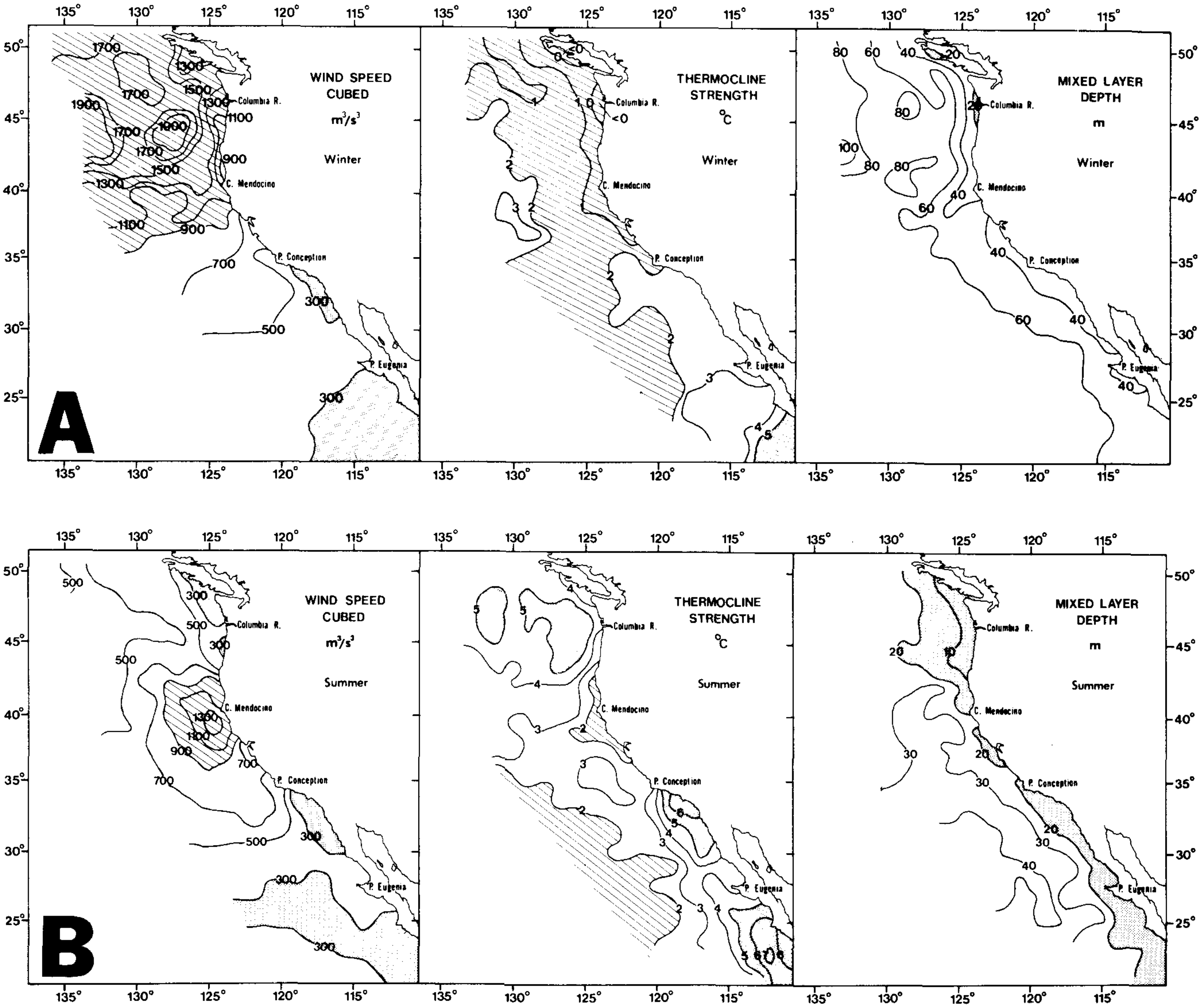

Figure 4. Mean distributions of wind speed cubed (m^3s^{-3}) indicating the rate of turbulent energy production, thermocline strength (°C), and mixed layer depth (m) for *(A)* winter (December-February) and *(B)* summer (June-August). Wind speed cubed is contoured at intervals of 200 m^3s^{-3}. Values less than 300 m^3s^{-3} are shaded, and values greater than 900 m^3s^{-3} are hatched. Thermocline strength is contoured at intervals of 1°C. Shaded areas are greater than 5°C; hatched areas denote a thermocline strength less than 2°C. Mixed layer depth is contoured every 20 m, and values less than 20 m are shaded.

completely described. Lower values of wind speed cubed (<200 m^3s^{-3}), stronger stratification, and shallower mixed layers (~30 m) occur close to the coast. The local spatial minimum in wind-generated turbulence in the Southern California Bight persists throughout the year and is consistent with a decrease in the magnitude of the equatorward surface wind in the lee of Point Conception. A nearshore maximum in wind speed cubed just south of Punta Baja (near 30°N values approach 500 m^3s^{-3}) corresponds to a permanent region of negative wind stress curl that reaches the coast in the vicinity of Punta Eugenia (Nelson 1977). High turbulence production, weak stratification, and deep mixed layers characterize the entire region north of San Francisco, with the exception of a small area off the mouth of the Columbia River, for which mixed layer structure is not completely defined by temperature alone (see Figure 2A).

The similarities among the distributions of wind speed cubed and the two indices of upper-layer stratification are obvious in summer (Figure 4B). South of Point Conception, the two regions of low turbulence production are associated with shallow mixed layers (~20 m) and the highest values of thermocline strength. These features (i.e., high stability in combination with low turbulence) are not particularly well related to the central stock's spawning cycle, which passes through a minimum between July and

October (Smith and Richardson 1977). This simply indicates that factors other than the simultaneous occurrence of low turbulence and high stability influence the timing of peak spawning. The highest values of wind speed cubed occur in the region of maximum upwelling off Cape Mendocino, which is also characterized by the weakest stratification. Off the Columbia River there is a strong correspondence between the patterns of wind speed cubed, thermocline strength, and mixed layer depth and Richardson's (1980) distributions of eggs and larvae of the northern subpopulation of *E. mordax*. The strong influence of the Columbia River plume is apparent in the high values of thermocline strength and the shallowest thermal MLD's in the entire California Current region. It is possible that, because of this strong upper-layer stratification, higher values of turbulence production may be associated with spawning success for the northern subpopulation in summer (e.g., the area within the 500 m^3s^{-3} contour off Vancouver Island, Washington, and Oregon, Figure 4B) than for the central and southern subpopulations in winter (Figure 4A).

Seasonal Variability

Annual cycles of wind speed cubed (Figure 5A, B) and thermocline strength (Figure 5C) are shown for selected 1-degree squares near the principal spawning grounds for the three subpopulations of the northern anchovy. A strong correspondence between the timing of peak spawning and the magnitude of the mean wind-generated turbulence can be demonstrated for each of the three regions. However, the relationship of the spawning cycle to the annual cycle of vertical stability (thermocline strength) shows less consistency between regions.

The southern stock spawns off southern Baja California (25-28°N) during winter and spring; peak larval abundance occurs from January to March (Smith 1972). Wind speed cubed fluctuates about a nominal value of 300 m^3s^{-3} from September to February (curve 1, Figure 5A); mean values exceed 400 m^3s^{-3} after the onset of upwelling-favorable winds in March and April (Bakun and Nelson 1977). During this period, thermocline strength decreases from a maximum (>6°C) in October to a minimum (~0-1°C) in January (curve 1, Figure 5C).

The central stock spawns in the Southern California Bight (30-34°N) throughout the year, with a maximum from February to April (Smith and Richardson 1977). The Southern California Bight is characterized by uniformly low turbulence production throughout the year (curve 2, Figure 5A). At this location, the small peak in the annual cycle (~300 m^3s^{-3}) occurs during the peak spawning season; thermocline strength is nearly constant, but at a minimum (~2°C), from January to April (curve 2, Figure 5C). The seasonal

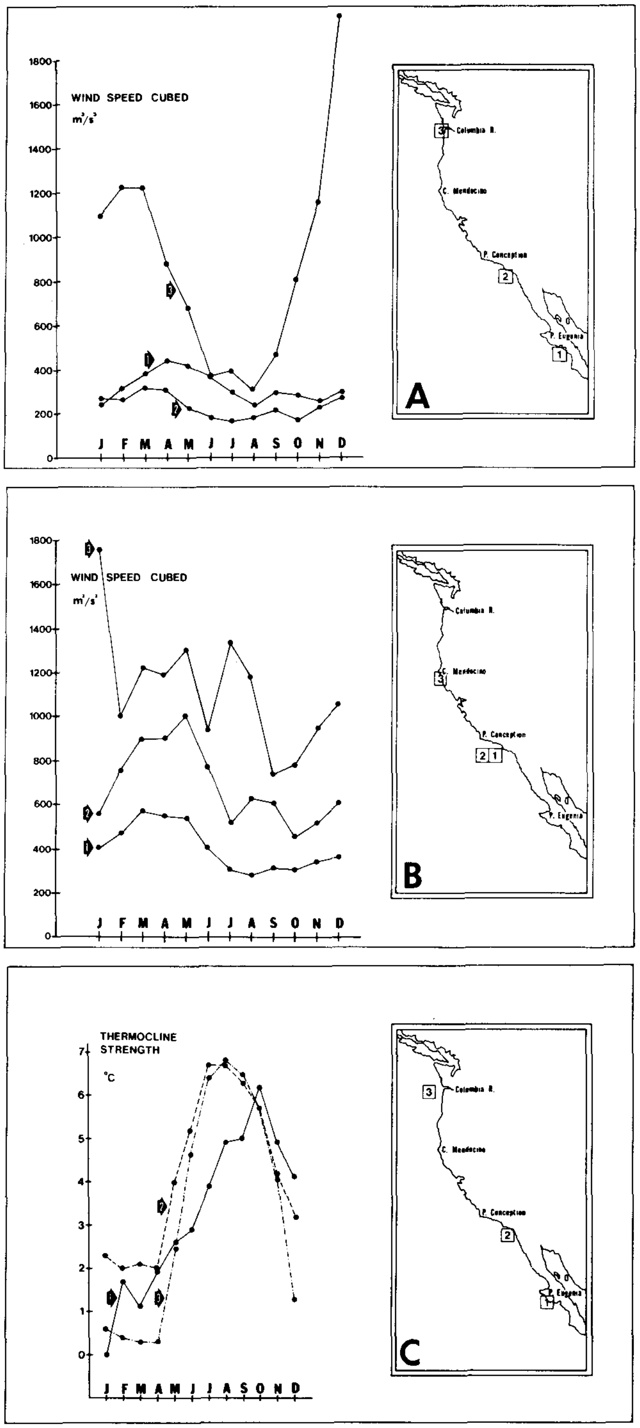

Figure 5. Annual cycles of wind speed cubed (m^3s^{-3}) and thermocline strength (°C) at selected 1-degree squares along the coast. Characteristic values of wind speed cubed and thermocline strength in the three northern anchovy spawning areas are shown in panels *A* and *C*. Mean values of wind speed cubed typical of the offshore regions of the Southern California Bight and the region of maximum upwelling off Cape Mendocino are displayed in panel *B*.

transition to a shallow mixed layer structure (i.e., strong upper-layer stratification) occurs between April and May, but the precise timing of the transition period cannot be resolved by these long-term mean data. According to Richardson (1980), the northern stock spawns in the Columbia River plume (44-46°N) from June to August; spawning is concentrated in July. Off the mouth of the Columbia River, upper-layer stratification increases to a maximum (6-7°C) from July to September (curve 3, Figure 5C). It is also notable that mean wind speed cubed decreases to a minimum (350-400 m^3s^{-3}) through the spawning season (curve 3, Figure 5A).

Taken in isolation, these data suggest a relationship between peak spawning periods and optimum levels (not necessarily minimum levels) of wind-generated turbulent mixing. We note that the cube roots of the mean values associated with the spawning seasons (200-400 m^3s^{-3}) lie close to an apparent low wind-speed threshold for the formation of oceanic whitecaps (Monahan 1971), a more obvious, visual index of wind-generated turbulence production. In this context, the proper relationship between the mean wind speed cubed and the mode of the wind-speed probability distribution (which typically shows Poisson rather than Gaussian behavior) is important. From an examination of selected frequency distributions presented by Nelson (1977), we concluded that mean values of 200-400 m^3s^{-3} are entirely consistent with modal wind speeds in the range 3-5 m s^{-1}. This range of values is just below the threshold wind speed (~5 m s^{-1}) that Therriault and Platt (1981) used to distinguish biological (low turbulence) from physical (high turbulence) control of phytoplankton patchiness.

The data plotted in Figure 5B demonstrate a large offshore increase in turbulence production in the Southern California Bight (curves 1 and 2) and illustrate the seasonal progression of wind speed cubed that characterizes the region of maximum upwelling (curve 3). The zonal section represented by curve 2 (Figure 5A) and curves 1 and 2 (Figure 5B) shows a monotonic increase in wind speed cubed from values less than 300 m^3s^{-3} near the coast to values exceeding 900 m^3s^{-3} offshore. The amplitude of the annual cycle is substantially larger at the offshore locations as well. Off Cape Mendocino, wind-generated turbulence production is high throughout the year; highest values are associated with winter storms and strong equatorward surface winds during summer.

Seasonal isogram plots of wind speed cubed and thermocline strength (Figure 6A) and two independent estimates of mixed layer depth (Figure 6B) were constructed from the long-term monthly mean values within 3 degrees of the coast. Wind speed cubed was plotted for the 1-degree squares immediately adjacent to the coast. The stability indices were averaged over three 2-degree squares at each latitude to increase the number of observations per averaged value.

The seasonal cycles of wind speed cubed and thermocline strength (Figure 6A) show strong similarities among the timing and locations of regions characterized by low wind-induced turbulence (<300 m^3s^{-3}) and strong vertical stability (thermocline strength >5°C). The relative minima (wind speed cubed) and maxima (thermocline strength) in the time-space domain nearly coincide with the known spawning periods and spawning grounds for the northern anchovy. The notable exception occurs between 30°N and 35°N in the Southern California Bight.

The coastal region between 43°N and 48°N is characterized by low turbulence and strong upper-layer stratification from June to September. During this same period, the thermal MLD's are less than 20 m over the entire region north of 40°N (Figure 6B). Minimum MLD's occur in May and June in response to peak freshwater discharge from the Columbia River. Between Cape Mendocino (40°N) and Point Conception (35°N) high values of wind speed cubed, low stability, and shallow mixed layers are associated with strong coastal upwelling during spring and summer. During winter, frequent and severe storms cross this region (north of 40°N), drive the mixed layer deeper (Figure 6B), and decrease upper-layer stratification to a minimum (Figure 6A).

Because of the strong influence of the Columbia River plume on vertical stability, we checked the consistency of the thermal mixed layer depths (based on MBT data) by constructing a seasonal isogram plot of pycnocline depth. Pycnocline depth was defined as the upper depth of the interval for which stability (defined by Equation 1) was a maximum, and mean values were computed from the hydrographic data in the NODC SDII file. Comparison of the two panels in Figure 6B shows close agreement between thermal MLD and pycnocline depth along the entire coast during the summer. A weaker relationship is evident during winter, although the two methods show similar seasonal trends.

The nearshore region in the Southern California Bight (30-35°N) is characterized by uniformly low values of wind speed cubed (<300 m^3s^{-3}) throughout the year, with the exception of a local maximum at 33°N from February to April (Figure 6A). Upper-layer stratification follows a well-defined, large-amplitude annual cycle. There is a lack of agreement between the peak spawning period for the central subpopulation of *E. mordax* (January-April) and maximum thermocline strength (July-September). Thus the simultaneous oc-

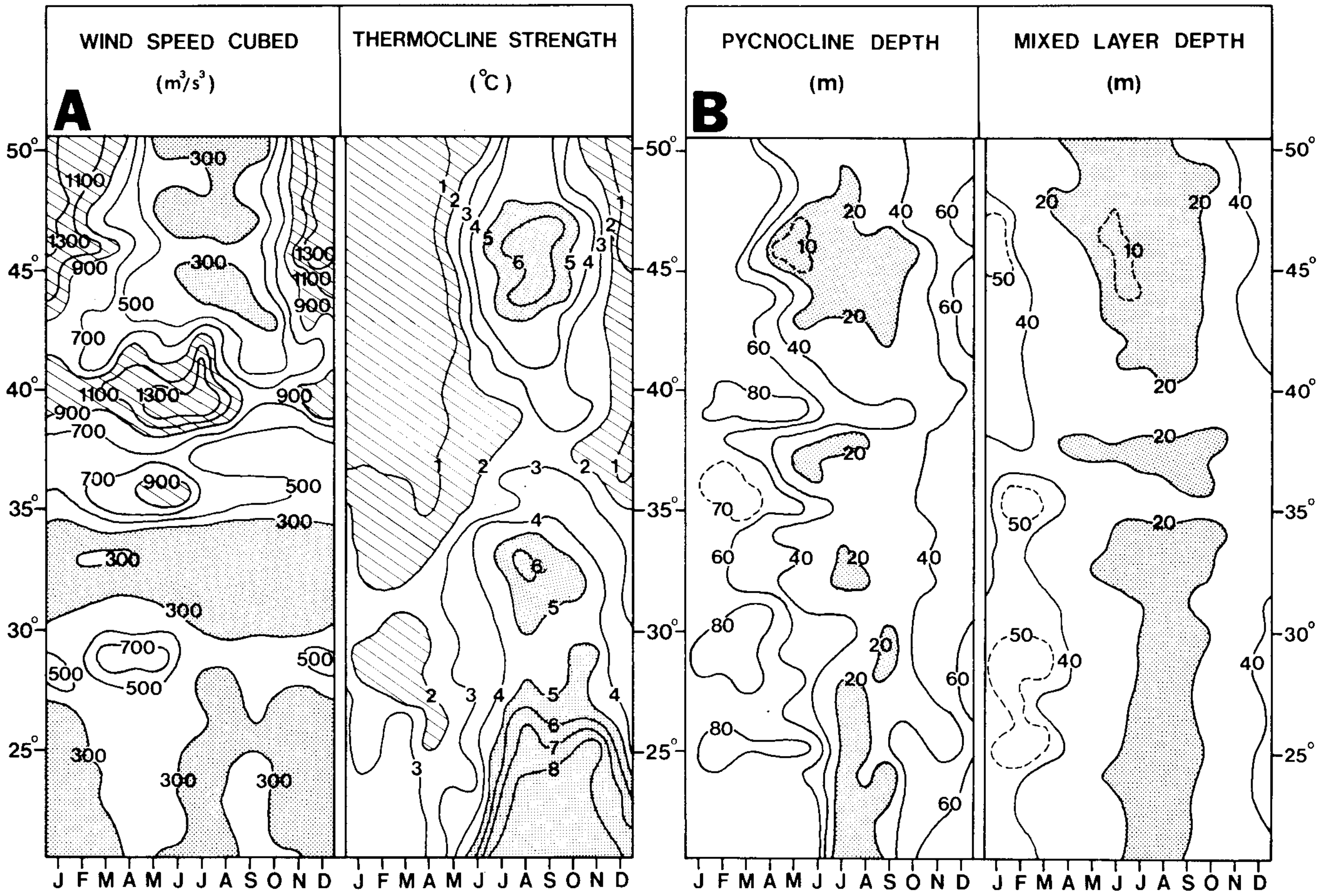

Figure 6. Seasonal cycles of (*A*) wind speed cubed (m^3s^{-3}) and thermocline strength (°C) and (*B*) pycnocline depth (m) and mixed layer depth (m) near the coast. Means of wind speed cubed were computed by month for 1-degree squares immediately adjacent to the coast. Monthly means for thermocline strength, pycnocline depth, and mixed layer depth are averages of the values within 3 degrees of the coast at each latitude. In panel *A*, wind speed cubed is contoured at intervals of 200 m^3s^{-3}. Values less than 300 m^3s^{-3} are shaded, and hatched areas correspond to mean values greater than 900 m^3s^{-3}. Thermocline strength is contoured every 1°C. Shaded areas are greater than 5°C; hatched areas are less than 2°C. In panel *B*, pycnocline depth and mixed layer depth are contoured every 20 m. Layer depths less than 20 m are shaded.

currence of high stability and low turbulence may not be necessary for spawning success. This also suggests that high stability (and shallow mixed layers) prior to or during the peak spawning months may also contribute to adverse spawning conditions, for example, by inhibiting the upward flux of nutrients into the mixed layer and thereby decreasing primary production.

South of 30°N, a pattern of low turbulence production is broken twice over the annual cycle: (1) from March to June in conjunction with strong, upwelling-favorable surface winds, and (2) during the fall when tropical storms occasionally impinge on Baja California. This region is also characterized by relatively strong thermal stratification (values exceed 3°C; maximum stability occurs from August to November, Figure 6A) and shallow mixed layers (20-40 m) throughout the year. If upper-layer stability and wind-generated turbulent mixing were the only two factors associated with the "critical period" for larval anchovies, then the extended period of low turbulence and relatively high stability near the coast and south of 27°N suggests that spawning conditions might be more favorable for the southern subpopulation than for the central stock. Of course, other factors, such as the spatial structures of predator-prey populations (Smith and Lasker 1978), may interact with the processes addressed in this paper to regulate spawning success, particularly in regions of low mean values of wind speed cubed (e.g., in the Southern California Bight).

Turbulence, Transport, and Stability on the Principal Spawning Grounds

The long-term mean distributions mapped in Figures 4-6 corroborate Lasker's (1975, 1978) explanation of the "critical period" concept (i.e., a stable ocean in the absence of turbulent mixing is a prerequisite for larval survival). The spawning grounds for each of the three subpopulations of the northern anchovy are characterized by low values of wind speed cubed during the peak spawning seasons; mod-

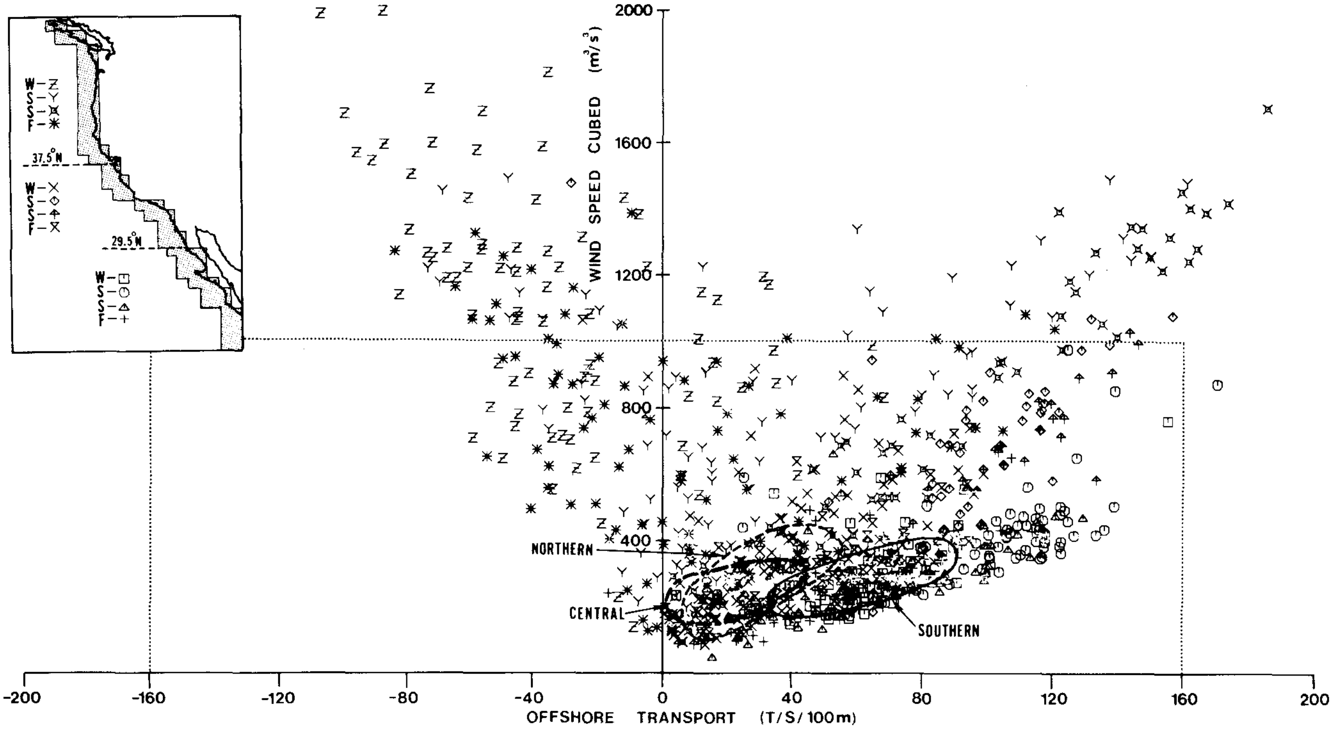

Figure 7. Scatter diagram of wind speed cubed (m^3s^{-3}) versus offshore Ekman transport (t s^{-1} per 100 m). Mean monthly values are plotted for each 1-degree square within the shaded region shown in the inset. Negative values denote onshore transport. Symbols are coded according to season (W,S,S,F) within each of the three coastal regions shown in the inset. Winter corresponds to December-February. Values of wind speed cubed and offshore transport associated with the peak spawning months and spawning grounds for the southern, central, and northern subpopulations of *E. mordax* are enclosed by solid, dashed, and dotted lines, respectively. The dotted lines at 1000 m^3s^{-3} and ± 160 t s^{-1} per 100 m correspond to the limits of the expanded scatter diagrams in Figure 8.

erate to strong upper-layer stratification is associated with two of the three spawning seasons and locations. During the peak spawning season for each subpopulation, low values of wind speed cubed correspond to equatorward surface wind stress (Nelson 1977), implying some degree of offshore transport in the surface layers and upwelling near the coast. Surface transport has been discussed (Parrish et al. 1981) as an alternate but not mutually exclusive "critical period" hypothesis. Therefore, an index of offshore Ekman transport was used as an additional variable to characterize the wind field over the principal spawning grounds.

Scatter diagrams of turbulence versus transport were constructed by plotting the long-term monthly mean values of wind speed cubed against estimates of offshore Ekman transport (Figures 7 and 8). Nelson's (1977) surface wind-stress values were used to compute the offshore directed component of surface Ekman transport (using the method described by Bakun and Nelson, 1977) for each 1-degree square area within a region extending from the coast to 2 degrees of longitude offshore. The total ensemble of approximately 720 possible monthly mean pairs of wind speed cubed and offshore transport was partitioned into three geographic regions with breaks at 29.5°N and 37.5°N (approximate stock boundaries) and into four quarters, with winter defined as December-February. Twelve different symbols were used to distinguish the spawning seasons and spawning grounds. The total data set was subsampled and replotted in four additional scatter diagrams to illustrate the salient points more clearly (Figure 8). Different letter symbols are shown in Figure 8, analogous procedures were used to construct the diagrams. Each of the points plotted in these diagrams corresponds to a pair of long-term monthly means. Sampling variability produces large scatter about the means. Thus, these diagrams do not represent all possible combinations of turbulence and transport and should be considered as mean "envelopes" characterizing the average environmental conditions in the region.

Low turbulence and weak offshore transport are common to all three spawning regions (Figure 7), which occupy overlapping positions near the origin in the diagram. Four distinct regimes are evident in this diagram: (1) the entire left portion (i.e., onshore transport) is characteristic of fall-spring off the Pacific Northwest; (2) the high wind speed cubed/high offshore transport region (i.e., greater than 600 m^3s^{-3} and 80 t s^{-1} per 100 m) distinguishes the region of maximum upwelling from Point Conception (35°N) to Cape Blanco (43°N) in spring and summer; (3) the

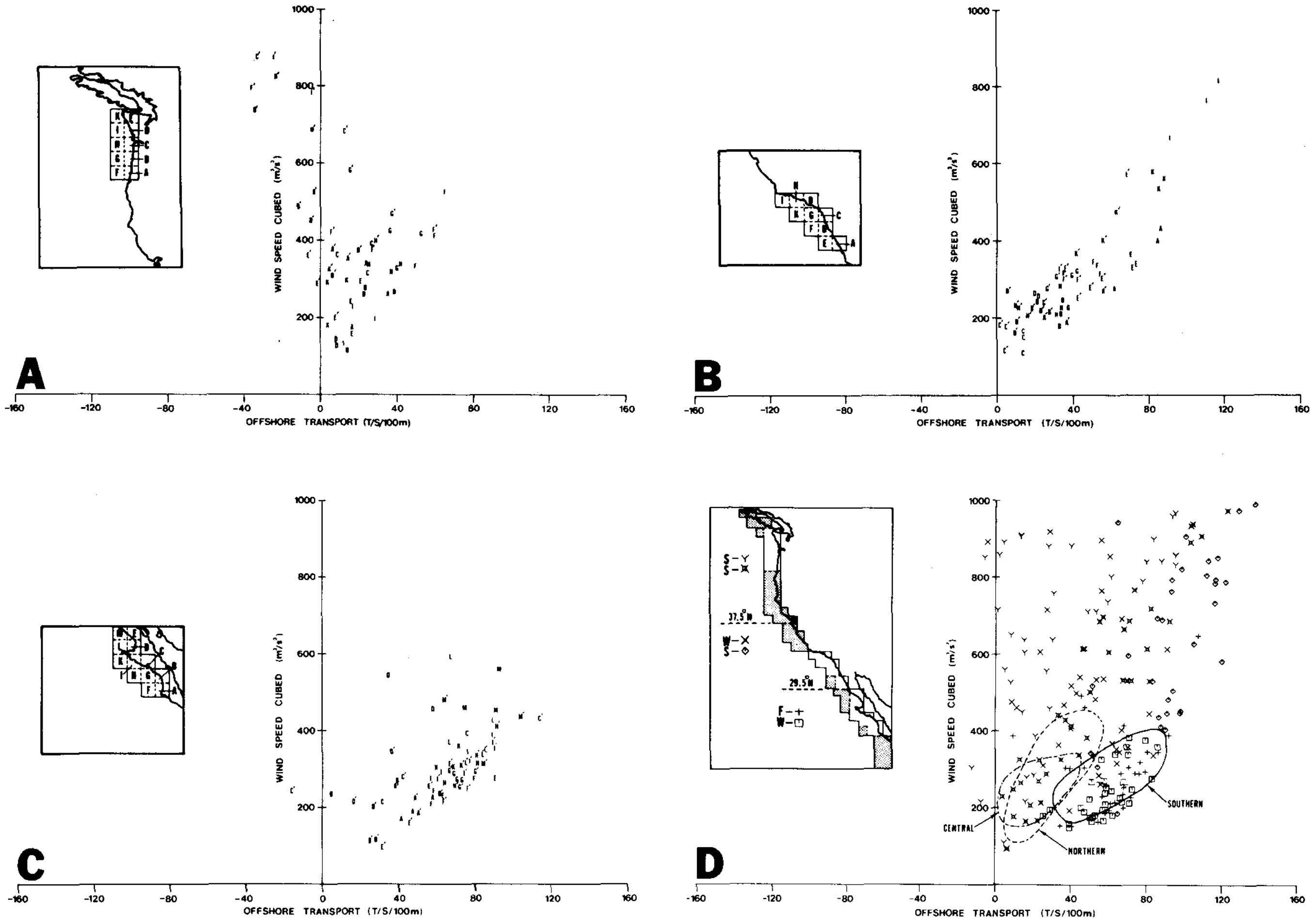

Figure 8. Scatter diagrams of wind speed cubed (m^3s^{-3}) versus offshore Ekman transport (t s^{-1} per 100 m) in the (*A*) northern, (*B*) central, and (*C*) southern spawning regions. Values for the nonspawning areas are plotted in panel *D*. Mean monthly values are plotted for March-August in panel *A*; December-May in panel *B*; and September-February in panel *C*. Negative values denote onshore transport. Symbols are coded according to the location of the 1-degree squares shown in the insets, and primed letters correspond to the first three months of the six months plotted in each of panels *A, B,* and *C*. Values plotted in panel *D* correspond to the shaded regions outside the principal spawning areas (inset), but during the peak spawning seasons in each of the three regions. The symbols are coded according to season (W,S,S,F) and region, and the enclosed portions of the scatter diagram labeled northern, central, and southern are the same as those shown in Figure 7. Note the change of scale for wind speed cubed in this figure compared to Figure 7.

low-turbulence/high transport area is associated with the Baja California upwelling system in the spring; and (4) the low wind speed cubed/weak offshore transport region (i.e., less than 400 m^3s^{-3} and 80 t s^{-1} per 100 m) almost exclusively encompasses data from the principal spawning regions during the peak spawning seasons. The overlap among the three spawning regions would have been more pronounced if we had plotted wind speed cubed against the alongshore component of surface stress (thereby removing the effect of latitudinal variation in the Coriolis parameter; offshore transport is inversely proportional to the Coriolis parameter f, where $f = 0.0001458$ SIN ϕ s^{-1} and ϕ is the geographic latitude).

Separate scatter diagrams were constructed for each of the three principal spawning regions but only for the 6 months spanning the spawning season in each region (Figure 8A, B, and C). Data for the nonspawning regions during the same 6-month periods are plotted in Figure 8D to identify other coastal locations characterized by low turbulence and weak offshore transport. Our interpretation of these scatter diagrams follows the main conclusion drawn from the spatial and temporal distributions: the months and locations associated with low wind-generated turbulence (and weak offshore transport) are also the principal spawning seasons and spawning grounds for each of the three subpopulations of the northern anchovy.The lowest values of wind speed cubed and offshore transport correspond to the squares immediately adjacent to the coast (e.g., symbols A, B, C, D, and H in Figure 8B). Examination of anchovy larvae distributions for 1966-1979 (Hewitt 1980) suggests a tendency for higher larval abundance within 100 km of the coast than offshore, which would be consistent with greater spawning success in the nearshore, low-turbulence regions.

There are a few locations and months for which the mean wind speed cubed/offshore transport pairs fall within the areas on the diagrams occupied by the spawning stocks (Figure 8D). For the southern stock, most of these data are from 1-degree squares located well offshore (e.g., the entire shaded block south of Cabo San Lucas at 25°N). Virtually no other locations between 29.5°N and 37.5°N can be characterized by the low-turbulence/weak transport values associated with the central stock's spawning grounds. The additional data coinciding with the position occupied by the northern stock come from the 1-degree squares adjacent to Vancouver Island and from the nearshore region in the vicinity of San Francisco. Recent data suggest that the coastal waters adjacent to San Francisco Bay provide a suitable habitat for winter-spring spawning of *E. mordax* (Stepanenko 1981[1]).

Analogous procedures were used to construct a scatter diagram of wind speed cubed versus thermocline strength (Figure 9). For this diagram, quarterly mean values of wind speed cubed and thermocline strength were used. Thus the numbers of wind speed cubed/thermocline strength data pairs have been reduced by a factor of three relative to the data points plotted in Figure 7. Although this particular diagram shows a great deal of scatter, there is evidence for an inverse relationship between wind speed cubed (turbulence) and thermocline strength (stability). High turbulence (large wind speed cubed) and weak stability (low thermocline strength) correspond to winter storm activity and deep mixed layers off the Pacific Northwest, although similar turbulence/stability conditions occur off Cape Mendocino during spring and summer. High stability and relatively low values of wind speed cubed characterize Baja California in the fall (symbol D, Figure 9). The majority of the months and locations associated with the peak spawning seasons on each of the spawning grounds (symbols A, B for the southern stock; E, F for the central stock; L for the northern stock) lie within a relatively narrow range of values for wind speed cubed (200-400 m^3s^{-3}) and thermocline strength (2-5°C). This is evident in the close agreement among the three envelopes enclosing these points for each stock. For similar values of wind speed cubed in each region, stability (thermocline strength) is slightly higher on the spawning grounds for the southern and northern stocks of *E. mordax* than for the central stock.

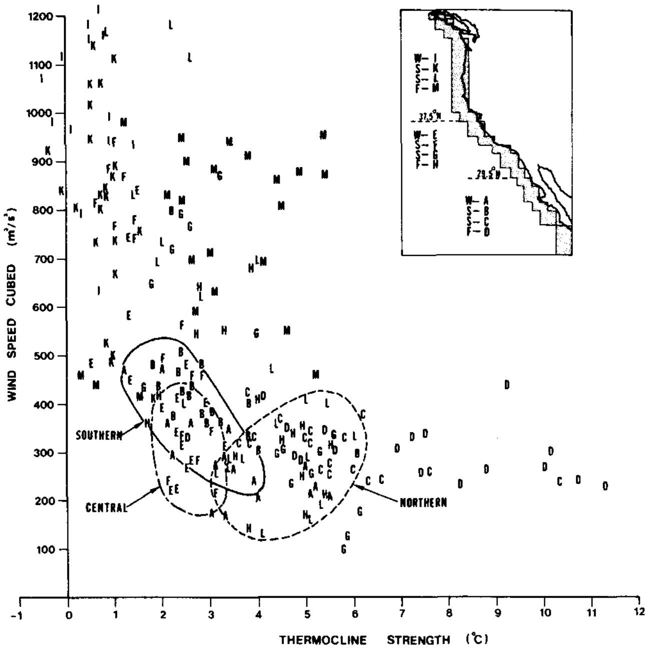

Figure 9. Scatter diagram of wind speed cubed (m^3s^{-3}) versus thermocline strength (°C). Mean quarterly values are plotted for each 1-degree square within the shaded region shown in the inset. Symbols are coded according to season (W,S,S,F) within each of the three coastal regions. Winter corresponds to December-February. Values of wind speed cubed and thermocline strength associated with the peak spawning months and spawning grounds for the southern, central, and northern subpopulations of *E. mordax* are enclosed by solid, dashed, and dotted lines, respectively.

DISCUSSION

Historical surface wind observations and subsurface temperature data from the California Current region have been used to compile long-term monthly mean distributions of two indices related to (1) the rate of turbulent energy production by the wind (wind speed cubed), and (2) the vertical stability of the upper water column (thermocline strength). Characteristic spatial patterns (Figure 4) and annual cycles (Figures 5 and 6) of these indices were discussed in relation to the principal spawning grounds and peak spawning seasons of the three subpopulations of the northern anchovy, *Engraulis mordax*. A strong correspondence was shown among the locations and seasons characterized by low wind speed cubed (turbulent mixing) and the timing of the spawning cycle for each stock. A weaker correspondence of the spawning cycle to relatively high thermocline strength (vertical stability) was demonstrated. Each of the spawning regions in the California Current is also associated with weak coastal upwelling and offshore transport during the respective spawning season (Figures 7 and 8). Bakun and Parrish (1982) show similar relationships among the regions of low turbulence production and the principal spawning grounds of the Peruvian anchoveta, *Engraulis ringens*.

One interpretation of these long-term mean data is

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[1] Stepanenko, M.A. Assessment of stocks and reproduction conditions of some commercial fish off the Pacific coast of the North America in 1980. Mimeograph report, Pacific Research Institute of Fisheries Oceanography (TINRO), Vladivostok, 1981, 21 p.

that reproductive strategies have evolved in response to "optimum" levels of turbulent mixing in the stable layers of the upper ocean, rather than to minimum levels of turbulence (or to maximum vertical stability). There are two important aspects to this rationale. In the complete absence of wind stirring or (upwelling), nutrient fluxes into the mixed layer would be substantially reduced, and phytoplankton production would decrease. Therefore, some degree of mixing and entrainment of nutrients at the base of the mixed layer would be required to maintain adequate concentrations of food for first-feeding larval anchovies. On the other hand, if the "optimum" level of turbulent mixing was frequently exceeded by large amounts, then destruction of fine-scale food strata and dispersion of larval anchovies could lead to recruitment failure, particularly if unfavorable conditions persisted through the spawning season (Lasker 1978). A similar argument can be made that too much stability prior to or during a spawning season might produce equally adverse spawning conditions by severely inhibiting the upward flux of nutrients and reducing primary production. There is evidence to suggest that the long-term monthly mean values of wind speed cubed that characterize the spawning grounds of the three subpopulations of *E. mordax* are consistent with a "threshold" wind speed ($\sim$5 m s^{-1}) associated by Kullenberg (1978) and Therriault and Platt (1981) with horizontal patchiness in phytoplankton distributions.

Mean distributions of environmental indices, which represent highly nonlinear, time-dependent physical processes (e.g., wind speed cubed), are meaningful to investigations of recruitment variability if, for example, pattern recognition can be used to identify normal requirements for reproductive success. In this context, the spatial patterns and annual cycles of wind speed cubed and thermocline strength discussed in this paper are useful, and corroborate Lasker's experimental evidence (1975, 1978). However, to determine the degree to which turbulence and stability have exerted a limiting control on spawning success of the northern anchovy over the past 14 years, reasonably complete time series data, on space and time scales appropriate to the biological processes, are required. Because the linkage between the physical processes (wind speed cubed) and recruitment success (year-class strength) is by no means direct, it is not reasonable to expect "any single mechanism to explain larval survival in all cases" (May 1974).

A 14-year time series (1968-81) of daily mean wind speed cubed indices (Figure 10) was constructed for a representative location in the Southern California Bight (33°N, 119°W). An estimate of the surface wind was computed from the 6-hourly northern hemisphere surface pressure analyses available at Fleet Numerical Oceanography Center, using the method described by Bakun (1973). The daily values displayed in Figure 10 are means of the cube of the wind speed for the four synoptic samples per day. These time series data are characteristic of physical processes integrated over spatial scales (typically 3-degree resolution) which are 1 to 2 orders of magnitude larger than the horizontal scales associated with plankton patchiness and larval feeding. The indices are also uncalibrated in terms of absolute magnitude (Bakun 1973). Nevertheless, we feel that the analyzed meteorological fields offer a means of reconstructing consistent time-histories of the physical processes (e.g., wind speed cubed, offshore transport) that may have limited recruitment, thus causing the wide variations in year-class size over the past 14 years of the anchovy fishery. A similar time series of the stability indices could not be assembled because appropriate subsurface data do not exist.

The striking features of the daily wind speed cubed series are the large pulses over relatively restricted time periods during the spawning season (December-April). The characteristics distinguishing the spawning season of one year from that of another seem related to the frequency of occurrence of wind speed cubed "events" above a threshold value. In terms of Lasker's first-feeding hypothesis, favorable spawning seasons leading to strong year classes (e.g., 1976, 1978) contain relatively fewer events of magnitude exceeding a critical value, whereas spawning seasons resulting in poor year classes (e.g., 1975, 1977) are characterized by relatively more frequent, extended periods of intense wind events. Indeed, the first-feeding hypothesis has been largely formulated on the basis of field observations obtained before and after a period of strong winds during 1975 (Lasker 1975, 1978) and during the drought year spanning the 1975-76 spawning season (Lasker 1981b). Interestingly enough, the period of strong winds in February 1975 (also a period of strong upwelling) was followed by an even more intense mixing event (also strong upwelling) near the end of March—the largest such event during the spawning season over the 14-year record. It is likely that the occurrence of both of these events within one month contributed to the highest estimated recruitment failure in the history of the anchovy fishery (Smith et al. 1981).

One simple way of reducing the daily time series data to a quantitative index relating to the history of the fishery is to integrate the wind speed cubed index over the spawning season (i.e., form the December-February mean). These values (or the means for several different combinations of months from December

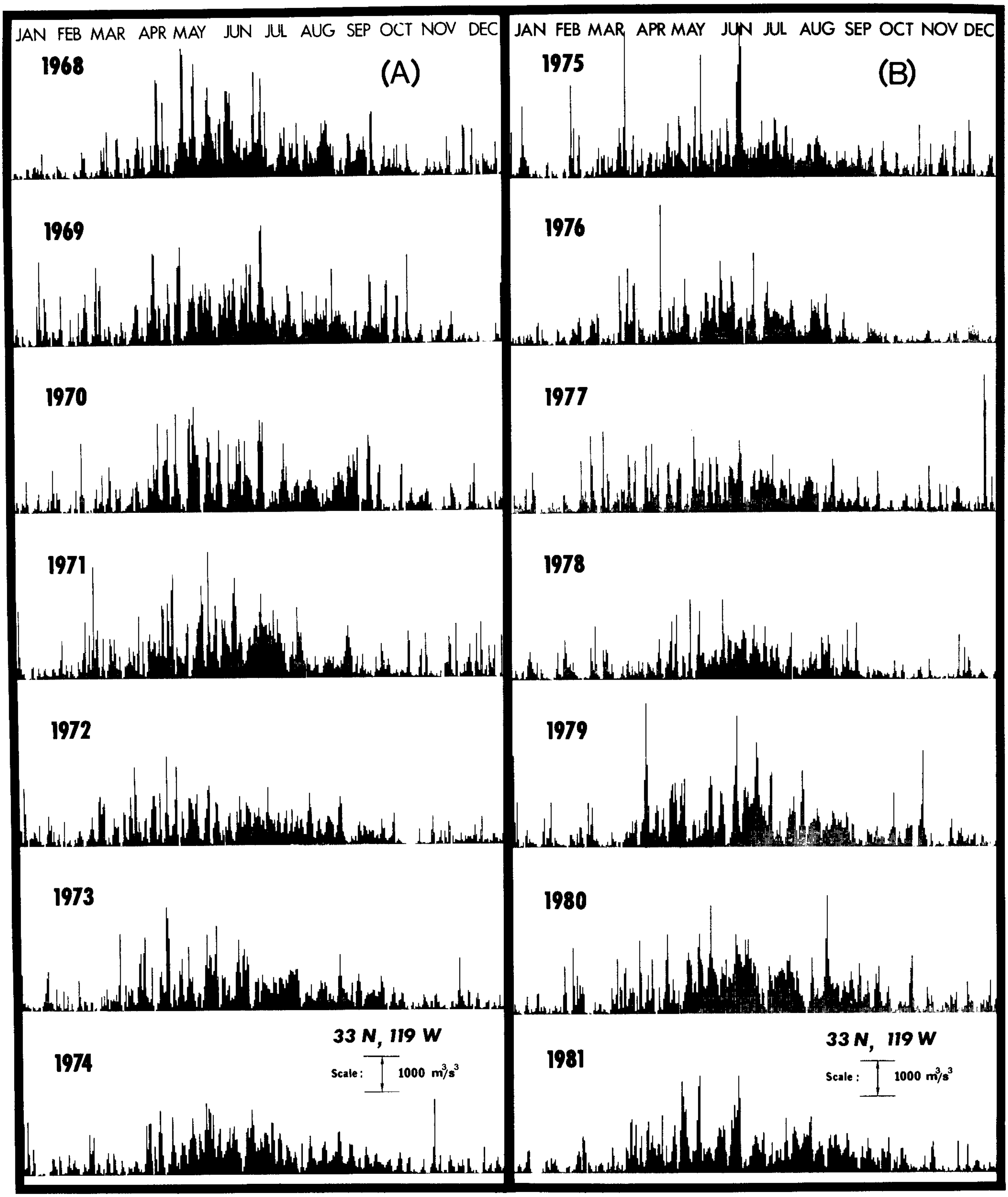

Figure 10. Daily indices of wind speed cubed (m^3s^{-3}) at 33°N, 119°W for *(A)* 1968-74, and *(B)* 1975-81. Daily values were derived from 6-hourly surface atmospheric pressure analyses. Values are scaled according to the key on each plot.

to April) could be used to test the relationship of wind-induced turbulence to recruitment and year-class strength, for example, by regressing the values of the intensity of wind speed cubed, averaged over the spawning season, against estimates of year-class size (Mais 1981) or by using rank correlation methods to compare the relative ranks of wind speed cubed with relative ranks of spawning success (Smith et al. 1981). Such statistical tests are beyond the scope of this paper. However, it is unlikely that the variability in year-class strength would be well described by a linear correlation with bulk estimates of a highly nonlinear process, particularly considering the limited degrees of freedom in the data.

This is not to imply that turbulence and stability may not exert a control on spawning success (i.e., the lack of a significant statistical relationship would not be sufficient to reject the wind-turbulence hypothesis), but rather to suggest that the mean intensity of wind speed cubed over the spawning season may not provide a useful way to quantify the integrated effects of physical processes on time scales critical to larval first feeding. A simple calculation demonstrates our point. A sequence of 30 days in which the (uncalibrated) daily wind speed cubed averages 300 m^3s^{-3} would have exactly the same monthly mean as a sequence of 30 days in which periods of 4 days with daily means of 125 m^3s^{-3} are followed by an event of magnitude 1000 m^3s^{-3}. In the first situation, mixing and stability conditions would most likely favor the formation of chlorophyll maximum layers, leading to recruitment success. In the second case, recruitment failure would result from episodic destruction of stratified layers during the critical period (2-3 days) after yolk-sac absorption (Lasker et al. 1970).

It is likely that the most favorable conditions for larval survival correspond to extended periods of low-turbulence "windows" prior to and continuing through the critical period. In terms of this requirement, at least five important features in the wind speed cubed time series need to be quantified in relation to the "critical period" requirements of larval anchovy: (1) the required length of the low-turbulence "windows," (2) the magnitude and duration of events exceeding the low-turbulence threshold, (3) the frequency with which high-turbulence events recur, (4) the association of high-turbulence events with coastal upwelling or downwelling processes, and, perhaps most important, (5) the timing of the spawning cycle in relation to the sequence of turbulence events. A proper analysis of the last feature would require detailed information on the birthdate distributions of surviving anchovy (Methot 1981).

We suggest two methods that might be used to further investigate the effects of physical mechanisms on reproductive success. A statistical approach could be used to search through a time series of daily (or 6-hourly) values of wind speed cubed, to find the combinations of low-turbulence "windows" and high-turbulence "events" that best characterize a spawning season as favorable or unfavorable in terms of the stability requirements of Lasker's first-feeding hypothesis. Examination of these data in relation to data on intensity of spawning, birthdate distributions (Methot 1981), and year-class survival (Mais 1981; Smith et al. 1981) might suitably test the wind turbulence hypothesis.

An alternate method would be to investigate the evolution (generation, maintenance, and destruction) of fine-scale food strata in the upper layers of the ocean by coupling existing state-of-the-art one-dimensional mixed layer models (e.g., Garwood 1977) with appropriate biological models (Steele 1977) to test the sensitivity (biological response) to different characterizations of atmospheric forcing and to different initial conditions. Substantial new field measurements of both physical and biological processes over an extended period of the spawning season would be required to initialize and verify the model predictions. A carefully designed physical/biological mixed layer model would complement existing laboratory and field programs, and offers a method to properly integrate the effects of wind-generated turbulence over a spawning season, thereby contributing to our understanding of the important linkages of physical processes to recruitment success of the northern anchovy.

ACKNOWLEDGMENTS

We thank Drs. C.N.K. Mooers and R.W. Garwood for reviewing an early version of this paper, and J. Cropp for typing the manuscript. Access to historical surface and subsurface data and computing and plotting facilities was provided by the U.S. Navy, Fleet Numerical Oceanography Center, Monterey, California.

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LARGE-SCALE RESPONSE OF THE CALIFORNIA CURRENT TO FORCING BY THE WIND STRESS CURL

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ABSTRACT

Seasonal distributions of zooplankton volume in the California Current show a maximum at a distance of about 100 km offshore between San Francisco and northern Baja California. It is shown that this coincides with a region of offshore upwelling of the thermocline associated with a nearshore counterflow. This counterflow is evident year-round at depths below the thermocline (the California Undercurrent) but appears only seasonally in the upper 200 m (the Davidson Countercurrent). However, the integrated nearshore transport in the upper 500 m is poleward year-round.

The seasonal California Current-Countercurrent system is shown to have a nonseasonal (anomalous) counterpart that fluctuates with a time scale of 5-6 months. The region of offshore upwelling associated with this anomalous pattern is found to be located somewhat farther (about 200-300 km) offshore than in the seasonal pattern. Statistical analysis of this anomalous pattern of variability reveals a response resembling that expected from a simple model of offshore Ekman pumping (upwelling) driven by the wind stress curl. As such, this upwelling is not a boundary phenomenon and is therefore quite distinct from coastal upwelling in this region.

It is proposed that this Ekman pumping mechanism upwells nutrients into the euphotic zone, and is therefore indirectly responsible for the offshore peak in zooplankton abundance north of the northern Baja California border.

RESUMEN

Las distribuciones estacionales del volumen del zooplancton en la Corriente de California señalan un máximo a unos 100 Km. mar afuera, entre San Francisco y la zona norte de Baja California. Se demuestra que ésto coincide con la región de surgencia de la termoclina, asociada con una contracorriente costera. Este flujo costero se manifiesta todo el año a profundidades por debajo de la termoclina (contracorriente de California), pero es de régimen estacional por encima de los 200 m de profundidad (contracorriente Davidson). Sin embargo, integrando el transporte costero de componente norte que abarca de los 500 a los 0 m de profundidad, puede considerarse que dicho flujo dura todo el año.

Se demuestra que el sistema estacional, Corriente de California-Contracorriente, tiene una anomalía que no es estacional, y que fluctúa en periodos de 5-6 meses. La región de surgencias asociada con estas anomalías, se encuentra localizada más lejos, hacia los 200-300 Km. mar afuera del patrón estacional. El análisis estadístico de la variabilidad en este tipo de anomalía revela una respuesta similar a la que pudiera resultar de un simple modelo de Ekman, bombeo en las surgencias, desarrollado por la acción de los remolinos del viento. En este caso la surgencia no es producida por la acción de zonas limítrofes, siendo por lo tanto distinta a las surgencias costeras que se presentan en esta región.

Se considera que este mecanismo de bombeo Ekman aporta nutrientes a la zona eufótica, y es responsable indirectamente de los máximos en la abundancia de zooplancton al norte de Baja California.

INTRODUCTION

Through the persistent efforts of CalCOFI over the past 30 years, sufficient data has now accumulated to allow statistical examination of physical and biological interaction in the California Current over a broad range of time and space scales. Past investigations by Bernal (1979; 1981), Bernal and McGowan (1981), Chelton (1981), and Chelton, Bernal, and McGowan (in press) have focused on the very large spatial scales of variability. These studies have demonstrated that zooplankton biomass and the transport of the California Current are dominated by variability with time scales of 2 years and longer. A rather surprising discovery from these studies has been that these interannual variations appear to be unrelated to local wind forcing over the California Current.[1] This study represents an attempt to isolate some (secondary) aspect of the flow of the California Current that *is* driven

[Manuscript received February 15, 1982.]

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[1] An apparent weak relation between the flow of the California Current and basin-wide scales of wind forcing over the North Pacific has been shown by Chelton, Bernal, and McGowan (in press) to actually reflect a coupling between the California Current and occurrences of El Niño in the eastern tropical Pacific. This results from the fact that large-scale winds over the North Pacific are significantly correlated with El Niño events.

by the local wind forcing in this region and to compare it with dynamical expectations.

The conventional view of the dynamics of epipelagic ecosystems in eastern boundary currents is that biological productivity at all levels of the food chain is indirectly controlled by wind-driven coastal upwelling of deep-water nutrients (see, for example, Smith 1968; Cushing 1969; 1975; Walsh 1977). Winds over the California Current are generally upwelling-favorable year-round south of San Francisco. Although this is undoubtedly an important factor contributing to the high nutrient concentrations found in the California Current (and thus the high levels of productivity), it is not necessarily the only controlling factor. Advection of nutrient-rich waters from higher latitudes by the equatorward transport of the California Current may also be important. The fact that the dominant large-scale variations in zooplankton abundance are unrelated to variations in wind forcing indicates that coastal upwelling must play at best a secondary role in the biological variability. The earlier studies by Bernal, Chelton, and McGowan have presented rather convincing evidence that advection is the dominant mechanism controlling large-scale, year-to-year variations in zooplankton abundance.

Although the dominant signals of variability in the California Current are unrelated to the local wind field, it seems reasonable to expect that some secondary aspect of variability in the physical characteristics must be related to wind forcing. If such a relationship could be identified, the results might have important biological implications.

ZOOPLANKTON DISTRIBUTION IN THE CALIFORNIA CURRENT

A limitation of the earlier studies by Bernal, Chelton, and McGowan has been that the large spatial averaging used to isolate the larger scales of variability precludes the possibility of detecting any cross-shore structure in either zooplankton biomass or current velocity. For example, if coastal upwelling were solely responsible for productivity, we might expect zooplankton abundance to be maximum at the coast, decreasing offshore. This relationship between nearshore and offshore zooplankton biomass would be obscured in the large areal averaging of zooplankton volume. However, the spring-summer distribution of zooplankton volume shown in Figure 1 indicates that this anticipated nearshore-offshore structure is present only south of CalCOFI line 100. Between San Francisco and northern Baja California the highest zooplankton biomass is located a distance of about 100 km from the coast. It is worth noting that satellite images of this region from the Coastal Zone Color Scanner (CZCS) frequently indicate extremely high chlorophyll concentrations immediately adjacent to the coast (within 10-20 km), presumably reflecting a phytoplankton response to nutrients from coastal upwelling (see, for example, Smith and Baker 1982). Thus, it is possible that an even larger peak in zooplankton biomass may exist very close to the coast, but this narrow region is not well sampled by the standard CalCOFI station pattern. Even if concentrations are higher near shore, the offshore peak in zooplankton abundance is an important biological characteristic of the California Current.

There are at least two possible explanations for this feature. The first is that nutrients upwelled at the coast by the longshore wind stress lead to high phytoplankton productivity within a relatively short time lag (the doubling time for phytoplankton is less than a few days). This high primary productivity would then result in a corresponding increase in secondary productivity. The zooplankton responding to the increased phytoplankton biomass would be passively carried offshore together with nonconsumed phytoplankton by Ekman transport from the longshore wind stress. However, since the doubling times for zooplankton are on the order of a month, the zooplankton biomass could actually increase offshore, even though the primary food source is at the coast. Eventually, as the zooplankton continued to drift offshore, food would become a limiting factor, and zooplankton biomass would decrease. Given an appropriate primary-secondary productivity model, this mechanism could, in principle, be quantitatively tested from the 30-year CalCOFI data set. However, the spatial and temporal sampling of both phytoplankton and zooplankton in the CalCOFI record are probably inadequate for this type of study.

An alternative explanation is that the region offshore is, for reasons yet to be determined, a more hospitable environment for the zooplankton and that the high zooplankton biomass is produced locally rather than being passively carried into the region by Ekman drift. Because the time scales are longer, this mechanism can easily be investigated from the CalCOFI data.

THE NEARSHORE COUNTERFLOW OF THE CALIFORNIA CURRENT

The July longshore integrated transport in the upper 500 m in the California Current is shown in Figure 2. (Most of this transport is generally confined to the upper 200 m.) Note that the peak in zooplankton abundance north of CalCOFI line 100 coincides with a region of maximum horizontal shear in the flow. The nearshore transport is poleward while the transport

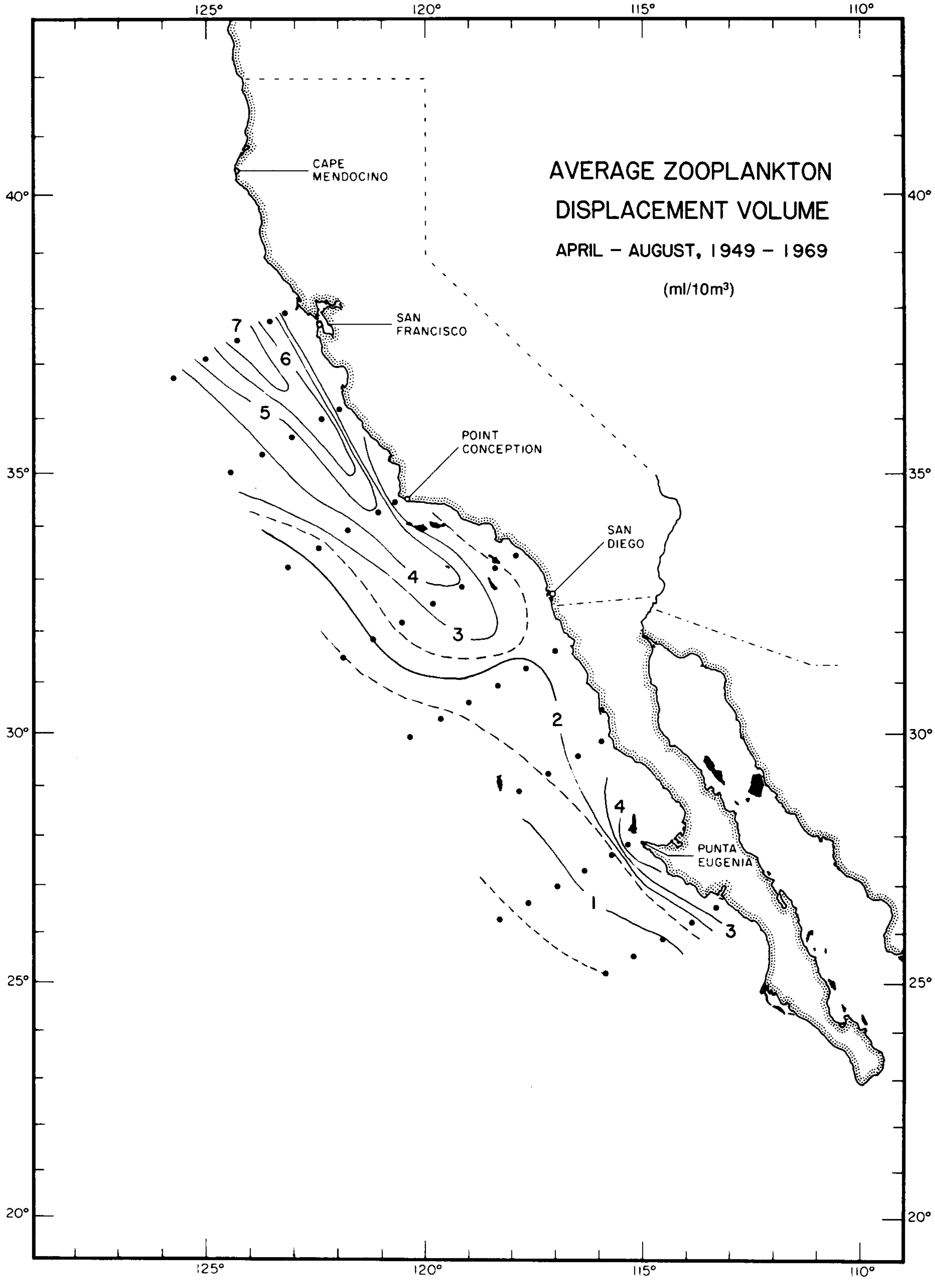


Figure 1. Spring-summer distribution of zooplankton displacement volume in the California Current. April-August long-term (1949-69) averages were computed over "pooled areas" measuring 200 km in the longshore direction and 65 km in the cross-shore direction (see Smith 1971). The dots represent the centers of the pooled areas. This spatial and temporal averaging removes the small-scale patchiness inherent in the zooplankton samples.

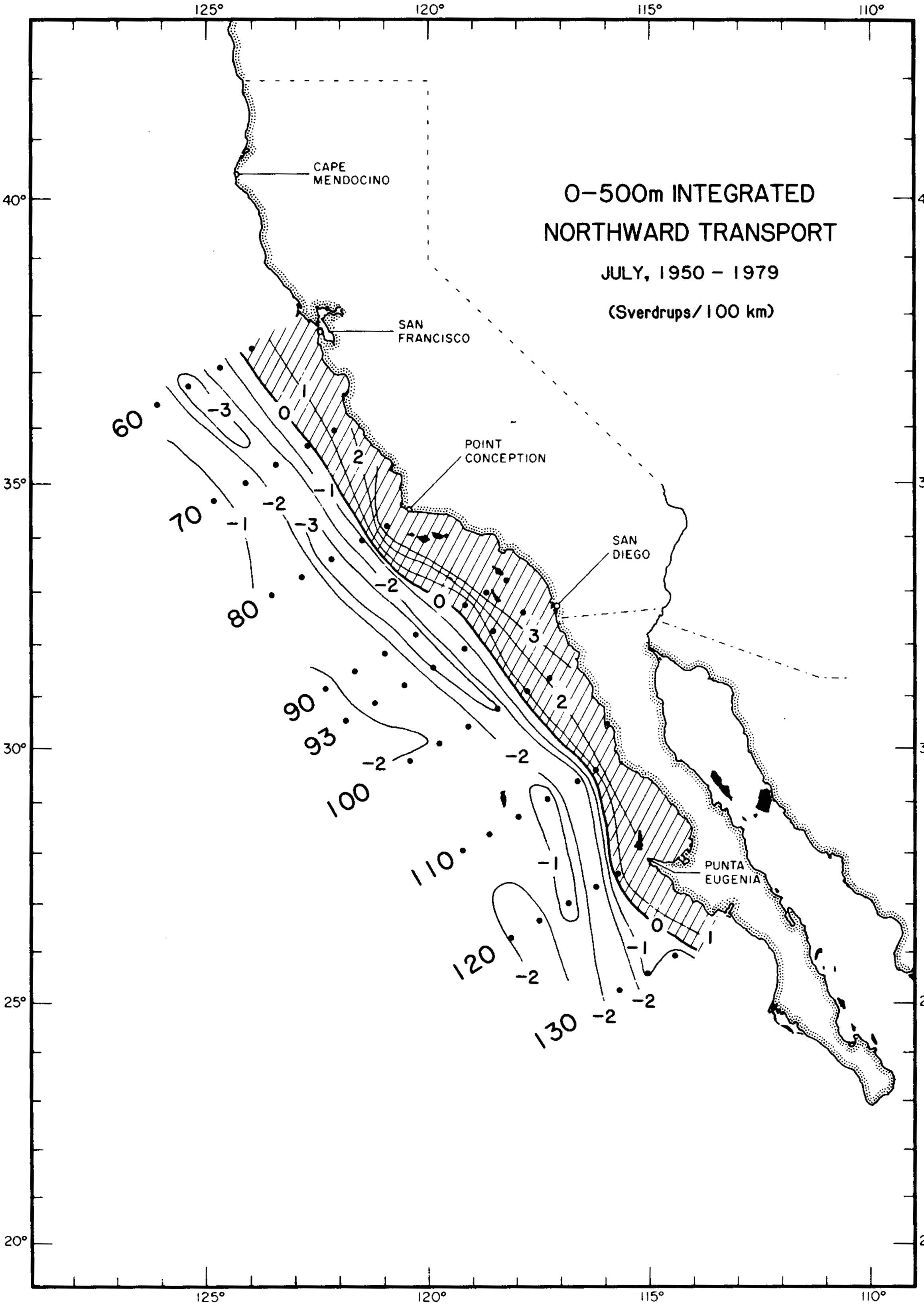


Figure 2. Seasonal average longshore integrated geostrophic transport in the upper 500 m in the California Current for July. Transport was calculated from geostrophic velocities relative to a reference level of 500 db (dots show location of stations used to draw contours, and the CalCOFI line numbers are labeled). Shaded region represents poleward transport. These seasonal mean values were determined by the harmonic method, which fits the full 30-year time series at each grid location to two harmonics (one with an annual and the other a semiannual period) by least squares regression.

farther offshore is equatorward. The flow in the region of maximum zooplankton biomass is very weak. This "recirculation" area would thus provide a very stable environment with little tendency to disperse the zooplankton populations.

The relation between zooplankton biomass and the transport of the California Current is shown in detail in Figure 3 for each of the CalCOFI cardinal lines from 60 to 120. For lines 60 through 90, the peaks in zooplankton volume are all located approximately 50-150 km offshore. In all cases, this very nearly coincides with the location of flow reversal as determined from the integrated transport in the upper 500 m. (The zooplankton maximum is located somewhat inshore of the flow reversal along line 70, but this may be attributable to the different methods used to compute the seasonal means; namely, long-term averaging for zooplankton and harmonic analysis for geostrophic transport.) For lines 100 through 120, the zooplankton biomass is maximum immediately adjacent to the coast, even though there is still a region of flow reversal 50-100 km offshore. Zooplankton productivity is apparently controlled by a different physical process in this southern region (perhaps coastal upwelling as opposed to the offshore upwelling that will be discussed for the northern area).

It should be emphasized at the outset that the analysis described here restricts attention to the physical characteristics of the California Current. Speculations about the possible biological response expected to be associated with the observed physical variability will be discussed. The validity of the proposed biological-physical connection could be easily tested from the 30-year CalCOFI record of zooplankton biomass.

The nearshore counterflow is a prevalent feature of the California Current system. The seasonal mean steric heights of the sea surface relative to 500 db for the months of January, April, July, and October are shown in Figure 4. Since gradients of steric height are proportional to the strength of the geostrophic flow, the steric height contours can be used to infer relative velocity. The nearshore surface counterflow is always present inside the Southern California Bight and present everywhere north of central Baja California during the fall and winter. (When it appears north of Point Conception, the nearshore counterflow is generally called the Davidson Countercurrent.) This feature exists year-round as a relatively steady "undercurrent" in the deeper water throughout the California Current as shown by the seasonal mean steric heights of the 200-db surface relative to 500 db in Figure 5.

Thus, the flow of the California Current can be characterized as a superposition of two "modes" of variability. One consists of a nearshore poleward counterflow extending from the surface down to at least 500 m and an equatorward flow from the surface to at least 500 m in the region offshore. This first

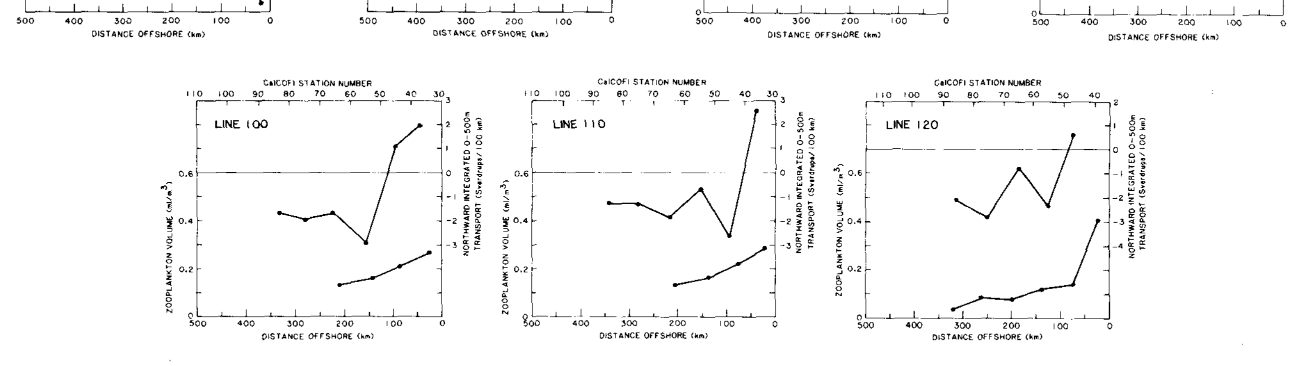


Figure 3. Cross sections of 0-500 m July seasonal average longshore integrated geostrophic transport (upper curves) and April-August average zooplankton displacement volumes (lower curves) for each of the CalCOFI cardinal lines from 60 to 120 (see Figure 2 for locations). Zooplankton averages were computed over 120-km-by-65-km pooled areas (see Smith 1971).

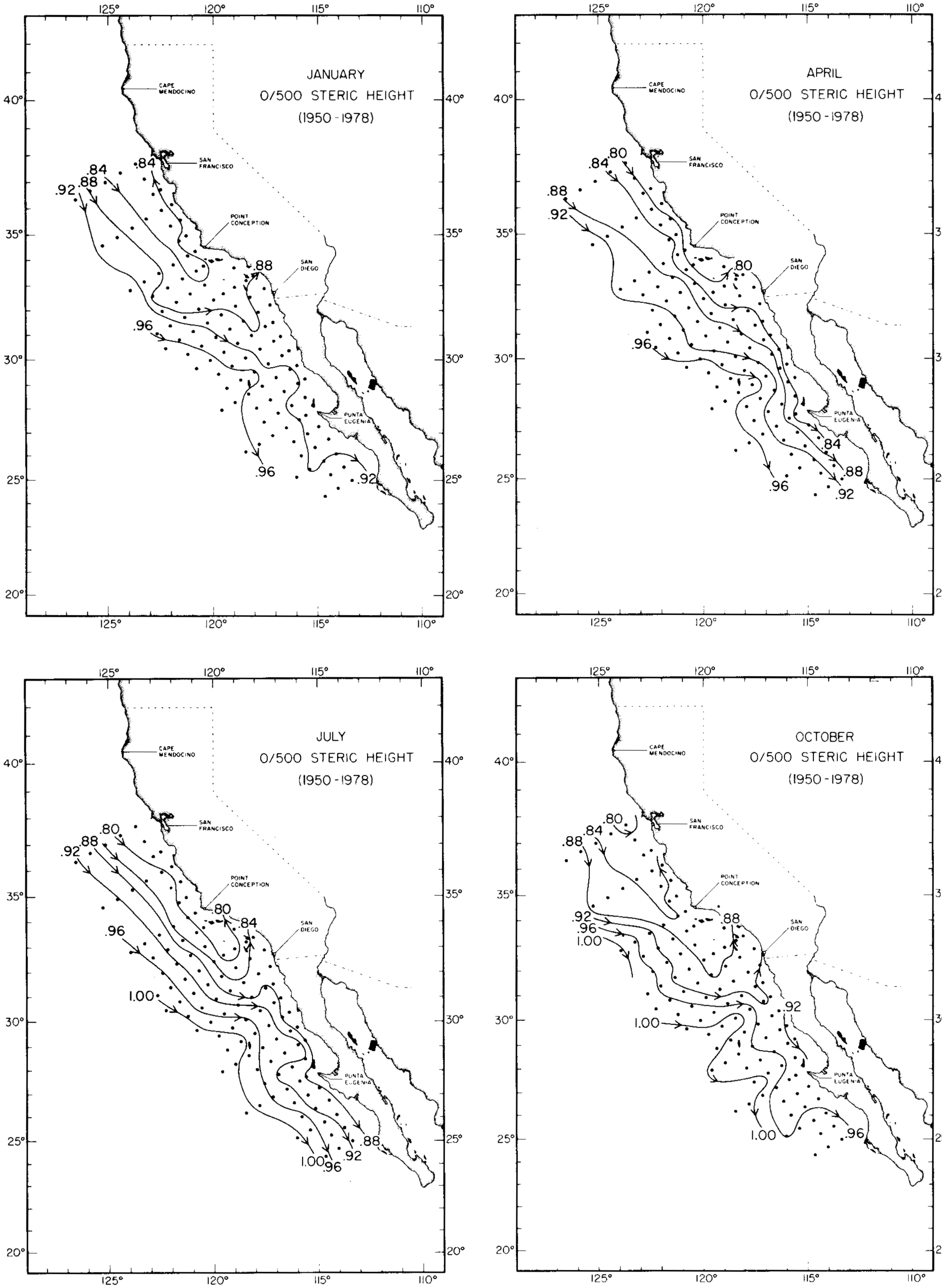


Figure 4. January, April, July, and October seasonal mean values of the steric height of the sea surface relative to 500 db. Arrows on contours indicate direction of geostrophic flow (computed from gradients of the steric height). Averages were computed over the 30-year period from 1950-80 using harmonic analysis as described in Figure 2.

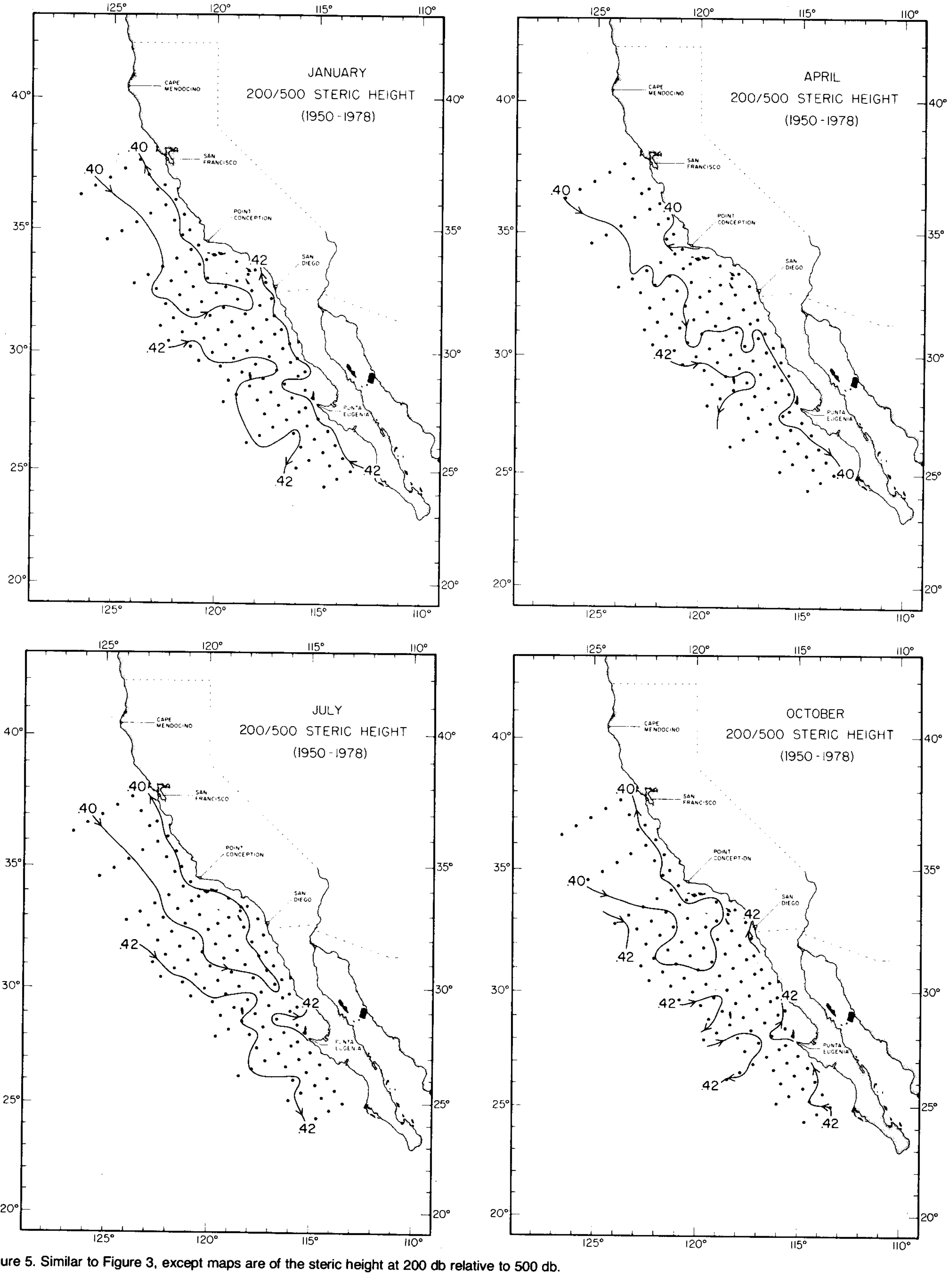


Figure 5. Similar to Figure 3, except maps are of the steric height at 200 db relative to 500 db.

mode varies only weakly over the seasonal cycle. The second mode consists of a shallow equatorward near-surface flow everywhere, with strong seasonal variability. When this second mode is weak (late fall and early winter) the nearshore counterflow associated with the first mode is evident everywhere from the surface to 500 m. However, when the second mode is strong (late spring and early summer) the nearshore counterflow associated with the first mode is reduced (or disappears altogether) near the surface. At these times the counterflow is evident only as a deep undercurrent.

A look at what a nearshore-offshore surface flow reversal means in terms of thermocline depth discloses a second important biological implication of this feature. A schematic diagram for a simple two-layer system is shown in Figure 6. For a nearshore surface poleward geostrophic flow, the sea surface must slope downward *away* from the coast. Correspondingly, an equatorward surface geostrophic flow in the region offshore requires a sea-surface slope downward *toward* the coast. The sea-surface height is minimum in the middle region where the flow is weak. If the flow in the deeper layer is zero or weak relative to the near-surface flow, then the offshore trough in sea level must be compensated by an offshore doming of the thermocline. Thus, in this simplified two-layer model, the region of flow reversal corresponds to a region of maximum vertical displacement (upwelling) of deep-water isotherms (and hence, nutrients). The deep-water nutrients supplied to the surface layer by this mechanism would result in high primary productivity, which would then lead to the observed high zooplankton abundance in this region (Figure 1).

Sections of temperature across the California Current verify the thermocline behavior suggested from the simple two-layer model (Figure 7). The upward doming of deep-water isotherms offshore is present year-round (with some seasonal variation) throughout the California Current. It should be emphasized that the upwelling discussed here is *not* directly a coastal boundary phenomenon. Coastal upwelling from the longshore wind stress is only a nearshore process restricted to within 20-50 km of the coast (Yoshida 1955; Allen 1973; Gill and Clarke 1974). This coastal-boundary-related upwelling is evident in Figure 7 as rising isotherms at the nearest inshore stations. The upwelling region emphasized in this study is located about 100-150 km offshore.

The section of nutrient concentrations along line 90 shown in Figure 8 indicates that this offshore upwelling is indeed an important source of nutrients to the euphotic zone (evident by the upward doming of nutrient contours about 100-200 km offshore). Measurements of nutrients are inadequate to construct long-term average distributions throughout the California Current. However, the 0-50-m integrated nitrate shown in Figure 9 indicates that the offshore nutrient enrichment was present everywhere north of northern Baja California during August-September 1969.

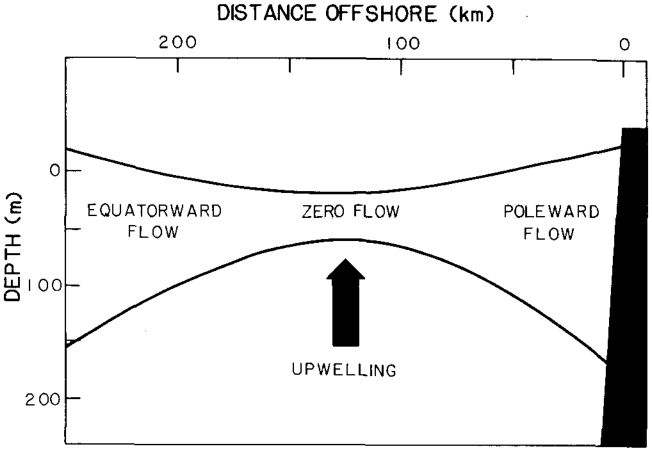
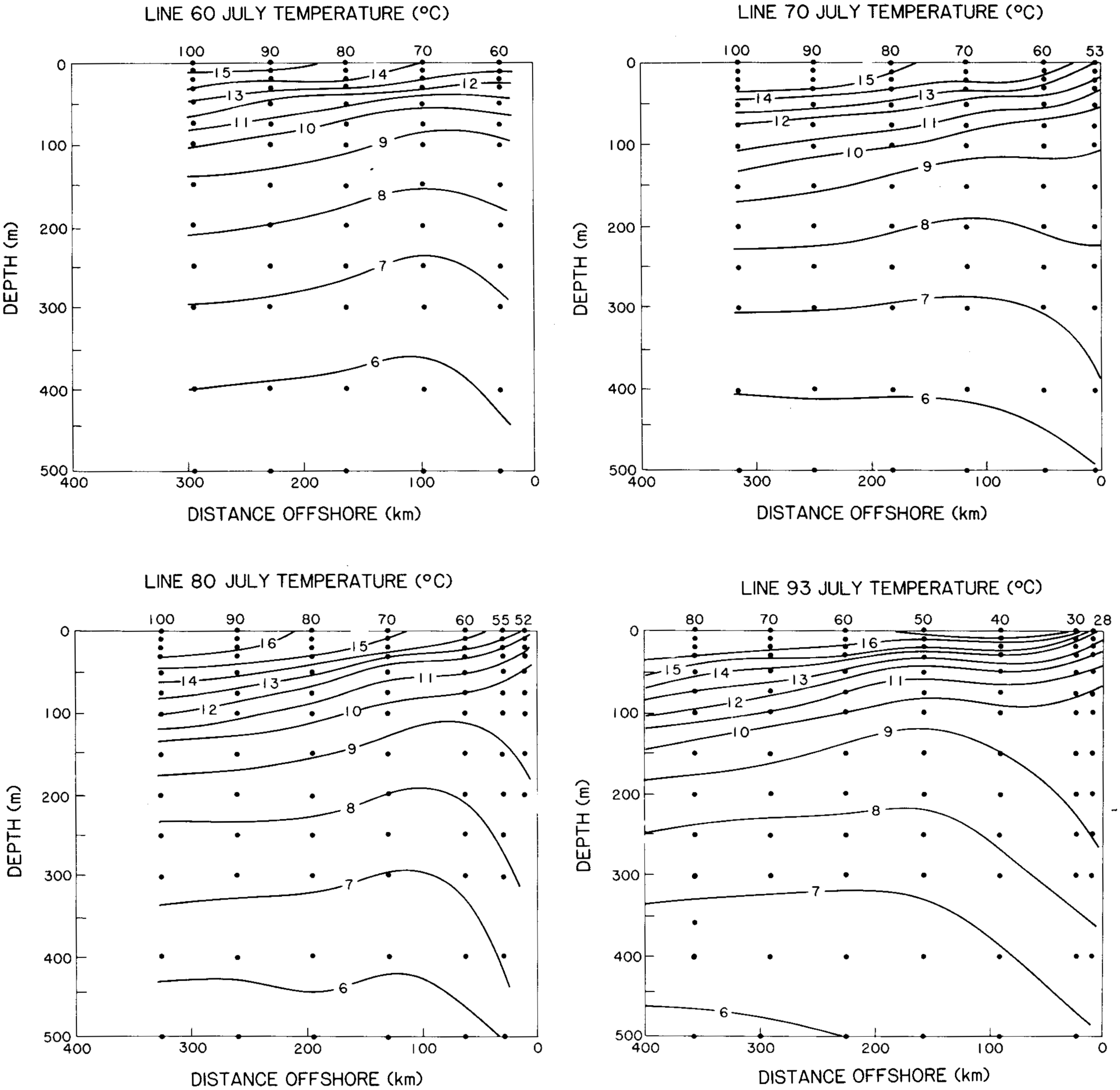


Figure 6. Schematic diagram of two-layer system showing the sea-surface and thermocline configuration corresponding to an equatorward flow offshore and a nearshore poleward flow.

Satellite chlorophyll images provide additional evidence for the existence of an offshore enrichment of nutrients. In addition to the coastally trapped high chlorophyll concentrations discussed previously, the CZCS images often show regions of high chlorophyll concentrations approximately 100-150 km offshore (see, for example, Smith and Baker 1982). These features are commonly referred to as "plumes," since they sometimes appear to extend offshore from Point Conception or other points farther north. This term is somewhat misleading because it implies that the high phytoplankton biomass is due to nutrients advected downstream from a source at the coast. Since these plumes of chlorophyll often extend several hundred kilometers, the supply of nutrients at a single upstream coastal source would have to be enormous. It seems more likely that the entire plume is a continuous source of nutrients brought to the sea surface by non-coastal upwelling.

A SEARCH FOR THE CAUSE OF THE NEARSHORE COUNTERFLOW

In the preceding section it was suggested that the offshore peak in zooplankton abundance in Figure 1 may be related to the upwelling of deep-water isotherms and nutrients associated with a nearshore counterflow. But what is the cause of this counterflow? It cannot be driven by the longshore wind stress itself because the prevailing winds over the



LINE 60 JULY TEMPERATURE (°C)

LINE 70 JULY TEMPERATURE (°C)

LINE 80 JULY TEMPERATURE (°C)

LINE 93 JULY TEMPERATURE (°C)

Figure 7. Average July temperature sections along CalCOFI lines 60, 70, 80, and 93 (see Figure 2 for locations) computed by the harmonic method (see text) over the 30-year period 1950-79. CalCOFI station numbers are shown along the top of each plot.

California Current are equatorward year-round south of San Francisco. So the counterflow, when it is present, is in opposition to the overlying winds.

It has long been recognized that the generally equatorward longshore winds over the California Current reach their maximum speed some distance offshore. This "jet" of winds results in a change in sign of the wind stress curl: inshore of the jet, the wind stress curl is positive, while farther offshore it is negative (as it is over most of the interior Pacific Ocean). These features are clearly evident in the seasonal mean wind stress curl maps shown in Nelson (1977) and Chelton (1980). The spatial resolution of existing historical data is too coarse to resolve the detailed characteristics of the wind field in this region. However, it appears that the boundary where the wind stress curl changes sign is roughly parallel to the coast and located somewhere between 200 and 400 km

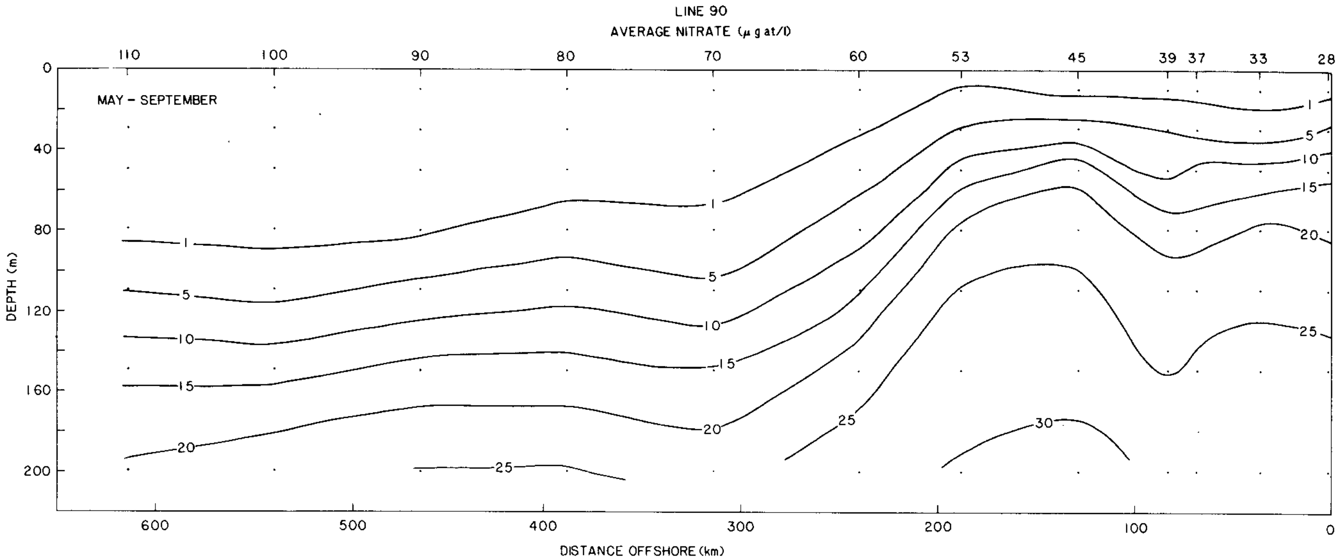


Figure 8. Spring-summer vertical distribution of nitrate along CalCOFI line 90. Data taken from 1969, 1972, and 1978.

offshore. The curl magnitude deduced from these coarse-resolution winds is largest immediately adjacent to the coast.

This nearshore positive wind stress curl makes the dynamics of the California Current system very interesting. If we denote the northward water velocity by v, the depth by z, the characteristic water density by ρ, the vector wind stress by $\vec{\tau}$ (with northward and eastward components τ_y and τ_x), and the Coriolis parameter by $f = 2\Omega\sin\theta$ (where Ω is the earth's rotation rate and the θ is the latitude), Sverdrup (1947) showed that the steady-state response to the wind stress curl is given by

$$\int_{-\infty}^{-0} v dz = \frac{1}{\rho\beta} \text{ curl } \vec{\tau} = \frac{1}{\rho\beta}\left(\frac{\partial \tau_y}{\partial x} - \frac{\partial \tau_x}{\partial y}\right).$$

Thus, because of the latitudinal variation of the Coriolis parameter $\beta = \frac{df}{dy}$, a positive wind stress curl leads to a poleward vertically integrated "Sverdrup transport." In the California Current, the nearshore positive wind stress curl would lead to a nearshore poleward water transport in opposition to the prevailing equatorward winds.

Munk (1950) used observations of winds over the California Current to show that the general character of the counterflow observed from hydrographic observations was consistent with the Sverdrup relation. This is also shown qualitatively in Figure 10 with more recent data. The upper panel shows the nearshore integrated transport in the upper 500 m at 36° N, 122° W. Except for April and May, when there is no net transport, the integrated transport is poleward all year with a maximum in November. This poleward transport appears to lag the wind stress curl (middle panel) by about 3-4 months and is in opposition to the consistently equatorward wind stress (lower panel).[2]

Yoshida and Mao (1957) later reexamined the wind-forced response of the California Current in somewhat greater detail. They pointed out that classical coastal upwelling is restricted to within a very narrow region close to the coast and that large-scale upwelling in the California Current must be driven by the wind stress curl. They also noted that the readjustment of the ocean to seasonally changing wind stress curl forcing cannot occur instantly. (This may account for the 3-4-month lag between wind stress curl and maximum poleward transport evident in Figure 10.) Thus, the thermocline depth is related to the integral effect of the wind stress curl, or, equivalently, the time rate of change of the thermocline depth (upwelling) is related to the instantaneous wind stress curl. This dynamical balance is now referred to as "Ekman pumping" (c.f., Pedlosky 1979) and can be expressed in terms of the sea-surface elevation h by:

$$\frac{dh}{dt} = -\frac{1}{\rho f} \text{ curl } \vec{\tau}.$$

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[2] The wind stress and wind stress curl data used in this study were computed from quasi-geostrophic wind vector estimates by Fleet Numerical Oceanography Center (FNOC). The FNOC grid spacing is about 300 km at the latitudes examined in this study. A detailed description of the method used by FNOC to compute the wind stress and wind stress curl can be found in Caton et al. (1978). Values were computed at 6-hourly intervals and then averaged to form monthly means. These are the best measure of wind stress and wind stress curl presently available for examining variability over the time scales of interest in this study.

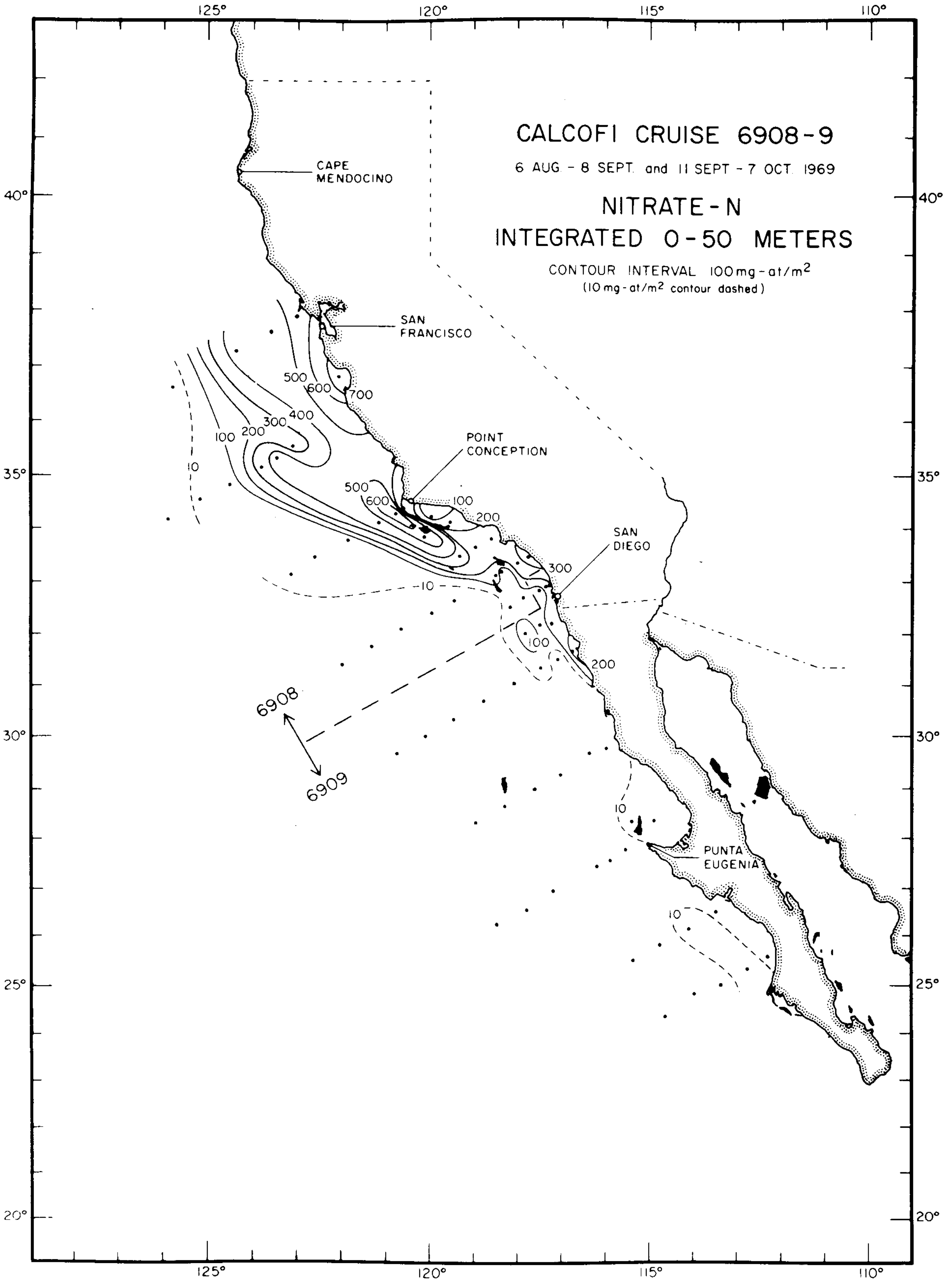

Figure 9. Horizontal distribution of 0-50-m integrated nitrate for CalCOFI cruises from August 6 to October 7, 1969 (from Thomas and Siebert 1974).

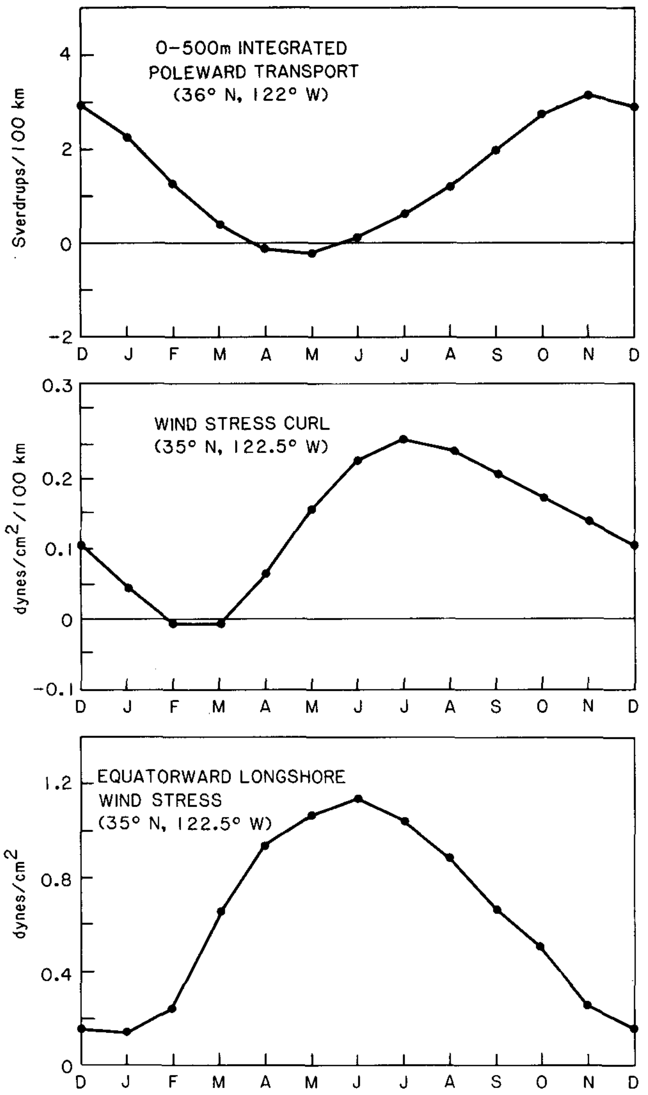

Figure 10. *Upper panel:* seasonal variation of the longshore integrated geostrophic transport in the upper 500 m (computed from geostrophic velocities relative to 500 db) between stations 55 and 60 along CalCOFI line 70 (located at 36°N, 122°W). Positive values correspond to poleward flow. *Middle panel:* seasonal variation of the wind stress curl at 35°N, 122.5°W. *Lower panel:* seasonal variation of equatorward longshore wind stress at 35°N, 122.5°W. Wind stress curl and wind stress data consist of FNOC quasi-geostrophic winds on a grid with approximately 600 km resolution (see text). These seasonal cycles were computed by the harmonic method discussed in Figure 2.

Thus, a positive wind stress curl causes a downward vertical velocity of the sea surface. This drop in sea level corresponds to a *rise* of the thermocline, i.e., a positive wind stress curl causes upward vertical velocity (upwelling) of the thermocline and a corresponding upwelling of deep-water nutrients.

It should be noted that, when the latitudinal variation of the Coriolis parameter is taken into account, the transient response to wind stress curl described by (2) generates westward-propagating Rossby waves, which ultimately bring the ocean into the steady-state Sverdrup balance (1). Since the phase speeds of Rossby waves are small (less than 10 cm/sec), the transient adjustment to changing wind stress curl would require a time scale of at least 2-3 months to bring the California Current into steady-state equilibrium.

STATISTICAL RELATIONSHIPS

The relationship between the wind stress curl and the countercurrent suggested qualitatively above cannot be examined quantitatively from the seasonal cycles. The reason for this is that nearly all geophysical quantities show a strong seasonal variation, and any two seasonal cycles are likely to be highly correlated if one allows for a phase lag. However, the statistical reliability of any resulting high correlation is very low. Chelton (in press) gives examples of how this can lead to erroneous conclusions about cause and effect.

Briefly, the presence of any narrow band signal (annual cycle, semiannual cycle, tidal cycle, etc.) reduces the effective number of degrees of freedom or independent realizations in a time series. A purely random, white-noise time series with N sample observations contains N degrees of freedom. At the other extreme, a pure-tone harmonic time series contains only 2 degrees of freedom, no matter how long the record length is or how frequently the harmonic signal is sampled. Since seasonal variability generally consists of two harmonics, one with an annual and the other with a semiannual period, the seasonal cycle contains, at most, only 4 degrees of freedom. Thus, the statistical significance of any correlation estimated from seasonal cycles is necessarily very low.

Therefore, to statistically explore cause and effect relationships between any two time series, it is essential to first remove the seasonal cycle, thereby increasing the effective number of independent observations in the sample records. Note that this does not remove any true physical relationship between the two time series. This is because the seasonal variation of a quantity is never a pure-tone harmonic. For example, the summer maximum wind stress curl over the California Current appears earlier or later than "normal" in some years or is stronger or weaker than "normal" during some months. If a connection between the wind stress curl and a nearshore countercurrent suggested from seasonal cycles is valid, the countercurrent should similarly appear early or late, strong or weak.

Accordingly, the seasonal cycles of the wind stress curl and the steric height of the sea surface relative to 500 db were removed from the data to produce time series of nonseasonal or anomalous variability. The CalCOFI grid points used in this analysis are shown by the dots in Figure 11 (these are the grid points occupied 40 or more times over the 30-year time period from 1950 to 1979).

The second analysis step was to extract the dominant recurring large-scale patterns of variability by computing the empirical orthogonal functions (EOFs) or principal components of nonseasonal 0/500 steric height and wind stress curl. A detailed description of this procedure and its implementation on the gappy CalCOFI hydrographic time series can be found in Chelton (1980). The principal EOF of 0/500 steric height, accounting for 31% of the overall variability, is examined in detail in Chelton (1981) and Chelton, Bernal, and McGowan (submitted). This is the mode of variability representing large-scale changes in the transport of the California Current that have been shown in the earlier studies to have an important influence on the large-scale biological variability in this region. Since it is unrelated to local wind forcing over the California Current, this pattern is not of interest to this study.

The second EOF of 0/500 steric height, accounting for 8% of the overall variability (or, equivalently, 12% of the residual variability not explained by the first EOF), is shown in Figure 11. The relatively small fraction of variability accounted for by this EOF reflects the presence of significant mesoscale energy contained in the higher order modes. This mesoscale variability is not adequately resolved (either spatially or temporally) by the CalCOFI sampling strategy, and can therefore be considered "noise" in the context of the present study. Thus, EOF analysis is a useful method for filtering this "noise" out of the data.

It can be seen from Figure 11 that this second EOF of anomalous 0/500 steric height resembles a nonseasonal analog of the seasonal California Current-Countercurrent system described earlier (with the region of flow reversal located somewhat farther offshore). The direction of geostrophic flow can be inferred from gradients of the steric height. When the time amplitude of this spatial pattern is positive, the flow in the offshore region is anomalously strong equatorward, and the nearshore flow is anomalously poleward. Correspondingly, a negative time amplitude indicates anomalous poleward flow in the region offshore, with anomalous equatorward flow nearshore. The trough (or ridge, if the sign of the time amplitude is negative) associated with these flow anomalies, shown by the dashed line in Figure 11, is located approximately 200-300 km offshore.

The time scales associated with this second EOF of nonseasonal 0/500 steric height can be determined from the autocorrelation plot in Figure 13. Typical time scales of steric height anomalies described by this pattern are around 5-6 months. This is similar to the seasonal time scales associated with an annual cycle, suggesting that this mode of variability may, indeed, represent nonseasonal (early, late, strong, or weak) variations in the seasonal countercurrent.

The hypothesis that the nearshore counterflow is forced by the wind stress curl can be examined by determining the relationship between the amplitude time series of this second EOF of anomalous 0/500 steric height and forcing by wind stress curl anomalies in this region. The most energetic aspects of large-scale wind stress curl forcing over the California Current can be described by the dominant EOF, shown in Figure 12. It is evident that the spatial resolution of these winds is very poor (the FNOC grid spacing is about 300 km at these latitudes). This coarse resolution is made even worse by the fact that the quasi-geostrophic wind stress at each grid point is determined using a differencing technique that computes pressure gradients across four grid points (a distance of about 1200 km). Then the curl of the wind stress is computed by again applying the same differencing method to the gridded wind stress values (see Caton et al. 1978 for a detailed description). Thus, the FNOC wind stress curl estimates represent only the very large-scale aspects of the wind field; spatial scales less than about 600 km are effectively filtered from the records. Even though any detailed spatial structure is obscured by this smoothing, it is still possible that the FNOC wind stress curl estimates may adequately resolve the principal time scales of the most energetic features in the wind field. The significant relation between steric height and wind stress curl demonstrated below supports this hypothesis.

In spite of the spatial smoothing, Figure 12 indicates that the first EOF of wind stress curl anomalies exhibits the general spatial characteristics desired for examining the relation between wind stress curl and anomalous nearshore countercurrents. (The correspondence between the detailed spatial structures of the steric height and wind stress curl EOFs is not as close as one would hope, but this may be due to the coarse spatial resolution of the wind data or the poor temporal resolution of the steric height data.) Wind stress curl anomalies associated with this pattern change sign some 500-600 km offshore. (Again, the sign reversal may actually occur closer to the coast, but it cannot be resolved with the coarse grid spacing of the smoothed FNOC data.) Positive time amplitudes associated with this spatial pattern correspond to anomalously high wind stress curl values nearshore. Correspondingly, negative time amplitudes refer to anomalously weak (or negative) nearshore wind stress curl. The ridge of maximum (or minimum, if the time

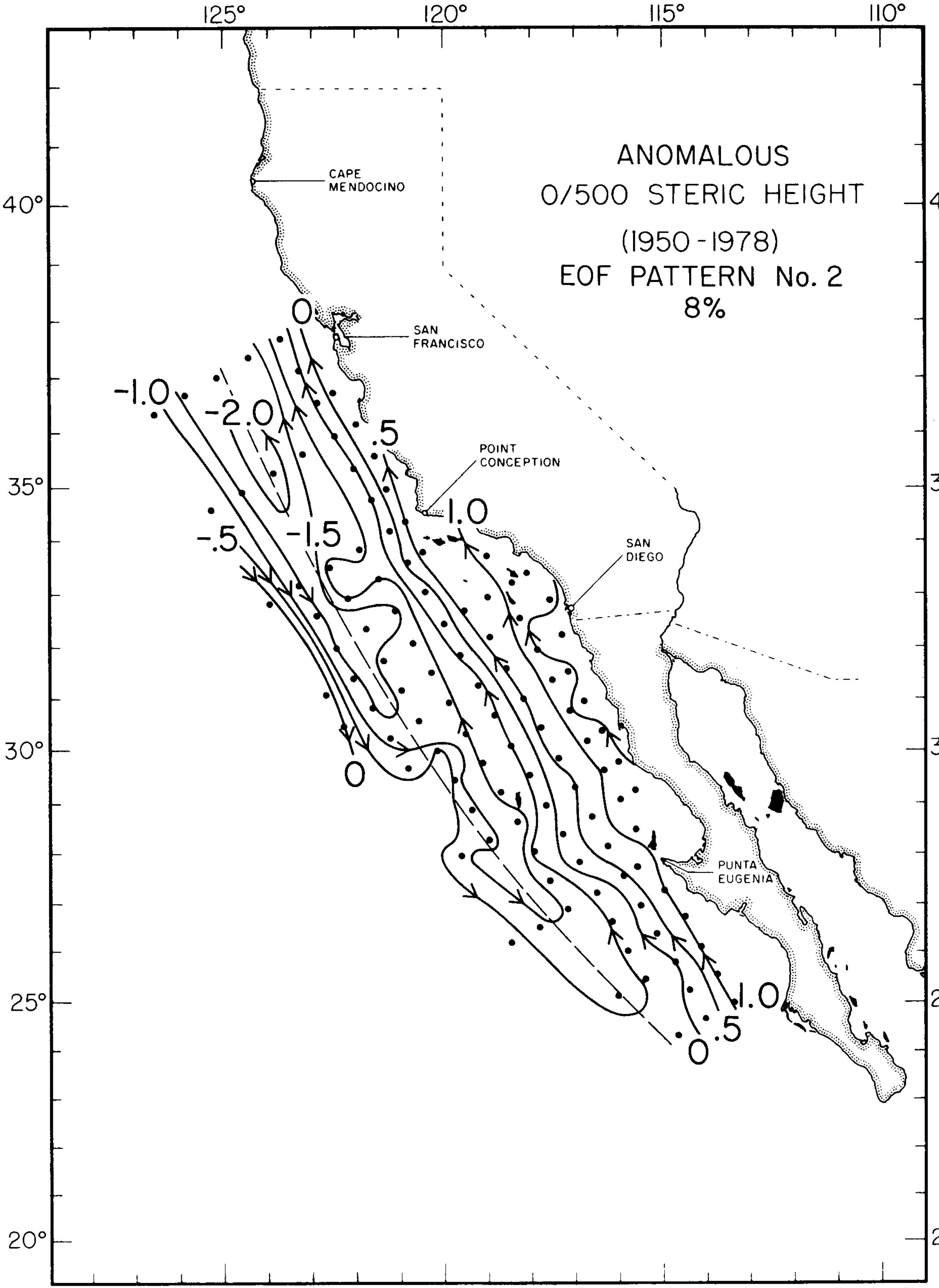

Figure 11. The second empirical orthogonal function (EOF) of nonseasonal 0/500 steric height. The seasonal means computed by the harmonic method (see Figure 4) have been removed. Dots correspond to locations of grid points over which the EOF was computed, and arrows indicate direction of geostrophic flow associated with the pattern when the time amplitude is positive.

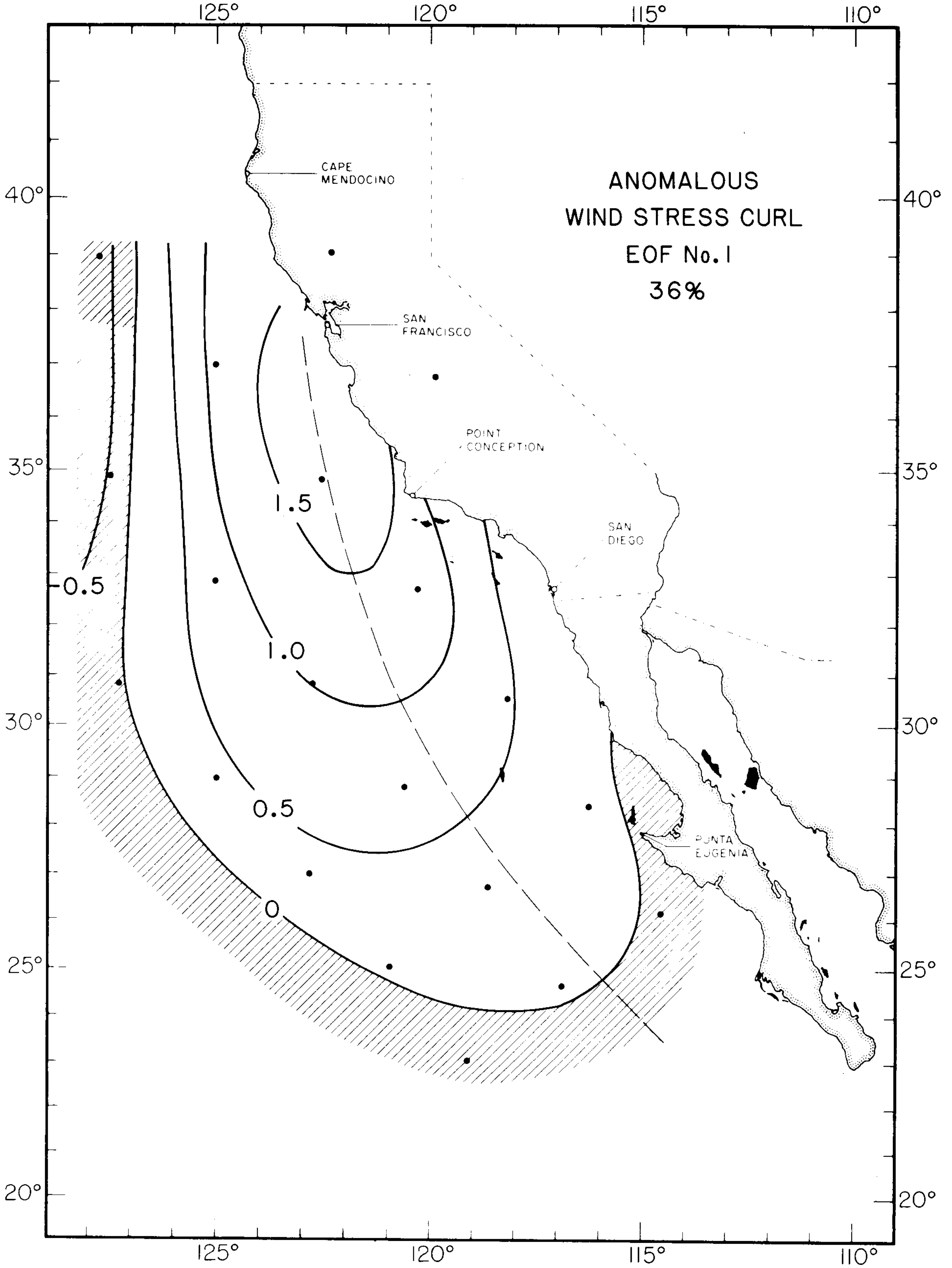

Figure 12. The first EOF of nonseasonal FNOC quasi-geostrophic wind stress curl. Again, the seasonal cycle was computed by the harmonic method and removed. Dots correspond to locations of FNOC grid points over which the EOF was computed.

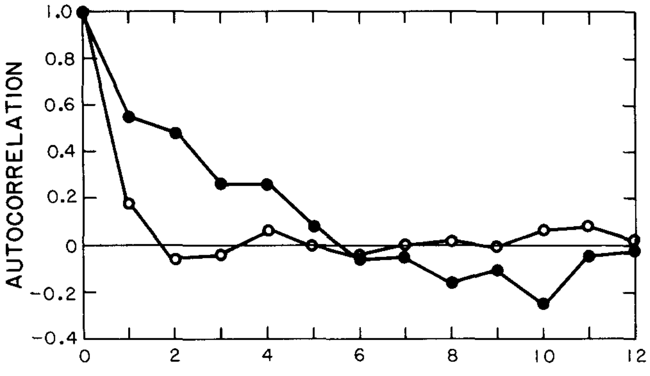

Figure 13. Autocorrelations of the amplitude time series of the second EOF of nonseasonal 0/500 steric height (solid circles) and the first EOF of nonseasonal wind stress curl (open circles).

amplitude of the pattern is negative) wind stress curl values, shown by the dashed line in Figure 12, is located 200-300 km offshore, roughly in the same location as the trough in anomalous steric height shown in Figure 11.

The time scales associated with this pattern of wind stress curl variability can be seen from Figure 13 to be very short (1-2 months). Thus, the amplitude time series of this first EOF of nonseasonal wind stress curl behaves approximately as a random, white-noise process. In view of these rapid month-to-month changes in the anomalous wind stress curl forcing, and the anticipated relatively sluggish transient adjustment of the ocean, the time-dependent Ekman pumping model (2) is likely to be a more appropriate dynamical balance than the steady-state Sverdrup balance (1).

This Ekman pumping model can be expressed in terms of centered finite differences of the amplitude time series of the steric height and wind stress curl by

$$h_2(t) - h_2(t-1) = -k \operatorname{curl} \vec{\tau}_1(t-½), \qquad (3)$$

where k is a constant, h_2 refers to the amplitude time series of the second EOF of steric height, and curl $\vec{\tau}_1$ refers to the amplitude time series of the first EOF of wind stress curl. The wind stress curl data was available from FNOC in the form of 10-day averages (which were, themselves, computed from 6-hourly values of the quasi-geostrophic wind stress curl). For the analysis here, the wind stress curl at time (t −½) was constructed by averaging the values from the last 20 days of month ($t-1$) and the first 20 days of month t. Thus, for example, the change of the time amplitude of the second EOF of steric height from January to February was compared with the wind stress curl averaged over the last 20 days of January and the first 20 days of February. These comparisons were made for each month when the time amplitude of the second EOF of steric height was available (a total of 90 months; see Appendix). The results were used to compute the correlation between month-to-month changes in the amplitude time series of the second EOF of steric height and the ½-month shifted-amplitude time series of the first EOF of wind stress curl. To check for the possibility of a lag in the relationship, $[h_2(t) - h_2(t-1)]$ was actually correlated with [curl $\vec{\tau}_1(t-½+T)$] for lags T ranging from −18 to 18 months. If the Ekman pumping model is valid, the only significant correlation should be at lag $T=0$.

The results are shown in Figure 14 in terms of the *skill* in estimating $\frac{dh_2}{dt}$ at time t from curl $\vec{\tau}_1$ at time $(t+T)$ (the skill is equivalent to the *squared* correlation; see, for example, Chelton, submitted[3]). The details of this skill calculation as it was applied to the gappy steric height time series are given in the Appendix. The results indicate that the only significant estimation skill indeed occurs at lag $T=0$, where the skill is 0.45 (equivalent to correlation of 0.67). This can be compared with a 95% significance skill level of 0.27 (computed as described in Chelton, submitted[3]). The positive correlation indicates that the response is as expected from the Ekman pumping model, i.e., a positive wind stress curl leads to poleward nearshore flow. This corresponds to a drop in offshore steric height and an upwelling of the thermocline offshore. (Note that the relatively large correlation at lag $T=-12$ months probably indicates the quasi-seasonality of the amplitude time series of the steric height pattern.)

This statistical result implies that, when the nearshore positive wind stress curl over the California

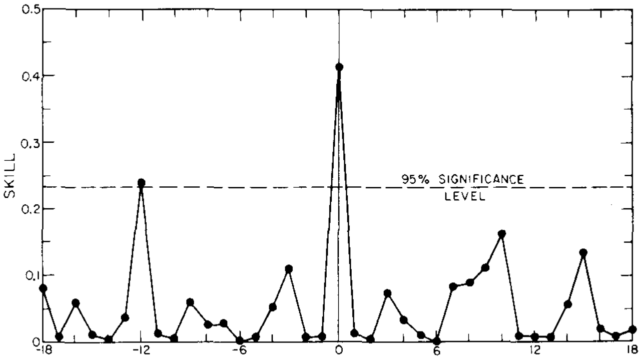

Figure 14. Skill in estimating $\frac{dh_2}{dt}$ at time t from curl $\vec{\tau}_1$ at time (t + lag), where h_2 refers to the amplitude time series of the second EOF of 0/500 steric height, and curl $\vec{\tau}_1$ refers to the amplitude time series of the first EOF of the wind stress curl. The quantities $\frac{dh_2}{dt}$ and curl $\vec{\tau}_1$ were approximated as centered finite differences by $[h_2(t) - h_2(t-1)]$ and curl $\vec{\tau}_1$ $(t-½)$, respectively. The 95% significance level of skill values is shown by the dashed line (computed as described in Chelton, submitted. See footnote 3.) Note that skill values are equivalent to the squared correlation.

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[3] Chelton, D.B. Effects of sampling errors on statistical estimation. Submitted paper.

Current is stronger than normal, the nearshore poleward counterflow is stronger than normal, and the drop in sea-surface elevation offshore (upwelling of the offshore thermocline) is greater than normal. When the nearshore positive wind stress curl is weaker than normal (or even reversed), the nearshore counterflow is correspondingly weak. In this case, the offshore sea-surface elevation is higher than normal, and the offshore thermocline is deeper than normal (upwelling is reduced).

SUMMARY AND CONCLUSIONS

The spring-summer distribution of zooplankton abundance in the California Current shown in Figures 1 and 3 reveals a somewhat surprising feature: the peak is located about 100 km offshore between San Francisco and northern Baja California. It seems unlikely that this offshore maximum is related to coastal upwelling driven by the longshore wind stress. Qualitative similarities with the seasonal nearshore counterflow and the associated offshore upwelling of the thermocline (and nutrients) suggest a possible physical-biological connection. This offshore upwelling could theoretically be forced by the unique wind stress curl conditions found to exist over the California Current. (It should be noted that similar meteorological conditions prevail over all eastern boundary currents, e.g. the Peru, Benguela, and Canary currents. Therefore, the results derived here for the California Current may be applicable to other eastern boundary currents as well.)

Although the nearshore counterflow could potentially be generated by other mechanisms (e.g., topographic steering in the Southern California Bight region), the mechanism proposed here has been demonstrated to be statistically consistent with temporal variations in the counterflow. That is, when the wind stress curl weakens, so does the nearshore counterflow. The region of offshore zooplankton maximum (San Francisco to northern Baja California) coincides with the region where the nearshore positive wind stress curl is strongest, both seasonally (see Nelson 1977; Chelton 1980) and nonseasonally (see Figure 12). To the south, where the wind stress curl is much weaker, the zooplankton maximum is located immediately adjacent to the coast.

It was emphasized that quantitative statistical examination of the relationship between the wind stress curl and the nearshore counterflow is not possible from the seasonal cycles because of the small number of degrees of freedom associated with this narrow-band process. To maximize statistical reliability, the time series must be seasonally corrected. Nonseasonal (anomalous) wind stress curl and steric height fluctuations reveal patterns analogous to their seasonal counterparts (Figures 11 and 12). These patterns can be used to statistically investigate the relationship between offshore upwelling and forcing by the wind stress curl.

From the statistical analysis of the seasonally corrected time series associated with these patterns, it is concluded that the second EOF of 0/500 steric height shown in Figure 11 resembles an Ekman pumping response to forcing by the first EOF of wind stress curl shown in Figure 12. An anomalously positive wind stress curl over the California Current generates an anomalous nearshore counterflow and upwelling of the thermocline in a region roughly parallel to the coast approximately 200-300 km offshore (coincident with the nonseasonal steric height trough in Figure 11). This large-scale upwelling is quite distinct from classical coastal upwelling, which is driven by the longshore wind stress and is limited to a region within 20-50 km of the coast. (Note that the offshore upwelling could be considered indirectly coastally related in the sense that the nearshore positive wind stress curl is ''anchored'' to the coast by the prevailing meteorological conditions in this region. However, the divergence of surface water responsible for the offshore upwelling is induced by horizontal shears in the long shore wind stress rather than by the discontinuity introduced by the presence of a coastal boundary.)

Although it has not been quantitatively examined in this study, it is anticipated that this Ekman pumping mechanism will prove to have important biological significance. The offshore upwelling of the thermocline provides a source of nutrients into the euphotic zone (see Figures 8 and 9) that would lead to increased productivity at all levels of the food chain. This mechanism may be responsible for the offshore peak in seasonal zooplankton abundance shown in Figures 1 and 3. In addition, the weak flow or recirculation associated with the flow reversal in the region of offshore upwelling would have little tendency to disperse the zooplankton populations, thus maintaining the high biomass. Efforts are presently under way to generate gridded time series of nonseasonal (anomalous) zooplankton biomass from the CalCOFI data. The resulting data set will allow quantitative statistical examination of the relation between the strength of the nearshore counterflow and fluctuations in zooplankton abundance.

If the hypothesis that wind stress curl-induced offshore upwelling is responsible for the offshore peak in zooplankton volume is true, then not only is coastal upwelling unimportant to the dominant large-scale variability of zooplankton abundance as demonstrated in earlier studies by Bernal, Chelton, and McGowan, but it is also not of secondary importance (at least over the large spatial scales considered here). This would indicate that coastal upwelling effects on biological variability must be only of very localized importance (both spatially and temporally).

ACKNOWLEDGMENTS

I would like to acknowledge that the analysis described here was made possible only through the persistent and dedicated efforts of CalCOFI in collecting and archiving the 18,000 hydrocasts used to construct the 30-year time series of steric height examined in this study. Together with the 25,000 zooplankton net tows collected by CalCOFI since 1950, the CalCOFI data base is unique in its ability to study large-scale, long-term physical and biological variability. The potential for statistical examination of physical and biological interaction from this valuable data base has only begun to be exploited.

Larry Eber kindly made the CalCOFI hydrographic data available in well-organized and compacted form, and Andrew Bakun provided the FNOC wind stress curl data used in this study. John McGowan provided the station seasonal zooplankton averages from which the "pooled area" spring-summer zooplankton volumes in Figures 1 and 3 were computed. Finally, I would like to thank Joseph Reid for his continued support and encouragement during analysis of the CalCOFI data.

This work was carried out at the Jet Propulsion Laboratory, California Institute of Technology, under contract with the National Aeronautics and Space Administration.

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APPENDIX

Computation of the correlation between time derivatives of the steric height and the wind stress curl is hindered by the fact that the steric height time series is gappy. This gappiness in both space and time required special techniques for generating the amplitude time series of the empirical orthogonal functions (EOFs). Computation of the time amplitude for a given month requires data values for that month at each of the N grid points used to generate the EOF. Since there were no months when all 150 of the grid points shown in Figure 11 were occupied, a technique for objectively estimating the EOF time amplitudes from the existing data values was required. The method developed by Davis (1976) was used, and the details are described in Chelton (1980). Objectively estimated time amplitudes for months with expected square errors exceeding 30% of the variance associated with the EOF were rejected, so that the time amplitudes for those months were considered "missing." For the time amplitudes of the second EOF of 0/500 steric height, this objective estimation scheme produced 90 months of "acceptable" data.

For ease of notation, define

$$H(t) = h_2(t) - h_2(t-1)$$
$$X(t) = \text{curl } \vec{\tau}_1(t-½),$$

where h_2 is the amplitude time series of the second EOF of steric height, and curl $\vec{\tau}_1$ is the amplitude time series of the first EOF of wind stress curl. Then the centered difference Ekman pumping model (3) reduces to

$$H(t) = -k\, X(t). \tag{4}$$

The most obvious method of examining this model statistically is to compute the time series $H(t)$ and $X(t)$ and simply correlate them. Using $< >$ to denote the expected or mean value, this correlation is given by

$$R_{HX} = \frac{<H(t)\, X(t)>}{[<H^2(t)> <X^2(t)>]^{½}} \tag{5}$$

However, although the number of sample values of $h_2(t)$ was 90, there were only 40 months t when both $h_2(t)$ and $h_2(t-1)$ existed, i.e. 40 values of $H(t)$. Then the correlation computed by (5) would be based on only 40 data values resulting in very low statistical reliability of the correlation estimate.

Therefore, an alternative method was developed; it involves computing the *statistics* of $H(t)$ rather than $H(t)$ itself. To see how this is done, substitute $[h_2(t) - h_2(t-1)]$ for $H(t)$ in (5) to get

$$R_{HX} = \frac{<h_2(t)\, X(t)> - <h_2(t-1)\, X(t)>}{2^{½}[(<h_2^2(t)> - <h_2(t)\, h_2(t-1)>) <X^2(t)>]^{½}} \tag{6}$$

In this last expression, the steric height EOF time series $h_2(t)$ has been assumed to be stationary. Since the wind stress curl time series $X(t)$ is complete, and only $h_2(t)$ is gappy, with the exception of the term $<h_2(t)\, h_2(t-1)>$, all of the statistical quantities in (6) can be estimated from all 90 months t when $h_2(t)$ exists: $<h_2(t)\, h_2(t-1)>$ must be estimated from only the 40 months when both $h_2(t)$ and $h_2(t-1)$ exist. Consequently, the statistical reliability of this quantity is lower than that of the others. However, since $<h_2(t)\, h_2(t-1)>$ is only about half as large as $<h_2^2(t)>$ (see Figure 13), the sensitivity of (6) to errors in this term is relatively small. Thus, use of (6) to compute the correlation between $H(t)$ and $X(t)$ is more reliable than first computing $H(t)$ and correlating the resulting time series with $X(t)$ as in (5).

In computing the correlation between $H(t)$ and $X(t)$, the model (4) was generalized to allow for the possibility of a lagged relationship:

$$H(t) = -k\, X(t+T)$$

where $X(t+T) = \text{curl } \vec{\tau}_1(t-½+T)$. The skill in estimating $H(T)$ from $X(t+T)$ is equal to the square of the correlation as computed by (6) [with $X(t)$ replaced by $X(t+T)$]. These skill values are plotted in Figure 14 for lags T ranging from -18 to 18 months.

HORIZONTAL TRANSPORT OF PHOSPHORUS IN THE CALIFORNIA CURRENT

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ABSTRACT

Horizontal transport of phosphorus (inorganic dissolved PO_4 and zooplankton P) to a depth of 200 m through an area of about 4.2 x 10^5 km^2 off California and Baja California has been calculated for four winter and six summer months of different years. Large seasonal and interannual variations occur in transport across CalCOFI lines 70, 80, and 110, and in the net P budget for the area. These variations are due to long-term changes in strength of the California Current and to small-scale, short-term variability caused by mesoscale turbulence and eddies. There is no correlation between upwelling indices and net P transport across lines by month. Mean summer and winter P transports were also calculated using CalCOFI PO_4 and geostrophic flow data from 1950 to 1978. The long-term mean transports for the area show a net export of about 300 g-at P/sec during winter and a net import of about 400 g-at P/sec during summer. This seasonal difference is probably due to (1) greater southward advection in summer and (2) higher mean phosphate concentrations throughout the area at all depths (0-200 m) during summer. Zooplankton contributes a mean of about 4 percent of the total P transports and budgets.

RESUMEN

Se calculó el transporte horizontal de fósforo (PO_4 inorgánico disuelto y zooplancton P) hasta una profundidad de 200 m por un área de aproximadamente 4.2 x 10^5 km^2, frente a California y Baja California, para cuatro meses de invierno y seis de verano de diferentes años. Ocurren grandes variaciones estacionales e interanuales en el transporte a través de las líneas 70, 80 y 110 de CalCOFI, así como en el presupuesto neto de P para este área. Estas variaciones se deben a cambios de largo período en la fuerza de la Corriente de California y también se deben a la variabilidad de pequeña escala y de corto período causada por turbulencia y remolinos de grande escala. No existe una correlación a través de las líneas entre índices de surgencia y el transporte P neto por mes. También se calculó el transporte P medio de verano y de invierno usando los datos CalCOFI de PO_4 y flujo geostrófico desde 1950 hasta 1978. El transporte medio de largo período para el área presenta una exportación neta de aproximadamente 300 g-at P/seg. durante invierno y una importación neta de aproximadamente 400 g-at P/seg. durante el verano. Esta diferencia estacional probablemente se debe a: (1) mayor advección hacia el sur en verano y (2) concentraciones fosfáticas medias más altas por todo el área y a todas profundidades (0-200 m) durante el verano. El zooplancton contribuye un medio de 4 por ciento del total de transportes P y presupuestos.

INTRODUCTION

The California Current off California, like most equatorward-flowing eastern boundary currents, has generally high primary productivity and high standing stocks of phytoplankton, zooplankton, and fish (Wooster and Reid 1963; Barber and Smith 1981). It is about 1000 km wide (Hickey 1979), with a gradient (increasing shoreward) of productivity and standing crop (Smith 1971; Owen 1974; Bernal and McGowan 1981) that begins about 500 km offshore and extends to, or near, the coast. Two important processes supporting this production are (1) advection of nutrient-rich water from the north, where nutrient concentrations throughout the water column are higher, and (2) coastal upwelling of nutrient-rich water.

Coastal upwelling drives a large part of seasonal variations in coastal production. Some of this production can be advected offshore a few hundred km in highly localized, ephemeral plumes (e.g., Traganza and Conrad 1981), but most effects probably do not extend much beyond 50 to 75 km offshore (Barber and Smith 1981). Long-term (interannual) variations in zooplankton biomass occur, however, from the coast out to about 500 km between Pt. Reyes and Cabo San Lazaro, an area of about 6.6 x 10^5 km^2 (Bernal 1979, 1981). These variations have little or no relationship to indices of upwelling (Bakun 1973; Chelton 1981); rather, they appear related to measures of advective strength of the California Current (Bernal and McGowan 1981; Chelton 1981). Bernal and McGowan argue that variations in zooplankton stocks off California and Baja California are due to fluctuations in abundances of species occurring only in those areas, hence the variations cannot be due solely to advection of northern stocks. They must result from variations in

[Manuscript received January 28, 1982.]

the area's underlying primary productivity. Productivity depends in part on available supplies of preformed nutrients, hence variations in advection of these nutrients from the north are probably responsible for part of the changes in zooplankton abundance. Here we attempt to quantify advection of the important plant nutrient phosphorus (P) into and out of a large region of the California Current (Figure 1).

METHODS

We used 1950-78 California Cooperative Oceanic Fisheries Investigations (CalCOFI) data (Table 1) on temperature, salinity, phosphate (PO_4), and zooplankton abundance. PO_4 was the nutrient most frequently sampled in both time and space.

The region analyzed (Figure 1: about 4.2 x 10^5 km^2) includes CalCOFI cardinal lines 70, 80, and 110, all out to station 90. Selection of these lines was based upon frequency of sampling and proximity to points for which Bakun (1973) calculated indices of upwelling derived from wind-stress (Figure 1). This latter criterion allowed us to compare variations in P transport across these lines with variations of upwelling indices. We investigated seasonal effects, considering cruises in December (month 12), January (01), and February (02) as "winter," and June (06), July (07), and August (08) as "summer."

Our transport calculations cover 0-200 m (*re.* 500 db) because of (1) data availability (PO_4 data from most CalCOFI cruises [Table 1] extend to at least 200 m); (2) the region's euphotic zone is always <<200 m (Owen 1974); and (3) 200 m is well into the thermocline and below the mixed layer during all seasons (Wyllie and Lynn 1971).

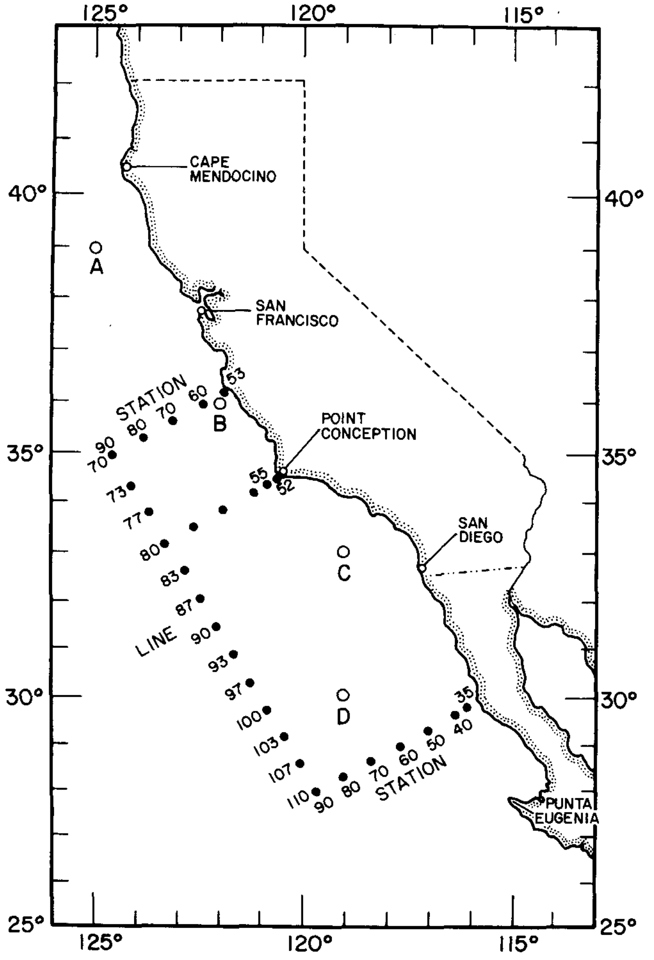

Figure 1. Region of the California Current for which phosphorus budgets were computed from transport across lines 70, 110, and the western edge (stations 90). Letters designate points for which Bakun (1973) calculated upwelling indices.

TABLE 1
CalCOFI Cruises Used for the Analysis of Horizontal Phosphorus Transport

5002*	(SIO**, 1960a)	6401[c]	(SIO, 1965a)	7008	(SIO, 1980b)
5007	(SIO, 1960a)	6407	(SIO, 1966)	7102	(SIO, 1980b)
5008	(SIO, 1960a)	6501	(SIO, 1965b)	7201	(SIO, 1980c)
5102[a]	(SIO, 1963a)	6507	(SIO, 1967)	7202	(SIO, 1980c)
5106[a]	(SIO, 1963a)	6806	(SIO, 1971)	7207	(SIO, unpublished data)
5107	(SIO, 1963a)	6901	(SIO, 1976)	7712	(SIO, unpublished data)
5108	(SIO, 1963a)	6902	(SIO, 1976)	7801	(SIO, unpublished data)
5112	(SIO, 1963a)	6906	(SIO, 1977)	7807	(SIO, unpublished data)
5508	(SIO, 1960b)	6907	(SIO, 1979)	7808	(SIO, unpublished data)
6107	(SIO, 1962)	6908[c]	(SIO, 1979)		
6301[b]	(SIO, 1963b)	6912	(SIO, 1980a)		

*First two digits = year, second two = month. Underlined cruises used to calculate individual cruise transport.
See Table 2 for limitations of these data sets.
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[a] Line 113
[b] PO_4 to 50 m only
[c] Some stations to less than 200 m, but not less than 100 m

PO_4 values were interpolated to standard depths 0, 10, 20, 30, 50, 75, 100, 150, 200, and 500 m. These data represent only dissolved inorganic P. We ignore dissolved organic P because little is known about its form and distribution (e.g., Corner and Davies 1971), and because it appears insignificant in phytoplankton ecology (Strickland and Solórzano 1966; Perry 1976).

Particulate organic P may occur as seston, bacteria, phytoplankton, zooplankton, and nekton; only zooplankton has been included here. There are no suitable data for bacteria and seston in the California Current. Phytoplankton has also been ignored because of lack of plant biomass data and because calculations using chlorophyll *a* measurements (Owen 1974) suggest that phytoplankton made up <<1% of inorganic P transport (both summer and winter, 1969). We did not treat P in fish and other nektonic organisms because the animals' mobility and migratory habits would probably invalidate any relation to water-transported dissolved inorganic P.

Zooplankton displacement volumes (ml/1000 m^3) were taken at the same stations as PO_4 data. P transported in zooplankton tissue was calculated as volume transport between adjacent stations (0-200 m) multiplied by the mean of those adjacent stations' zooplankton displacement volumes. Zooplankton transport was converted to P transport by assuming (1) displacement volume (cc) = wet weight (grams), (2) dry weight = 0.13 wet weight, (3) organic weight = 0.8 dry weight, (4) P = 0.02 organic weight, and (5) atomic weight of P = 31.

Geostrophic flows were referred to an assumed level of no motion at 500 db except in shallower water, where flows were referred to the deepest depth sampled. We did not make shallow-water corrections to geostrophic flow using the interpolation methods discussed in Reid and Mantyla (1976) because the available data do not include stations shallower than 500 m on either the northern or southern lines. North-south transport was calculated across CalCOFI station lines 70, 80, and 110 (Figure 1); east-west transport was calculated across a western boundary formed by station 90 on all lines between 70 and 110 (inclusive). Flow calculations used MLRG (SIO) program CADV, based on Sverdrup et al. (1942: p. 463).

Transport of PO_4 was calculated as geostrophic flow times mean PO_4 concentration. Mean PO_4 values were computed from concentrations at the four corners of each cell formed by two adjacent stations and two adjacent standard depths (e.g., station 70.80 at 75 and 100 m, and station 70.90 at 75 and 100 m). Each mean PO_4 value was multiplied by its corresponding volume transport to give PO_4 transport (g-at P/sec) for each cell. Cells were then summed vertically, east-west along lines, and north-south along the west edge to give net transport (0-200 m) of P across each line.

We made two estimates of P transport: (1) for seasons and years by using PO_4, volume transport, and zooplankton data from all cruises with complete data sets (underlined in Table 1) for winter and summer; (2) mean P transport over 29 years by using mean vertical distributions of PO_4 and volume transport from 1950 through 1978. In the 29-year mean analyses, all available PO_4 data for winter and summer (Table 1) were averaged for each depth at each station (Figure 2). Mean volume transports across lines 70, 80, and 110 were obtained from profiles of monthly mean geostrophic velocity from 1950 through 1978 (Figure 3, modified from Lynn et al., in press). For transport across the western edge, we used the overall mean summer and winter transports calculated in (1) above. For zooplankton, we used means obtained from individual cruises in (1) above.

Several aspects of the data limit both possible manipulations and confidence in calculated results. These are (1) problems of sampling design, (2) changes in analytical techniques between years, and (3) possible computational artifacts.

(1) Sampling and analyses for PO_4 were not always done to the same depth nor at a consistent set of depths. Many cruises sampled slightly (or radically) different station plans, and different years varied in areal coverage. Few cruises provided a complete data set for lines 70, 80, and 110 (Table 1); the cruises chosen represent the most complete available coverage (for any nutrient) by season and line. Similarly, few summer or winter cruises provide true replicate or duplicate sets of PO_4 observations. Consequently, spatial and temporal coverage are much less than ideal, and the data set is internally heterogeneous.

(2) Analytical and/or sampling techniques changed from 1950-78. From 1965 to 1969 (excepting a few cruises in 1966), hydrographic casts using Nansen bottles were supplemented by casts using salinity-temperature-depth (STD) recorders. At any given station, these casts were not simultaneous in time and space. When bottle casts did not go to 500 m, or when no bottle cast was made at an STD station, we have used STD data for geostrophic flow calculations. Each 1969 cruise included T and S data from both STD and bottle casts. In 1972, only STDs were used. Cruise 7712 and all 1978 cruises used bottle cast data for T and S. We have not assessed any errors or biases introduced by this variety of sampling techniques.

Before 1968, measurements of PO_4 were made manually with a spectrophotometer. From 1968 on, a Technicon AutoAnalyzer (AA) was used. Hager et al. (1972) showed the two methods to be comparable;

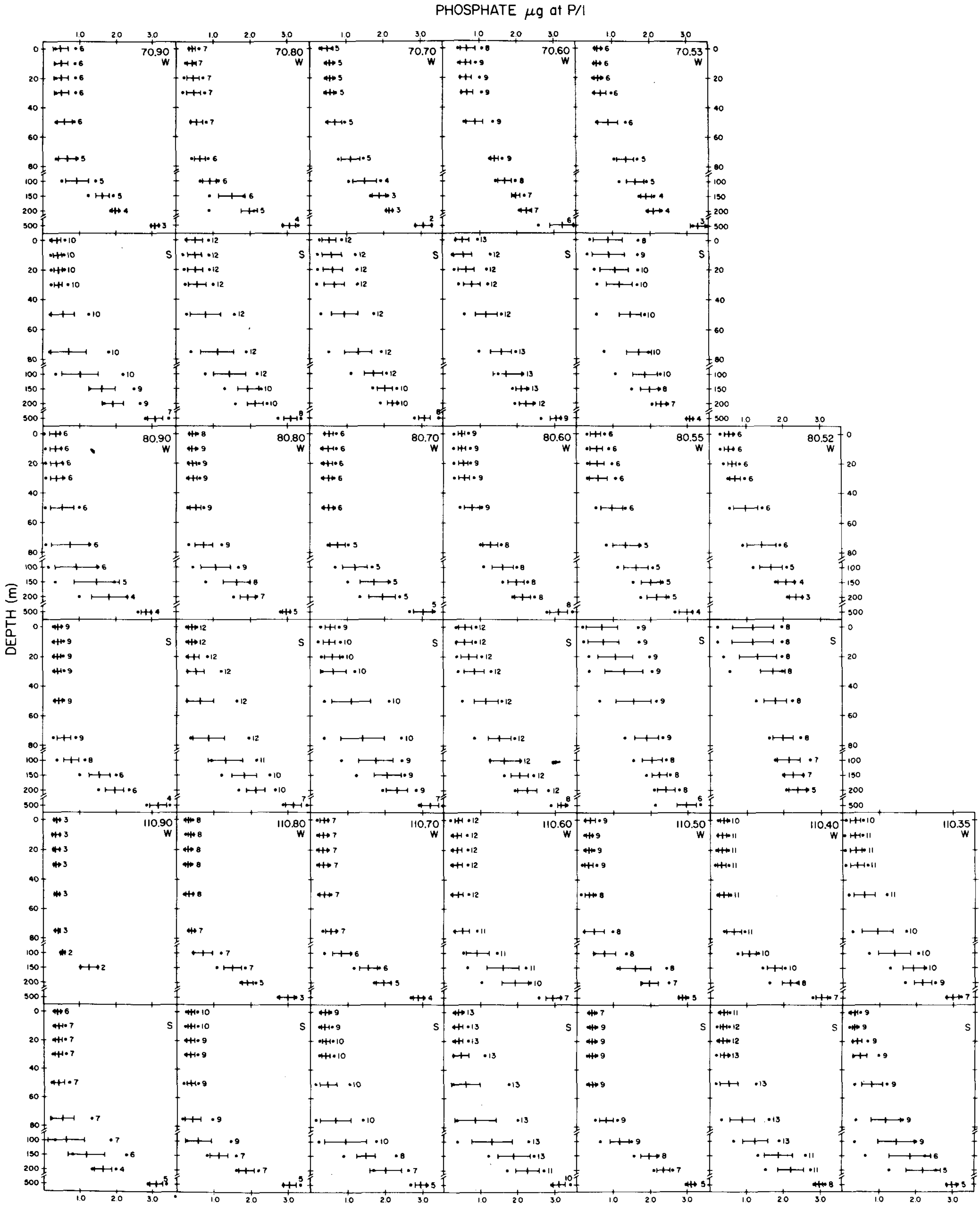

Figure 2. 1950-78 mean winter (W) and summer (S) vertical profiles of PO_4 from 0 to 500 m for CalCOFI lines 70, 80, and 110. Central heavy vertical bar = mean; horizontal bar = ± 1 S.D.; dots = range. Number of samples is beside each upper range dot.

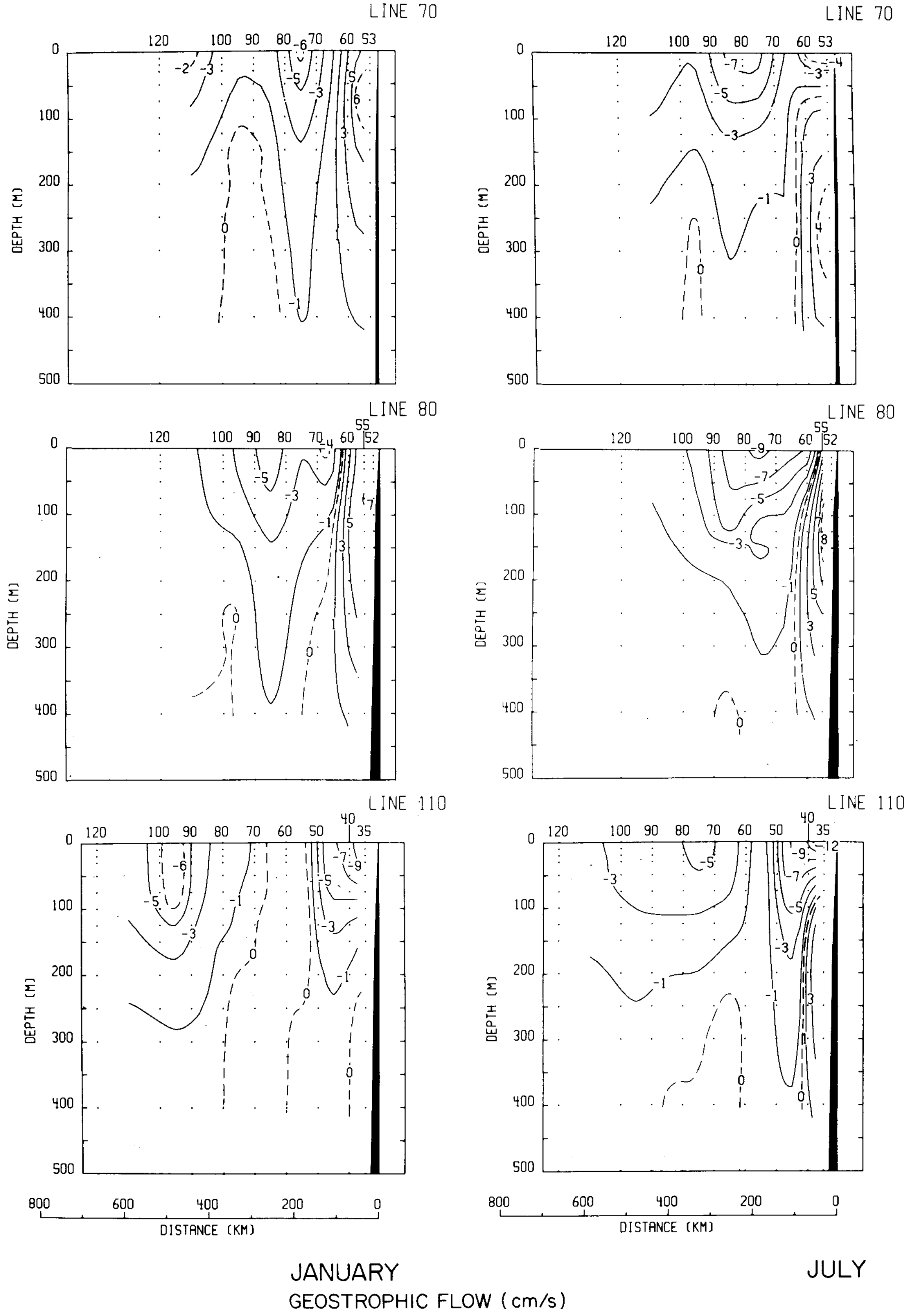

Figure 3. 1950-78 mean January and July geostrophic velocity profiles for CalCOFI lines 70, 80, and 110. Velocity in cm sec^{-1}; flows south are negative, north are positive (from Lynn et al., in press).

however, in routine AA work (as on CalCOFI cruises), baseline drift is a problem that renders absolute P values less reliable than in spectrophotometric data. We assumed no differences in accuracy and precision between methods, and combined all years' data in obtaining 1950-78 statistics.

Zooplankton sampling design changed over the years (Smith 1971, 1974; Smith and Richardson 1977). Sampled depths were 0-70 m (1950), 0-140 m (1951-68), and 0-210 m (1969 onwards). Displacement volumes for 1951-68 have been adjusted to be comparable to 0-210-m volumes (per Smith 1971). No conversion factor is available for 1950 volumes; this causes a slight increase in the zooplankton contribution to calculated P transport for 1950. Changes in mesh size and net type that occurred during the period were also ignored.

(3) Potential computational artifacts exist, especially in geostrophic flow calculations. If 500 db is not a true level of no motion (see "Discussion"), 0-200-m flow may be superimposed upon a deeper flow for which we cannot compensate accurately. In addition, any error in reference level will probably not apply uniformly to all four lines of stations.

Nearshore, shallow-water regions are potentially important contributors to mass-balance calculations. Chelton (1980) showed that high-frequency (>1 cycle yr^{-1}) variations in steric height do not match sea-level changes, which implies the existence of either deeper flows or significant currents between shore and the first offshore station. Further, shallow water is likely to have the greatest upwelling and most vigorous lateral transport. Unfortunately, these nearshore regions (with their attendant problems in geostrophic flow computations) have not received sampling sufficiently intensive to allow us to either incorporate their flows directly into our calculations, or to apply shallow-water corrections (Reid and Mantyla 1976).

Nutrient data also had to be manipulated. In a few cases where bottles were very widely spaced, interpolations for up to three depths between bottles have been made. In a few other cases the terminal value for a depth profile was extrapolated. On three cruises noncardinal lines were used (Figure 1; Table 1) because cardinal lines were not sampled. The footnotes of Table 3 list limitations of other data sets.

RESULTS

We calculated mass balances for water transport (0-200 m) using individual cruise geostrophic flows and mean 1950-78 January and July geostrophic velocities. Geostrophic flow estimates contain by far the largest potential sources of error (selection of level of no motion and inability to include nearshore transports) in PO_4 transport calculations, and are therefore discussed before other results dependent upon them.

TABLE 2
Mass Balance of Flow through Area*
Flow across boundaries

Cruise	Line 70	Line 110	West side	Net
		Winter		
5002	1.2880	−2.7460	1.9083	0.4503
6501	2.9091	−2.2340	0.3993	1.0744
6902	0.1107	−1.4003	1.4835	0.1939
7801	0.4794	0.7299	0.8861	0.6356
				$\bar{x}$ = 0.5886
				s.d. = 0.3711
		Summer		
6107	2.2979	−2.7885	1.5862	1.0956
6407	1.9003	−3.4782	2.0590	0.4811
6507	1.6534	−0.7582	0.2734	1.1686
6907	1.7743	−1.5955	0.2734	0.4522
7807	2.4616	−2.9153	0.6965	0.2428
				$\bar{x}$ = 0.6881
				s.d. = 0.4165
		1950-1978 Mean		
Winter	0.1793	−1.3585	0.9232	−0.2560
Summer	1.2771	−2.3467	1.3282	0.2586

*Units are Sverdrups (10^6 m^3 sec^{-1})
Flow in is positive, flow out is negative.

All net budgets for individual cruises (Table 2) are positive; mean input to the area is 0.64 Sv sec^{-1} (std. dev. = ± 0.37). This suggests (1) a consistent difference between lines in how well the assumption of no motion at 500 db is met, (2) failure to account for the wind-driven surface Ekman transport, or (3) failure to include nearshore flows. The third possibility, as mentioned above, cannot be addressed with our data. Considering the assumption of no motion at 500 db: Wyllie (1966, Chart 4) gives a 1960-65 mean geostrophic flow at 500 m *re.* 1000 db. There is a steric height difference of about 2 dyn cm at 500 m between lines 70 and 110. Wyllie also shows northward flow at line 70, southward flow at line 110, and a weak net eastward flow across the western edge. Accordingly, our estimates of transport would be too large across line 70 and too small across both line 110 and the western edge. The result is an overestimate of the net flux into the area, agreeing with the positive bias shown in Table 2.

Considering surface Ekman transport: Parrish et al. (1981) presented figures of mean surface transport by quarter for the California Current region. For winter and summer, there is no net across-line transport at lines 70, 80, and 110. Transport out of the area across the western boundary was about 0.6 Sv sec^{-1} in winter and 0.9 Sv sec^{-1} in summer. The seasonal difference agrees with the difference in our mean seasonal inputs. The good agreement in magnitude is

TABLE 3
Summary of Horizontal Phosphorus Transport* during Individual Cruises

	Winter					Summer				
Line	70**	80**	110**	West†	Net†† budget	70**	80**	110**	West†	Net†† budget
					Inorganic dissolved phosphate					
1950	1184a	−311b	1577	916	523	1002	1311	ND	2555	—
1961	ND	ND	ND	ND	—	2461	1627	1959	1161	1663
1964	ND	ND	ND	ND	—	2035f	2300f	3261f	938	−288
1965	2781	988c	2194c	328	915	3076g	592g	97g	511	3490
1969	−291	946	766d	1357	300	1079	1062	951c	82	210
1978	325	−1217	93e	396	628	1878	815	1114	253	1017
Mean	1000	102	1158	749	591	1922	1285	1476	917	1363
					Zooplankton phosphorus					
1950	8	−32	49	166	125	47	20	—	42	—
1961	—	—	—	—	—	19	19	14	5	10
1964	—	—	—	—	—	18	61	24	6	0
1965	18	1	17	7	8	54	14	9	5	50
1969	−5	8	6	5	−6	29	17	3	0	26
1978	5	−25	5	19	19	46	102	39	−1	6
Mean	7	−12	19	49	37	36	39	18	10	28
% (h)	0.7	11.8	1.6	6.5	6.3	1.9	3.0	1.2	1.1	1.5
					Mean total phosphorus: inorganic plus zooplankton					
	1007	90	1177	798	628	1958	1324	1494	927	1391

* In g-at P-sec.
** Transport north is negative, south positive.
† Transport east (in) is positive, west (out) negative.
†† Sum of transports into (+) or out of (−) area shown in Figure 1.
ND No data.
a No PO_4 available for station 70.55, values at station 70.60 used as an approximation.
b PO_4 values from line 83.
c Station 80.90 and 110.90 interpolated
d No station 110.90 data, value underestimates transport south.
e No station 110.80 or 110.90 data, value underestimates transport south.
f Some PO_4 to 150 m only, missing values to 200 m obtained from 1950-78 mean
g Some PO_4 to 100 m only, missing values to 200 m obtained from 1950-78 mean
h Percent of P transport contributed by zooplankton P.

probably fortuitous, considering the approximations in all the calculations, but it is clear that Ekman transport can help account for net input due to geostrophic flow.

Several cruises show large departures from the mean net budget that do not seem related to seasonal differences alone. This is not surprising, however, considering observational and analytical problems in geostrophic calculations (see "Methods"). Because of the small number of observations, and their limitations, the magnitude of variations in flow (Table 3) suggests that little significance can be placed on any but the largest differences in between-cruise P transport. We do not try to quantify that variability or to test for statistically significant differences. Despite data limitations, mean 1950-78 mass balances are quite close to zero (Table 2). In our data set we cannot separate signal (i.e., actual cruise-to-cruise and year-to-year variations) from noise (i.e., random errors due to measurement or other analytical errors). However, other studies have shown that flow of the California Current is extremely variable on many spatial and temporal scales (e.g., Sette and Isaacs 1960; Owen 1980; Chelton 1980), and much variation in our calculated flow is probably real. As a result, much of the variation in P transport is also likely to be real (see "Discussion").

Table 3 presents (1) north-south P transport (PO_4 + zooplankton P) across lines 70, 80, and 110; (2) east-west transport for the four winters and six summers; (3) net P budgets for the area by cruise; and (4) overall seasonal means for transports and budgets for both PO_4 and zooplankton P.

Table 4 shows mean P transports and budgets for 1950 through 1978. These data were derived from mean PO_4 data (Figure 2) and mean geostrophic velocity data (Figure 3).

DISCUSSION

The range in PO_4 concentration at a depth within the upper 200 m (Figure 2) is about a factor of 2 to 3, with greater ranges in the nutricline and at all depths near the coast (because of upwelling). Water fluxes vary by factors of 100 or more, and are negative in many cases. As a result, the first-order cause of variation in

TABLE 4

Phosphorus Transport Using All Phosphate and Geostrophic Velocity Data from 1950 to 1978*

	Inorganic dissolved phosphate	Zooplankton phosphorus	Total	Percent zooplankton
Winter				
Line 70	−130	−8	−138	6.2
Line 80	−510	3	−507	0.6
Line 110	869	6	875	0.7
West edge	704	16	720	2.3
Net budget	−295	2	−293	0.7
Summer				
Line 70	1216	26	1242	2.1
Line 80	883	34	917	3.9
Line 110	1829	13	1842	0.7
West edge	1017	8	1025	0.8
Net budget	404	21	425	5.2

*in g-at P/sec. Sign notation as in Table 3.

P transport and budgets is variation in advection, not changes in concentration of PO_4.

Large between-year, within-season variability in P transport (e.g., compare winters of 1965 and 1969 for line 70, or summers of 1964 and 1965 for line 110) suggests that, data problems aside, the changes are real. Some contributing factors are week-to-month variability caused by eddies (e.g., Owen 1980) and quasi-random turbulence of length scales similar to the sampling grid (75 x 75 - 225 km). Large-scale (current-wide) interannual variations in current strength also contribute (Wickett 1967; Saur 1972; Chelton 1980, 1981; Bernal and McGowan 1981).

Smaller-scale fluctuations in flow driving short-term variations in P transport can be seen clearly in geostrophic flow contours for cruises 5007, 6107, and 6407 (see Wyllie 1966, Charts 42, 142, 155). While long-term mean flows are generally southerly across all lines everywhere except near the coast (Figure 3), even our limited data set showed that net northerly flow could occur between station pairs anywhere from the coast out to station 90, on any line, in either season. Flow across the western edge also varied in direction, depending on mesoscale physical structure. Such variations have strong effects on net transport across entire lines and thus on P budgets. A northerly flow at some point on a line of stations may be only one side of an eddy carried on a more generalized southerly flow; we are unable to resolve this, and our budgets use the numbers with their calculated signs.

P transport and budgets for single cruises (i.e., small time and space scales) are very sensitive to these unresolved problems. This makes it difficult to quantify long-term interannual variations caused by current-wide variations in transport, and we have not attempted to do so. We did look qualitatively at possible consequences of long-term changes in advection of P on interannual, current-wide zooplankton fluctuations. Those fluctuations were identified by Bernal (1979) and shown to be correlated with advection (Bernal and McGowan 1981; Bernal 1981; Chelton 1981). Bernal (1979) identified several anomalous zooplankton biomass periods between 1959 and 1969; only two (in 1950 and 1964) coincide with our P data. In addition, Chelton and Bernal identified 1978 as an anomalous year (Chelton 1980, 1981). In both summer and winter of these three years—1950, 1964, 1978—we find no obvious relation between P transport across lines and anomalous zooplankton biomasses. Neither do we find a relation between total P budgets and biomasses. Clearly, more detailed data will be needed to detect correlations, on time scales of years, that must exist between plant nutrient supply and primary or secondary productivity.

Bernal and McGowan (1981) and Bernal (1981) also showed that between 1950 and 1969 interannual fluctuations of zooplankton biomass about the long-term mean were not correlated with deviations from long-term means of Bakun's (1973) upwelling index. Because of our limited data set, we were able to look only at correlations between P transport during individual cruises and corresponding upwelling indices. Magnitudes of P transport across lines 70, 80, and 110 were ranked within seasons. Kendall's rank difference correlation coefficients (r_d; Tate and Clelland 1957) were determined for the relationship of these rankings to upwelling indices at nearby points (Figure 1). Indices for the same month or the one or two months preceding were used, depending on distance of the line from the point where upwelling indices were calculated. There is no significant correlation ($p>0.20$) (Table 5) of variations in P transport across lines with variations in upwelling index. We also calculated correlation coefficients between transport across line 70 and upwelling indices off Washington (45°N, 125°W) with lags of 0 to 2 months. Again, no significant ($p>0.20$) correlations were found.

Because variations in near-surface PO_4 concentrations for individual cruises could reflect variations in upwelling intensity, we also calculated r_d between upwelling indices and integrated P (0-50 m) at the two stations nearest the coast on lines 70, 80, and 110. No significant correlations (all $p>0.20$) were found.

Tables 3 and 4 show that P transports across lines are generally greater in summer than winter, although there is considerable variability in individual cruise data (Table 3). The 1950-78 mean P transports also show a net northward flux of P across lines 70 and 80 during winter (Table 4); this is evident in only a few individual cruises. The seasonal difference could be

TABLE 5

Transport of Inorganic Dissolved Phosphorus* across CalCOFI Lines 70, 80, and 110 during Individual Cruises Compared to Upwelling Indices at Four Stations before or during those Cruises

Line 70					Line 80				Line 110					
		Upwelling Index					Upwelling Index				Upwelling index			
PO_4	Station:[a]	A	A	B	PO_4	Station:	B	C	PO_4	Station:	C	C	D	D
Transport	Time:[b]	t-1	t-2	t=0	Transport	Time:	t-1	t-1	Transport	Time:	t-1	t-2	t=0	t-1
1184		24	11	3	−311		35	42	1577		42	9	58	60
2781		−11	−5	7	988		10	36	2194		36	19	44	73
−291		−8	−39	−1	946		−3	4	766		4	6	45	8
325		−49	14	−36	−1217		−10	−5	93		−5	37	9	13
	r_d =	0.0	0.20	0.82		r_d =	0.40	0.40		r_d =	0.80	−0.20	0.40	0.80
1002		121	210	115	1311		153	191	—		—	—	—	—
2461		102	75	134	1627		139	241	1959		241	351	94	158
2035		149	140	313	2300		296	515	3261		515	469	176	204
3076		230	300	228	592		280	322	97		322	295	95	142
1079		145	112	303	1062		245	377	951		377	353	219	194
1878		233	289	252	815		240	306	1114		306	195	184	224
	r_d =	0.20	0.17	0.09		r_d =	−.09	0.09		r_d =	0.10	0.50	−0.20	0.35

* g-at P/sec

[a] See Figure 1 for locations.

[b] Same month as transport calculation t = 0.
month previous to transport calculation t-1.
two months previous to transport calculation t-2.

[c] 1977-78 upwelling indices from National Marine Fisheries Service, La Jolla, courtesy Paul Smith.

r_d = Kendall rank difference correlation coefficient; in all cases, $P_{(r_d)} > 0.20$.

due to increased advection across lines during summer (Table 2) and to increased PO_4 concentration at all depths (0-500 m) over most of the study area. Table 6 summarizes 178 comparisons of summer and winter mean PO_4 values at standard depths by line and station: summer values exceed winter values 147 times. This is a highly significant difference ($p << 0.01$, H_0: $\phi = 0.50$, binomial distribution, Tate and Clelland 1957). Similarly, integrated PO_4 (mg-at P/m^2) to 75 m and 500 m were generally higher in summer than in winter (Table 7). The higher summer integrated PO_4 values may be due to shoaling of isopycnals during this season (Eber 1977). The shoaling brings colder water with higher nutrients up to within the depth range used for our calculations of integrated PO_4.

Net P budgets for the area reflect seasonal differences in P transport: summer P import is greater than winter for mean budgets of individual cruises (Table 3), and there is summer import but winter export of P in 1950-78 mean seasonal budgets (Table 4). Given

TABLE 6

Comparison of Summer vs. Winter Phosphate Concentrations at Standard Depths from 0 to 500 m. Using Station Means, 1950-78*

		Line 70			Line 80			Line 110	
Station	S>W	S<W	S=W	S>W	S<W	S=W	S>W	S<W	S=W
35							7	3	0
40							9	1	0
50					Coastline		10	0	0
52		Coastline		9†	0	0	NS	NS	NS
53	9	1	0	NS	NS	NS	NS	NS	NS
55	NS	NS	NS	9	1	0	NS	NS	NS
60	5	4	1	10	0	0	10	0	0
70	9	0	1	9	0	1	9	1	0
80	10	0	0	10	0	0	7	3	0
90	2	7	1	7	3	0	6†	2	1
	35	12	3	54	4	1	58	10	1
			Totals	S>W	S<W	S=W			
			N = 178	147	26	5			

NS No station.

* E.g., for line 70, station 53, at 9 of 10 standard depths, the mean summer PO_4 concentration was greater than the winter concentration.

† No 500 m PO_4.

TABLE 7

Winter and Summer Water Column Phosphate (mg-at P/m^2) Integrated to 75 m and 500 m

	Line 70				Line 80				Line 110			
	Winter		Summer		Winter		Summer		Winter		Summer	
Station	75 m	500 m	75 m	500 m	75 m	500 m	75 m	500 m	75 m	500 m	75 m	500 m
35									52	1029	65	1052
40									37	996	59	1041
50					Coastline				31	905	43	1061
52	Coastline				82	658▽	146	750▽ 1072*	NS	NS	NS	NS
53	99	1125	116	1148	NS	NS	NS	NS	NS	NS	NS	NS
55	ID	ID	116	1185	77	1062	121	1171	NS	NS	NS	NS
60	79	1114	91	1108	71	1074	90	1123	36	928	51	1066
70	66	1058	79	1099	49	974	79	1137	35	920	43	950
80	46	957	67	1051	47	946	56	1042	29	911	34	901
90	49	966	46	949	44	876	40	952	33^+	115	37	118^+
S>W	0-75 m	4 ex 5		P<0.20	5 ex 6		P<0.10		7 ex 7		P<0.05	
	0-500 m	3 ex 5		P>0.20	6 ex 6		P≈0.05		6 ex 7		P≈0.05	

ID Insufficient data
NS No station
+ to 150 m only
▽ to 200 m only
* to 500 m

the small number and high variability of the data sets, the potential biases, and limitations due to analytical problems, seasonal differences in both P transports and net budgets are probably not significant. The most conservative interpretation is that, over the long term, the study area is neither a source nor sink of PO_4. The decrease in total PO_4 in the upper layers of the California Current from north to south (Reid 1962; Owen 1974) (especially in summer: Table 7) may be due to one or both of the following: (1) input (above 200 m) of high PO_4 water from the north and low PO_4 water from the west balanced by output of a relatively large volume of low PO_4 water to the south across line 110; (2) the possible mass imbalance for water above 200 m (Table 2), suggesting a net subsidence of PO_4-rich water out of the bottom of the area. Regardless of the long-term P balance, variability in net P budget occurs both within and between individual years and should have a marked effect on productivity of the California Current.

ACKNOWLEDGMENTS

We thank S. Anderson for help with physical data and geostrophic flow computations, T. Schultze for help with calculations and Figure 2, J. Thrailkill for zooplankton data not available in report form, and R. Lynn for use of geostrophic velocity information (Figure 3) in press (CalCOFI Atlas 30). The MLRG Illustration Facility prepared the final figures; S. McBride typed the manuscript. This research was supported by the Marine Life Research Program (Scripps Institution of Oceanography's component of the California Cooperative Oceanic Fisheries Investigations) and the Marine Biology Program of the U.S. Office of Naval Research (Code 484: Contract N00014-79-C-0200).

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NORTHERN ANCHOVY AND PACIFIC SARDINE SPAWNING OFF SOUTHERN CALIFORNIA DURING 1978-80: PRELIMINARY OBSERVATIONS ON THE IMPORTANCE OF THE NEARSHORE COASTAL REGION

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ABSTRACT

Estimates of egg and larval abundance of northern anchovy *(Engraulis mordax)* and larval abundance of Pacific sardine *(Sardinops sagax caeruleus)* from monthly Ichthyoplankton Coastal and Harbor Studies (ICHS) cruises during 1978-80 within the nearshore Southern California Bight (to the 43-m isobath) were contrasted with comparable estimates from CalCOFI region 7. The ICHS region encompassed 3.8 percent of the area in region 7.

Raw survey data, uncorrected for potential sampler biases, indicated that about 3 percent of northern anchovy larvae occurred within the nearshore zone relative to the entire region 7. This number may be equivalent to about 2 percent of the larvae spawned by the central subpopulation.

The abundance of Pacific sardine larvae in the coastal region increased from 1978-79 to 1979-80. Sardine larvae occurred most frequently during the summer and fall and were captured most often in Santa Monica Bay. CalCOFI data on Pacific sardine were too infrequent for comparison with ICHS data.

The ichthyoplankton data sets are discussed in relation to the nursery function of nearshore versus offshore waters and the need for additional criteria for assessing recruitment potential from the two regions.

RESUMEN

Se comparó la abundancia estimada de huevecillos y larvas de la anchoveta *Engraulis mordax* y la abundancia de larvas de la sardina del Pacífico *(Sardinops sagax caeruleus),* determinadas en los cruceros mensuales de Estudios del Ictioplancton en Puertos y la Costa (ICHS) durante 1978-80 en la zona costera del sur de California (hasta la isóbata de los 43 m.), con estimaciones comparables de la región 7 de CalCOFI. La región del ICHS abarcaba un 3.8 por ciento del área en la región 7.

Los datos sin procesar y sin corrección de los sesgos potenciales del muestreador mostraban que alrededor del 3 por ciento de las larvas de anchoveta ocurrieron en la zona cercana a la costa por toda la región 7. Este número podría ser equivalente a alrededor del 2 por ciento de las larvas producidas por la subpoblación central.

La abundancia de la sardina del Pacífico en la región costera aumentó de 1978-79 a 1979-80. Las larvas de sardina se observaron con mayor frecuencia durante el verano y otoño y se capturaron más a menudo en la Bahía de Santa Mónica. Los datos de CalCOFI referentes a la sardina del Pacífico eran muy poco frecuentes como para compararlos con los datos del ICHS.

Los datos del ictioplancton son discutidos en relación a la función de criaderos en las aguas cercanas a la costa contra aquéllos fuera de la costa, así como la necesidad de criterios adicionales para evaluar el potencial de reclutamiento de las dos regiones.

INTRODUCTION

The variable abundance and distribution of the early life stages of clupeiform fishes off the Pacific coast of North America have been investigated for more than three decades by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) (Ahlstrom 1966; Smith 1972). The time series on ichthyoplankton, developed by CalCOFI, was supplemented from 1978-80 by a regionally intensive project within the Southern California Bight; the project was entitled Ichthyoplankton Coastal and Harbor Studies (ICHS).

The ICHS data includes temporal and spatial features of ichthyoplankton abundance that are not available from CalCOFI cruises. Important differences exist in the species structure of ichthyoplankton between ICHS and adjacent CalCOFI regions (Brewer et al. 1980; Loeb et al.[1]). Other investigators have shown gradients in potential food for larval fishes—phytoplankton (Eppley et al. 1978; Kleppel 1980) and microzooplankton (Beers and Stewart 1967; Arthur 1977)—that increase toward shore. The ICHS data make it possible to assess longshore variability of ichthyoplankton within the bight and, with CalCOFI data, to evaluate nearshore versus offshore regions as spawning grounds for adult fishes and as habitats for the survival of larvae.

[Manuscript received February 8, 1982.]

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[1] Loeb, V., H. Moser, and P. Smith. Seasonal and geographic patterns of ichthyoplankton distributions in the CalCOFI area, 1975. Admin. Rep., unpub.

This report gives estimates of egg and larval abundance of northern anchovy *(Engraulis mordax)* and larval abundance of Pacific sardine *(Sardinops sagax caeruleus)* from monthly cruises within the nearshore ICHS region. These estimates are compared with similar estimates from an adjacent CalCOFI region. The data sets are discussed in relation to the nursery function of nearshore versus offshore waters and the need for additional criteria for assessing recruitment potential from the two regions.

ICHS sampled the nearshore Southern California Bight along the 8-m, 15-m, 22-m, and 36-m isobaths, inshore of most CalCOFI stations. The circulation and chemistry of these shallow waters are not well studied (Jones 1971; Tsuchiya 1980; Winant and Bratkovich 1981). Compared to offshore waters, coastal features are complicated by boundary effects, shoreline topography, local wind conditions, runoff from sporadic rainfall, and anthropogenic influences. Industrial, municipal, and thermal wastewaters from at least 24 discrete outfalls are discharged within the Southern California Bight (Southern California Coastal Water Research Project 1973).

MATERIALS AND METHODS

Sampling techniques and laboratory procedures used by the CalCOFI program have been discussed in detail by Kramer et al. (1972) and Smith and Richardson (1977). Briefly, 70-cm bongo[2] plankton samplers (0.505-mm mesh) were lowered to 210 m, depth permitting, and retrieved at 20-m•min^{-1} while a constant towing wire angle was maintained. Plankton samples were preserved and returned to the laboratory, where they were sorted and the fish eggs and larvae identified and enumerated. Data on tow depth, volume of water filtered, and numbers of eggs and larvae in each sample were then used to estimate ichthyoplankton abundance under unit areas of sea surface.

An important goal of the ICHS program was data compatibility with CalCOFI. Hence, a primary objective in the nearshore sampling (as in CalCOFI surveys) was an oblique tow trajectory with 70-cm bongos, whereby equal volumes of water were filtered per unit depth. Certain details of the ICHS methodology differed from CalCOFI techniques. ICHS sampled almost exclusively at night, whereas CalCOFI sampled during all hours. The ICHS bongo was fitted with a messenger release, opening-closing device as described by McGowan and Brown (1966). A steel bar, 0.7 m long and weighing about 40 kg, was tied 0.3 m below the bongo frame as a depressor weight. The nets were made of 0.333-mm mesh Nitex with a 1.5-m cylindrical section and a 1.5-m conical section leading to 0.333-mm mesh cod-end sock.

The ICHS bongo was slowly lowered to the bottom (canvas doors covered the mouths of the nets) with the ship under way. The angle and length of the towing wire were monitored in order to bump the depressor weight on the bottom. The canvas doors were then opened by messenger and the sampler retrieved immediately at a constant rate of 20-m•min^{-1} while maintaining a towing-wire angle of about 45°. A General Oceanics instrumented trawl block provided continuous readings of towing-wire angle, meters of cable out, and retrieval rate. Ship speed was monitored by a General Oceanics speedometer with a deck readout. General Oceanics flowmeters, located in the mouth of the bongo frame, were used to compute the distance traveled by the nets; from this data, the volume of water filtered was determined. With a combined ship speed and net retrieval rate of about 1.0-1.1-m•sec^{-1}, about 3-4 m^3 of water were filtered per meter of depth.

A depth transducer was mounted on the bongo frame beginning with cruise 12 to insure contact with the bottom by providing continuous depth readings of the sampler via a deck readout.

Fish eggs and larvae were carefully sorted from 25-100 percent of each sample with the aid of stereomicroscopes. Aliquots were made by using either the port or starboard bongo sample, and/or by splitting with a Folsom plankton splitter (McEwen et al. 1954). Ten percent of each sorted fraction was checked to ensure that sorting efficiency remained at least 90 percent. Fragmented larvae were counted, but were not considered in the determination of sorting efficiency prior to July 1979. Also, some samples collected prior to July 1979 were not sort-checked. Data for these cruises may underestimate abundance relative to subsequent cruises, but probably by no more than 5 percent, based on the numbers of fragments found and the sorting efficiency during the later cruises.

We have assumed that damaged specimens identified conservatively as engraulids and clupeids were, in fact, *Engraulis mordax* and *Sardinops sagax caeruleus,* respectively. Also, damaged specimens identified only as clupeiformes have been proportioned into the two specific categories for each sample, based on the ratio of individuals identified positively.

While the central subpopulation of northern anchovy encompasses at least eight CalCOFI regions and an area of about 571,000 km^2 (Vrooman et al. 1980), in this report data from region 7 only were compared with the ICHS data. The ICHS region is contiguous with region 7 (Figure 1), and region 7 is the center of

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[2] Cruise 7901 used the CalCOFI 1-m bridled net.

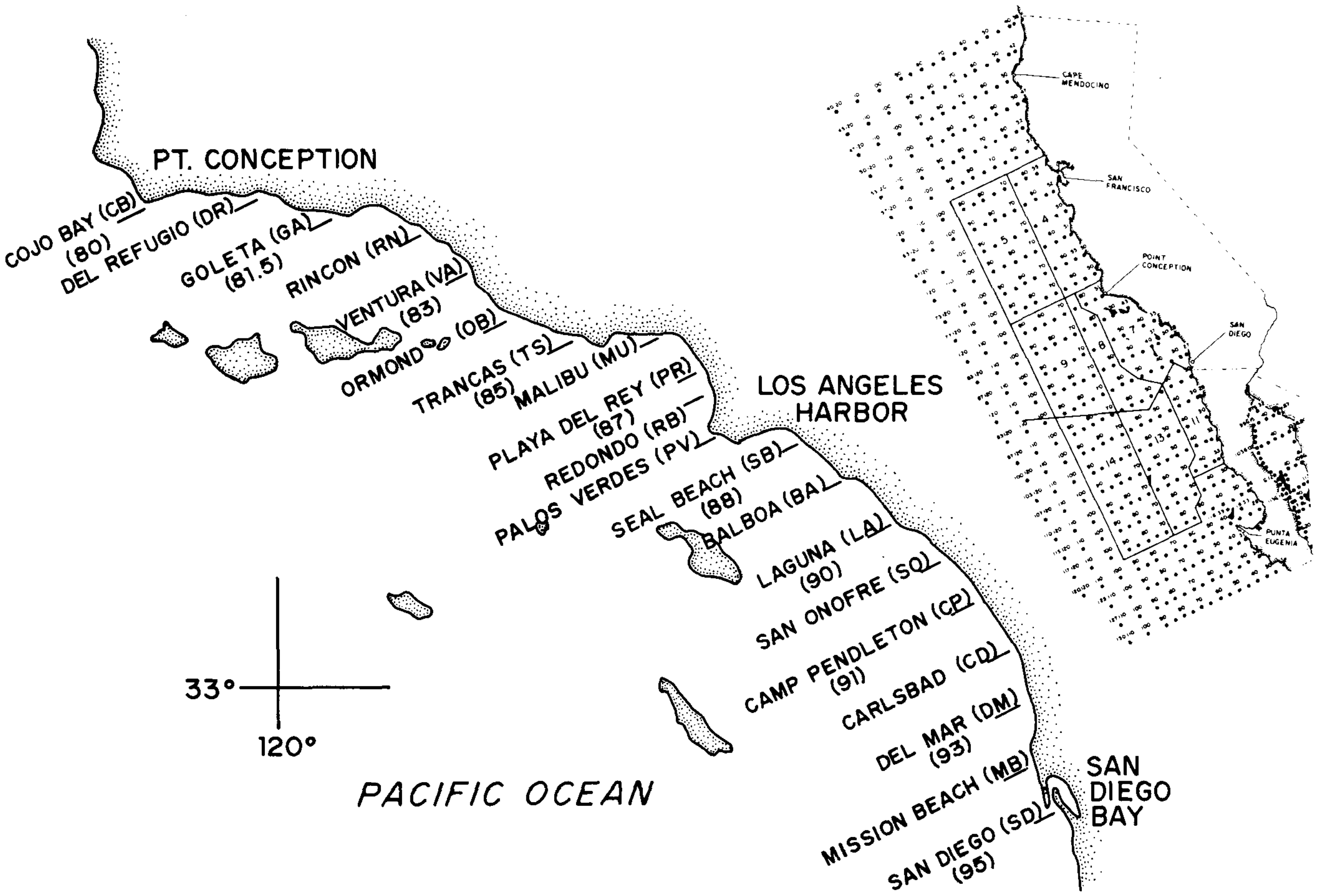

Figure 1. Locations of ICHS transects in relation to adjacent CalCOFI regions (inset). The ICHS region includes the area from shore to the 43-m isobath—approximately 3.8 percent of the area within region 7.

the northern anchovy central subpopulation biomass (Smith and Eppley 1981).

Station locations for ICHS and CalCOFI region 7 are listed in Tables 1 and 2, respectively. Stations occupied by ICHS varied between June 1978-July 1979 (Phase I) and August 1979-July 1980 (Phase II). Phase I sampling encompassed 10 transects and 4 stations per transect over isobaths of 8, 15, 22, and 36 m (Table 1). Data from eight ICHS cruises were available from this period. Phase II cruises occupied 46 stations each month along 20 transects. Only the 8-m and 22-m isobaths were sampled along 17 of the transects. Transects off Ormond, Redondo, and San Onofre beaches were sampled at 8-m, 15-m, 22-m, and 36-m isobaths. The volume of water filtered per unit depth was increased by a factor of four during Phase II, relative to Phase I. This was accomplished by decreasing the net retrieval rate from 20-m•min^{-1} to 10-m•min^{-1} and replicating each sample. The speed of the net (i.e., retrieval rate + ship speed) was maintained at about 1.0-1.1 m•sec^{-1} during both Phase I and II.

For purposes of this report, the ICHS stations represent a nearshore region that extends from just below the United States-Mexico border (32°24.5'N) to just above Pt. Conception (34°40.0'N). and extends offshore to the 43-m isobath (Figure 1). This area encompasses about 2652 km^2 that lie within the area (69,055 km^2) of CalCOFI region 7. The area of the ICHS region was determined by multiplying the longshore distance covered by the transects as determined from National Ocean Survey charts 19720 and 18740. The distance to the 43-m isobath was estimated by extrapolating the average seaward distance of the ICHS stations along the 8-m, 15-m, 22-m, and 36-m isobaths.

Station data from both CalCOFI and ICHS regions were scaled for each taxon to numbers of individuals under unit areas of sea surface (Smith and Richardson 1977). Regional census estimates (Smith 1972) for each survey cruise were computed from the mean number of eggs or larvae per m^2 of sea surface for all stations sampled, times the area within the respective region.

TABLE 1
ICHS Station Coordinates

Transect	Station (depth-m)	N. Latitude	W. Longitude	Distance from shore (km)
80 (Cojo Bay)	* 08	34°26.8′	120°26.7′	0.35
	15	34°26.7′	120°26.5′	0.79
	* 22	34°26.5′	120°26.5′	1.17
	36	34°26.2′	120°26.5′	1.20
DR (Del Refugio)	* 08	34°27.5′	120°03.0′	0.20
	* 22	34°27.3′	120°04.4′	0.31
81.5 (Goleta)	* 08	34°24.6′	119°47.4′	0.74
	15	34°24.1′	119°46.4′	1.00
	* 22	34°23.9′	119°46.5′	1.33
	36	34°23.5′	119°46.5′	2.04
RN (Rincon)	* 08	34°22.0′	119°27.5′	0.25
	* 22	34°21.4′	119°28.7′	1.40
83 (Ventura)	* 08	34°15.7′	119°16.6′	0.35
	15	34°14.9′	119°17.3′	1.79
	* 22	34°13.4′	119°21.5′	7.50
	36	34°11.9′	119°24.1′	11.95
OB (Ormond Beach)	* 08	34°07.3′	119°10.4′	0.28
	* 15	34°07.1′	119°10.9′	0.79
	* 22	34°06.6′	119°11.8′	1.70
	* 36	34°06.1′	119°12.8′	2.55
85 (Trancas)	* 08	34°03.1′	118°58.2′	0.37
	15	34°02.8′	118°58.0′	0.94
	* 22	34°02.6′	118°58.0′	1.26
	36	34°02.2′	118°58.0′	1.67
MU (Malibu)	* 08	34°02.2′	118°36.2′	0.11
	* 22	34°01.6′	118°37.4′	0.56
87 (Playa del Rey)	* 08	33°57.0′	118°27.2′	0.41
	15	33°57.0′	118°27.9′	1.48
	* 22	33°57.0′	118°28.6′	2.41
	36	33°57.0′	118°30.1′	4.43
RB (Redondo Beach)	* 08	33°50.3′	118°23.7′	0.20
	* 15	33°50.1′	118°23.8′	0.50
	* 22	33°50.0′	118°24.2′	0.82
	* 36	33°49.6′	118°24.9′	1.57
PV (Palos Verdes)	* 15	33°40.7′	118°24.7′	0.19
	* 22	33°44.4′	118°25.0′	0.39
88 (Seal Beach)	* 08	33°42.4	118°04.4′	0.93
	15	33°41.1	118°04.6′	3.52
	* 22	33°39.4′	118°05.0′	5.30
	36	33°37.2′	118°05.4′	8.37
BA (Balboa)	* 08	33°36.2′	117°54.5′	0.21
	* 22	33°35.9′	117°54.9′	0.62
90 (Laguna Beach)	* 15	33°30.3′	117°45.3′	0.52
	22	33°30.3′	117°45.5′	0.74
	* 36	33°30.2′	117°45.8′	1.24
SO (San Onofre)	* 08	33°21.7′	117°33.8′	0.50
	* 15	33°21.2′	117°34.6′	1.45
	* 22	33°20.7′	117°35.3′	2.01
	* 36	33°20.6′	117°35.8′	2.54
91 (Camp Pendleton)	* 08	33°15.1′	117°26.4′	0.70
	15	33°14.6′	117°27.2′	2.31
	* 22	33°14.3′	117°27.5′	3.26
	36	33°13.7′	117°28.2′	4.39
CD (Carlsbad)	* 08	33°07.4′	117°20.2′	0.27
	* 22	33°07.1′	117°20.7′	0.72
93 (Del Mar)	* 08	32°57.6′	117°16.3′	0.52
	15	32°57.6′	117°16.7′	1.04
	* 22	32°57.5′	117°17.1′	1.63
	36	32°57.5′	117°17.5′	2.22
MB (Mission Beach)	* 08	32°46.7′	117°15.4′	0.25
	* 22	32°46.3′	117°16.5′	1.13
95 (San Diego)	* 08	32°37.9′	117°08.7′	0.44
	15	32°37.8′	117°09.8′	2.00
	* 22	32°36.9′	117°11.3′	4.89
	36	32°35.8′	117°13.6′	9.07

Stations along numerically designated (CalCOFI) transects 80-95 were sampled from June 1978-July 1979 (Phase I). Stations marked by an "*" were sampled from August 1979-July 1980 (Phase II). Note that no samples were collected at the 8-m isobath along transects PV and 90.

TABLE 2
CalCOFI Region 7 Station Coordinates

Transect	Station	(Depth-m)	N. Latitude	W. Longitude	Distance from shore (km)*
80	51.0	110	34°27.0′	120°31.4′	4.6
	52.0	242	34°25.0′	120°35.6′	11.9
	55.0	763	34°19.0′	120°48.1′	30.9
	60.0	2151	34°09.0′	121°09.0′	66.5
82	46.0	539	34°16.2′	119°56.3′	16.1
	47.0	541	34°14.2′	120°00.5′	22.8
83	40.6	33	34°13.5′	119°24.7′	10.2
(83.3)	42.0	167	34°10.7′	119°30.5′	19.1
	51.0	213	33°52.7′	120°08.0′	63.5
	52.0	410	33°50.7′	120°12.1′	69.3
	55.0	981	33°44.7′	120°24.6′	77.8
87	32.5	24	33°54.4′	118°27.3′	2.8
(86.7)	32.7	33	33°54.0′	118°28.2′	4.3
	33.0	49	33°53.4′	118°29.4′	6.7
	34.0	70	33°51.4′	118°33.6′	14.1
	35.0	575	33°49.4′	118°37.7′	19.8
	36.0	801	33°47.4′	118°41.9′	24.8
	40.0	840	33°39.4′	118°58.5′	41.7
	45.0	1630	33°29.4′	119°19.1′	70.6
	50.0	77	33°19.4′	119°39.8′	99.6
	51.0	104	33°17.4′	119°43.9′	107.0
	55.0	1205	33°09.4′	120°00.4′	131.9
90	27.6	43	33°29.9′	117°44.4′	1.3
	28.0	302	33°29.1′	117°46.1′	2.8
	29.0	609	33°27.1′	117°50.2′	10.0
	30.0	616	33°25.1′	117°54.3′	17.2
	31.0	395	33°23.1′	117°58.5′	23.7
	33.0	751	33°19.1′	118°06.7′	36.5
	37.0	1173	33°11.1′	118°23.2′	58.9
	41.5	1372	33°02.1′	118°41.7′	84.1
	45.0	1720	32°55.1′	118°56.1′	103.7
	53.0	1138	32°39.1′	119°28.9′	157.4
93	26.7	45	32°57.4′	117°18.3′	3.5
	26.9	75	32°57.0′	117°19.1′	5.0
	28.0	553	32°54.8′	117°23.7′	10.9
	29.0	592	32°52.8′	117°27.8′	17.4
	30.0	779	32°50.8′	117°31.9′	23.3
	35.0	605	32°40.8′	117°52.4′	57.6
	40.0	1686	32°30.8′	118°12.8′	92.0
	45.0	1347	32°20.8′	118°33.3′	127.0
	50.0	1413	32°10.8′	118°53.6′	163.5
97	29.0	41	32°17.4′	117°04.8′	3.0
	30.0	59	32°15.4′	117°08.8′	10.6
	32.0	1289	32°11.4′	117°17.0′	25.0
	35.0	1183	32°05.4′	117°29.2′	47.6
	40.0	1489	31°55.4′	117°49.5′	84.6

*Nearest point on mainland.

RESULTS

Northern Anchovy Larvae

Northern anchovy spawn all year within the bight, but their estimated regional abundance may vary by a factor of 10 between adjacent months and a factor of 100 between adjacent seasons (Table 3). About 80 percent of northern anchovy spawning takes place in winter and spring (Stauffer and Parker 1980). CalCOFI sampling was concentrated during the months when anchovy spawning is greatest; ICHS sampled throughout the year. Seasonal spawning, possible biases resulting from different egg and larvae retention between the ICHS (0.333-mm mesh) net and the CalCOFI (0.505-mm mesh) net, and day-night differences in net avoidance require cautious comparison of ICHS and CalCOFI data.

The nearshore Southern California Bight contained an average of 38 *E. mordax* larvae per m^2 of sea surface during 1978-80 based on 861 plankton tows (Table 3). Similarly, during the same period, CalCOFI nets towed within region 7 captured an average of 102 larvae per m^2 from 466 plankton samples (Table 4). In order to eliminate temporal bias in comparing ICHS and CalCOFI regional abundance, nine surveys conducted during concurrent periods were contrasted (Tables 3 and 4). The relationship (Figure 2) between monthly census estimates of larval abundance in region 7 versus the ICHS region suggests that numbers of larvae covaried between the two regions. The overall means of the nine paired cruises were 5673 x 10^9 (82.4•m^{-2}) and 162 x 10^9 (61.1•m^{-2}) larvae in the two regions, respectively. The ICHS region, encompassing 3.8 percent of the area in region 7, contained about 3 percent of the northern anchovy larvae.

The abundance of larvae per m^2 varied directly with station depth within the ICHS region (Figure 3). This relationship indicates that the census data underestimated total numbers of larvae to the 43-m isobath during Phase II when stations over the 15-m and 36-m isobaths were not well represented (Table 1). Without data from the 15-m and 36-m isobaths, monthly census estimates were low by a factor of about 1.5 based on the regression equation in Figure 3. Figure 3 also shows that the average density of larvae (number per unit volume) rises to a near asymptote at the 36-m

TABLE 3

Summary of Egg and Larval Abundance of Northern Anchovy and Larval Abundance of Pacific Sardine from ICHS Cruises during 1978-80

		Engraulis larvae				*Engraulis* eggs				*Sardinops* larvae			
Cruise	Dates	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	Est. # larvae ICHS region (x 10^9)	# Sta./ positive	$\bar{x}$ eggs •m^{-2}	Std. dev.	Est. # eggs ICHS region (x 10^9)	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	Est. # larvae ICHS region (x 10^9)
	1978												
1*	12-24 Jun.	38/36	24.47	38.93	64.89	38/16	9.18	41.78	24.35	38/06	0.10	0.33	0.27
2*	10-21 Jul.	37/33	8.78	13.52	23.27	37/20	21.27	76.31	56.41	37/03	0.06	0.25	0.16
3	14-25 Aug.												
4	18-29 Sep.	39/35	12.76	18.93	33.85	39/18	11.67	44.27	30.95	39/03	0.04	0.13	0.10
5	16-27 Oct.	39/33	16.98	36.73	45.03	39/22	492.25	2878.47	1305.40	39/04	0.04	0.14	0.11
6	06-17 Nov.												
7	04-15 Dec.	39/36	32.18	45.64	85.33	39/27	14.69	54.12	38.96	39/01	0.01	0.09	0.04
	1979												
8*	08-19 Jan.	39/39	27.54	27.10	73.05	39/25	8.04	20.08	21.32	39/04	0.05	0.14	0.12
9	12-28 Feb.												
10*	12-23 Mar.	39/38	75.49	104.98	200.19	30/35	172.96	333.73	458.69	39/07	0.18	0.56	0.47
11*	02-21 Apr.	39/38	55.15	65.95	146.27	39/31	119.75	332.27	317.58	39/01	0.01	0.05	0.02
12	14-25 May												
13	11-22 Jun.												
14	10-18 Jul.												
15	13-24 Aug.	46/45	19.83	35.51	52.58	46/29	37.69	160.60	99.96	46/15	0.18	0.72	0.48
16	10-21 Sep.	46/46	15.05	27.60	39.90	46/24	2.61	6.90	6.93	46/21	0.31	0.66	0.83
17	08-18 Oct.	46/39	4.20	6.45	11.13	46/18	22.21	63.93	58.91	46/23	1.45	3.94	3.85
18	05-16 Nov.	46/25	2.73	9.66	7.25	46/25	15.11	46.76	40.07	46/12	0.18	0.44	0.49
19	03-13 Dec.	46/36	9.36	15.67	24.83	46/33	69.49	121.86	184.28	46/11	0.61	1.70	1.62
	1980												
20	07-19 Jan.	46/42	80.55	149.11	213.62	46/42	69.65	159.18	184.72	46/11	0.28	0.65	0.75
21*	11-28 Feb.	46/46	91.49	121.13	242.63	46/43	191.09	717.70	506.76	46/05	0.04	0.11	0.10
22*	10-22 Mar.	46/45	195.18	196.46	517.63	46/44	294.88	651.95	782.02	46/09	0.13	0.33	0.36
23*	07-17 Apr.	46/46	49.90	54.38	132.34	46/40	124.21	367.51	329.41	46/06	0.12	0.42	0.31
24*	12-25 May	46/43	22.17	38.47	58.79	46/33	33.92	117.21	89.96	46/10	1.93	11.43	5.11
25	16-26 Jun.	46/40	7.07	11.86	18.75	46/24	5.73	16.97	15.21	46/03	0.04	0.16	0.10
26	14-25 Jul.	46/30	1.63	2.24	4.31	46/15	4.26	23.54	11.29	46/00	0.00	0.00	0.00

*Cruises that were concurrent with CalCOFI cruises.

TABLE 4
Summary of Egg and Larval Abundance of Northern Anchovy and Larval Abundance of Pacific Sardine from CalCOFI Cruises during 1978-80

		Engraulis larvae				*Engraulis* eggs				*Sardinops* larvae			
Cruise	Dates	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	Est. # larvae region 7 (x 10^9)	# Sta./ positive	$\bar{x}$ eggs •m^{-2}	Std. dev.	Est. # eggs region 7 (x 10^9)	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	Est. # larvae region 7 (x 10^9)
	1978												
7801	05-24 Jan.	42/36	63.96	57.23	4,416.8	42/35	45.09	74.89	3,113.7	42/00	0.0	0.0	0.0
7803	18 Feb.-06 Mar.	42/42	267.81	356.41	18,493.6	42/36	79.99	133.41	5,523.7	42/02	0.071	0.39	4.9
7804	29 Mar.-14 Apr.	42/36	156.46	204.47	10,804.3	42/26	157.24	309.91	10,858.2	42/01	0.007	0.05	0.5
7805*	23 May-02 Jun.	34/29	42.74	134.14	2,951.4	34/13	10.96	36.21	756.8	34/01	0.029	0.17	2.0
7807*	20 Jun.-06 Jul.	41/18	6.75	8.64	466.1	41/08	1.47	5.89	101.5	41/02	0.039	0.17	2.7
7808	31 Jul.-16 Aug.	42/18	6.43	18.77	444.0	42/09	6.46	26.39	446.1	42/02	0.036	0.17	2.5
	1979												
7901*	15-22 Jan.	24/21	29.24	55.96	2,019.2	24/17	37.70	73.99	2,603.4	24/00	0.0	0.0	0.0
7902	19-28 Feb.	24/22	233.39	264.53	16,116.7	24/14	96.61	181.61	6,671.4	24/00	0.0	0.0	0.0
7903*	02-08 Mar.	27/25	117.38	144.40	8,105.7	27/17	44.80	80.31	3,093.7	27/00	0.0	0.0	0.0
7904*	06-17 Apr.	23/23	84.08	95.05	5,806.1	23/17	185.44	349.12	12,805.6	23/00	0.0	0.0	0.0
7905	30 Apr.-16 May	28/26	57.35	63.74	3,960.3	28/15	48.72	93.28	3,364.4	28/00	0.0	0.0	0.0
	1980												
8003a*	24 Feb.-02 Mar.	24/24	105.77	108.63	7,303.9								
8003b*	27 Mar.-06 Apr.	20/19	204.38	201.25	14,113.5								
8004*	11-29 Apr.	29/26	94.16	226.37	6,502.2		Data not available				Data not available		
8005*	24-30 May	24/17	56.75	117.63	3,918.9								

*Cruises that were concurrent with ICHS cruises.

isobath (2.2 larvae•m^{-3}). Extrapolation of a line fitted to the four X's in Figure 3 ($Y = 2.63 - 14.07/X$) gives an average density estimate of 2.3•m^{-3} at the 43-m isobath (i.e., 99•m^{-2}). The asymptote suggests that the majority of anchovy occurred within the vertical depth range sampled by ICHS. Ahlstrom (1959) found that 85 percent of the anchovy larvae were distributed in the upper 48 m.

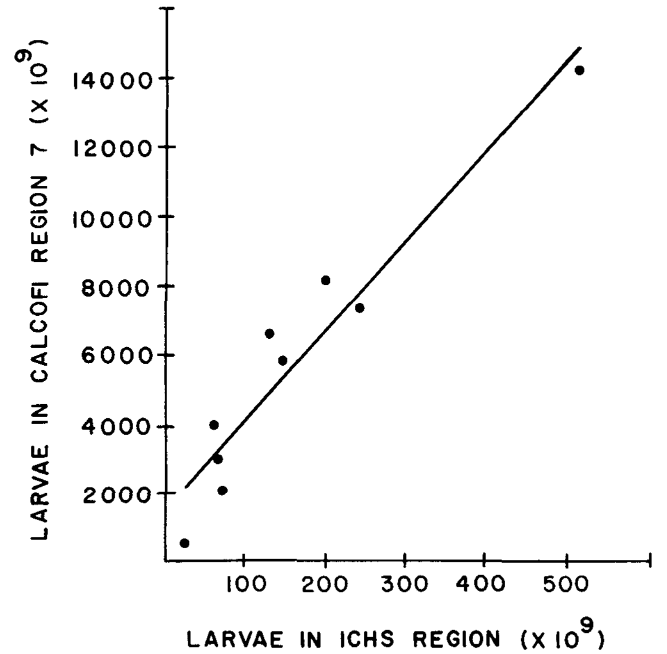

Figure 2. Monthly census estimates of northern anchovy larvae in the ICHS region versus CalCOFI region 7 ($Y = 1530.0 + 25.65X$; $r^2 = 0.92$).

Larval abundance was not well correlated with distance from shore within the ICHS region (Figure 4), and no clear relationship was evident between the highest mean station abundance and distance from shore based on five complementary CalCOFI-ICHS transects (Figure 5). For example, along transect 80,

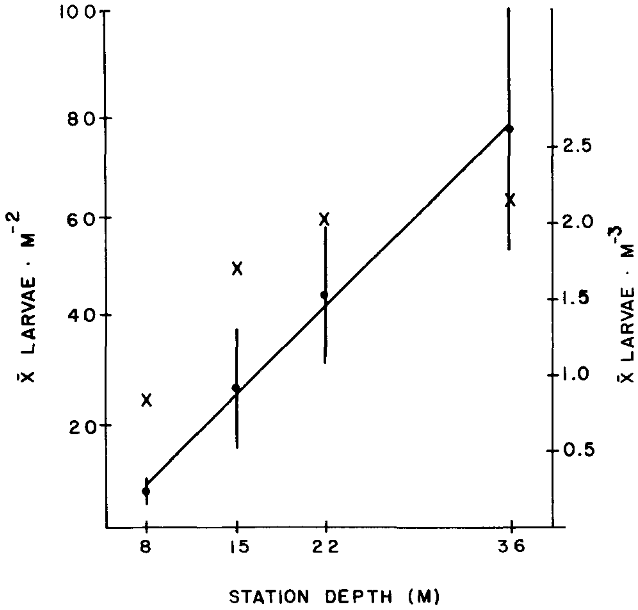

Figure 3. Average abundance per m^2 and 95 percent confidence intervals of northern anchovy larvae by station depth within the ICHS region ($Y = 11.76 + 2.51X$). The points represent mean abundance by isobath from all Phase I transects and from those Phase II transects (three) where data from 8-m, 15-m, 22-m, and 36-m isobaths were collected (N=453). The X's represent equivalent data, expressed as mean abundance per m^3.

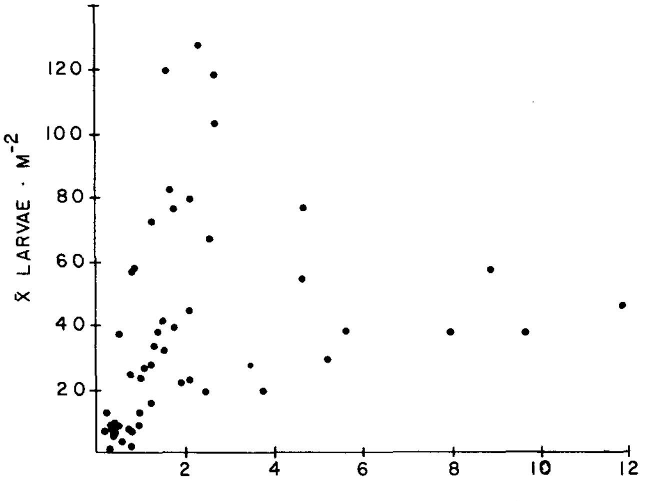

Figure 4. Mean station abundance of northern anchovy larvae by distance from shore. The points represent data from stations as described in Figure 3.

highest mean densities of larvae were found 1.2 km from shore; along transect 90, highest mean densities were found 103.6 km from shore. We have no explanation for the prominent dip in larval abundance that occurred along at least three of the five transects at distances between 10 and 20 km from shore.

We examined the variability of anchovy larvae in the longshore dimension by both average transect abundance and rank transect abundance (Tables 5 and 6). Table 5 summarizes all 1978-80 CalCOFI data along five transects and complementary data from nine CalCOFI-ICHS cruises. The within-transect averages between CalCOFI and ICHS are in surprisingly close agreement, while variability between transects is a factor of over 10 for CalCOFI transects and a factor of about 5 for ICHS transects. Because the standard deviations of the transect means were large, nonparametric techniques were used to test the signifi-

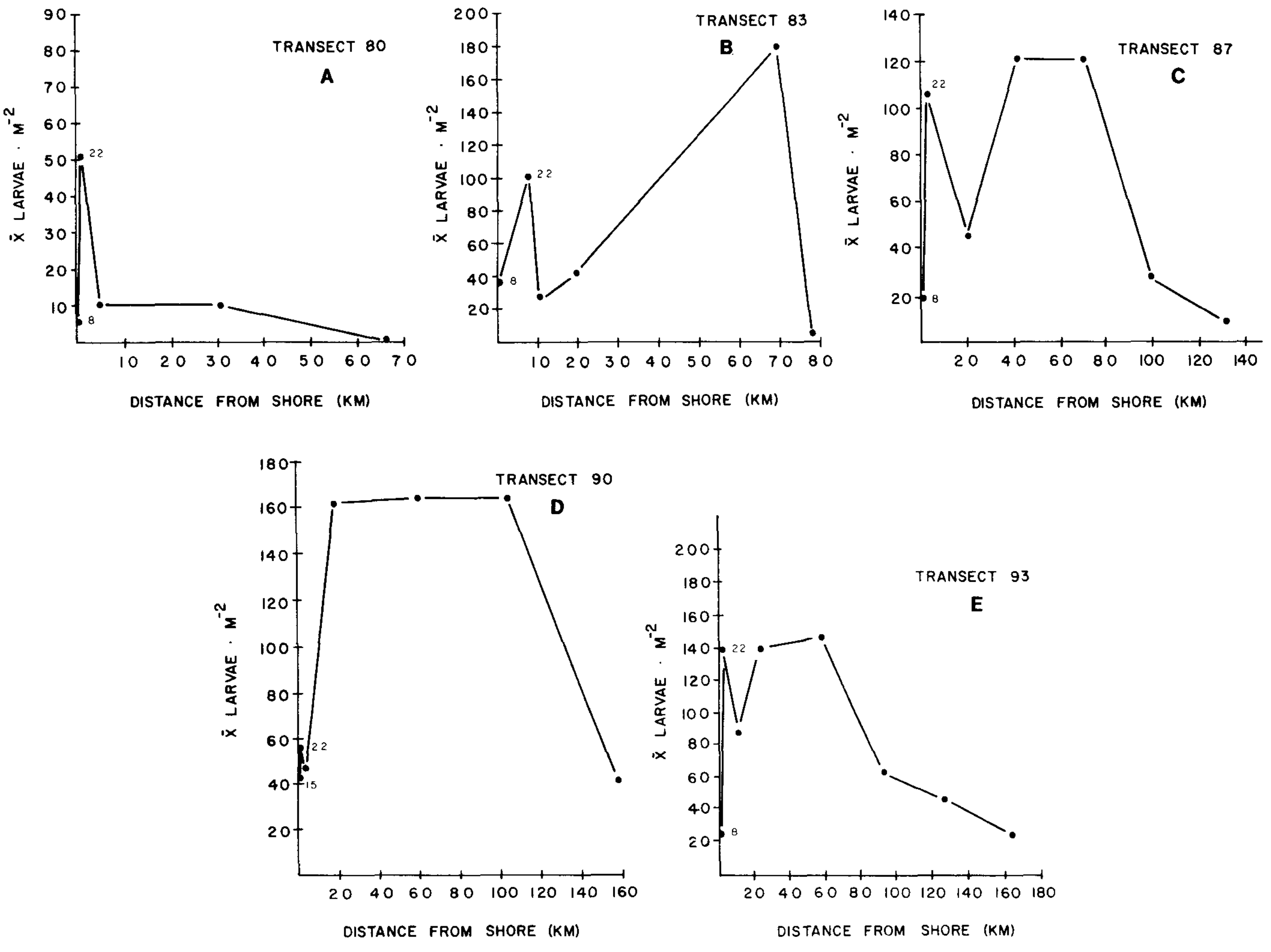

Figure 5. Average abundance of northern anchovy larvae along complementary CalCOFI-ICHS transects 80 *(A)*, 83 *(B)*, 87 *(C)*, 90 *(D)*, and 93 *(E)*. Mean station data were based on 9 concurrent CalCOFI-ICHS cruises (Tables 3 and 4) and only those CalCOFI and ICHS stations that were sampled during 1978, 1979, and 1980. ICHS stations are labeled.

TABLE 5

Abundance of Northern Anchovy Larvae along Complementary CalCOFI-ICHS Transects

	ICHS			CalCOFI					
	Nine concurrent cruises						All cruises 1978-1980		
Transect	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.
80	28/23	20.2	68.5	28/18	8.9	18.7	50/31	15.6	39.2
93	28/28	52.0	99.0	32/29	64.3	208.5	56/52	82.5	184.4
87	26/26	65.8	80.7	53/50	56.7	92.0	103/91	86.8	127.1
90	23/22	60.7	84.1	53/46	118.7	163.9	99/85	182.9	296.0
93	27/27	96.4	116.4	58/53	80.1	108.5	106/92	93.5	131.0

Concurrent cruises are designated in Tables 3 and 4.

cance of the transect differences. All station data from the complementary cruises were used to calculate mean transect abundance for each CalCOFI and ICHS cruise. Transects were ranked, and the ranks were summed across cruises for both CalCOFI and ICHS data. The results of the Kruskal-Wallis one-way analysis of variance by ranks (Siegel 1956) showed that transect ranks were significantly different (Table 7).

While a north (low)-to-south (high) gradient in abundance was suggested by the above rankings, a similar analysis of transect abundance within the ICHS region, which encompasses data from all seasons, showed different results. Table 6 summarizes ICHS transect data on the basis of stations over the 8-m and 22-m isobaths during Phase I and Phase II. We tested the rank sums of larval abundance for 10 transects across 20 months by the Kruskal-Wallis test as above.

TABLE 7

Transect Ranks of Northern Anchovy Egg and Larvae and Pacific Sardine Larval Abundance Based on the Kruskal-Wallis Analysis of Variance by Ranks

	CalCOFI		ICHS		
	Nine concurrent cruises		8- & 22-m isobaths across 20 months		
Transect	*Engraulis* larvae ranking		*Engraulis* larvae ranking	*Engraulis* egg ranking	*Sardinops* larvae ranking
80	5	5	10	10	10
81.5			3	3	8
83	4	4	1	1	3
85			6	6	7
87	3	2	7	2	1
88			2	4	2
90	1	3	8	9	6
91			5	7	9
93	2	1	9	5	5
95			4	8	4
	$p<0.01$	$p<0.02$	$p<0.30$	$p<0.001$	$p<0.01$

The probability of equal transect ranks is indicated below each column.

The 10 transects were not significantly different ($p<0.30$ of being equal), and no pattern or gradient was evident.

Northern Anchovy Eggs

Available data on *E. mordax* eggs are summarized in Tables 3 and 4. The highest mean density of eggs within the ICHS region was found in October 1978. However, over 99 percent of the eggs collected during the month were found along one transect (83), where stations over the 22-m and 36-m isobaths (4.5 km apart) yielded 997 and 17,904 eggs•m^{-1}, respectively.

TABLE 6

Transect Data on Northern Anchovy Egg and Larval Abundance along 8-m and 22-m Isobaths within the ICHS Region

	Engraulis larvae						*Engraulis* eggs					
	Phase I & II			Phase II			Phase I & II			Phase II		
Transect	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	# Sta./ positive	$\bar{x}$ eggs •m^{-2}	Std. dev.	# Sta./ positive	$\bar{x}$ eggs •m^{-2}	Std. dev.
80	40/30	32.2	111.0	24/19	47.9	141.0	40/12	4.0	21.5	24/06	6.3	27.8
DR	—	—	—	24/17	52.0	141.3	—	—	—	24/13	37.1	167.8
81.5	40/31	29.4	66.6	24/18	36.2	82.6	40/27	15.0	43.3	24/18	21.9	54.8
RN	—	—	—	24/24	82.6	171.9	—	—	—	24/21	277.1	697.7
83	40/40	45.6	86.9	24/24	60.7	108.0	40/36	240.1	522.5	24/22	252.1	622.1
OB	—	—	—	24/23	43.8	97.7	—	—	—	24/24	137.6	199.7
85	40/38	20.5	38.6	24/23	21.6	45.7	40/31	52.0	235.7	24/22	83.7	302.6
MU	—	—	—	24/23	46.0	114.8	—	—	—	24/16	34.7	100.8
87	38/33	39.4	69.0	24/21	41.4	74.3	38/27	156.4	776.4	24/19	247.3	972.8
RB	—	—	—	24/21	31.8	54.8	—	—	—	24/11	30.1	71.5
PV*	—	—	—	24/21	17.2	27.9	—	—	—	24/15	12.9	20.8
88	40/39	27.6	48.5	24/23	30.6	57.8	40/30	56.6	163.9	24/20	89.4	206.5
BA	—	—	—	24/19	19.2	45.1	—	—	—	24/16	8.3	16.3
90*	40/35	24.3	58.1	24/20	29.7	73.1	40/22	5.6	16.3	24/12	3.2	6.7
SO	—	—	—	24/20	26.5	66.7	—	—	—	24/16	22.3	85.3
91	40/35	23.6	50.9	24/22	28.2	61.3	40/23	44.1	134.2	24/14	21.3	46.6
CD	—	—	—	24/18	30.1	70.2	—	—	—	24/12	3.8	8.8
93	39/30	39.6	72.6	24/18	36.3	66.3	39/17	15.3	74.9	24/10	2.9	7.1
MB	—	—	—	24/18	21.3	45.8	—	—	—	24/11	4.3	11.5
95	40/35	17.7	32.7	24/20	16.7	31.9	40/28	30.1	84.8	24/16	17.8	52.3

*Data from 15-m isobath substituted for unavailable 8-m data.

The graph of anchovy egg abundance versus station depth (Figure 6) shows points that both include and exclude the catch of eggs at transect 83, 36-m isobath during October 1978. Also included in the graph are average abundance of eggs per unit volume of water. The mean density of eggs throughout the water column decreased between the 22-m and 36-m isobaths, probably because of their relatively shallow vertical distribution, as noted for the larvae.

Longshore variability of eggs, based on mean transect abundance along the 8-m and 22-m isobaths (Table 6), approached two orders of magnitude. The highest spawning activity occurred in the region off transect 83, as well as transects 87 and 88. The rank differences between transects were highly significant ($p<0.001$) based on the Kruskal-Wallis test as described above (Table 7). The longshore rank of anchovy larvae was related to the longshore rank of anchovy eggs ($p<0.20$) based on the Kendall coefficient of concordance ($w=0.80$) (Siegel 1956). Also, monthly mean egg abundance corresponded reasonably well with mean larval abundance (Figure 7).

Comparisons of egg abundance between ICHS and CalCOFI regions require additional data. Since the 1980 CalCOFI cruises were not sorted for eggs, data from only five concurrent cruises were available. The CalCOFI 0.505-mm mesh net may underestimate egg abundance by a factor of three or more as a result of extrusion, compared to the 0.333-mm mesh net used by ICHS (Smith, P. 1975. Time series of the abundance of anchovy eggs in the California Current region. Admin. Rep. Unpub.).

Pacific Sardine Larvae

Sardine larvae occurred infrequently during most months. Overall, 18 percent of the 861 ICHS samples captured sardine, but estimates of abundance during some months may be reliable only on a presence/absence basis. However, the increase in the number of stations within the ICHS region where sardine larvae occurred between 1978-79 and 1979-80 is noteworthy. Tables 3 and 4 suggest that sardine may have moved from offshore in 1978 to onshore during 1979, but this observation is based on only eight occurrences within the CalCOFI region.

The abundance of sardine larvae as a function of bottom depth within the ICHS region as shown in Figure 8 was based on 453 samples with 73 occurrences, i.e., the same sample data set used to summarize anchovy egg and larval abundance in Figures 3 and 6. These data indicate that the mean density of larvae was highest at the 15-m isobath.

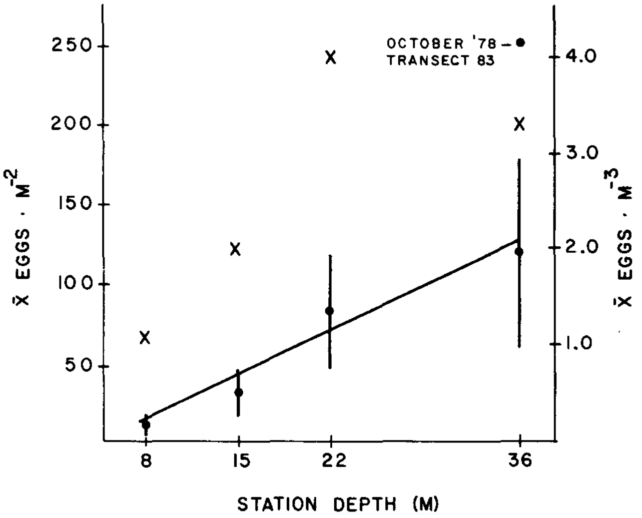

Figure 6. Average abundance per m^2 and 95 percent confidence intervals of northern anchovy eggs by station depth within the ICHS region ($Y=-22.03+4.12X$). The points and X's represent data from stations as described in Figure 3 with one exception: the datum from October 1978 transect 83, 36-m isobath was not included, as indicated. Inclusion of the one large sample gives a mean of 7.59-m^{-3} for the 36-m isobath.

Between June 1978 and July 1979, sardine larvae were found most often along transects 87, 88, 93, and 95; no larvae were found north of transect 85. By September and October 1979, sardine larvae were captured at ICHS stations throughout the bight. Transects from Santa Monica Bay to Seal Beach yielded frequent catches during 1980 (Table 8). A noteworthy peak in estimated abundance in May 1980 resulted primarily from a large number of larvae at the 22-m

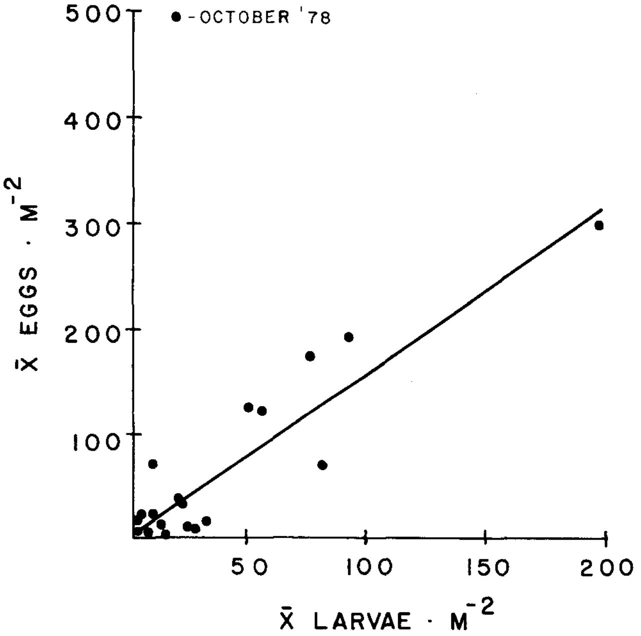

Figure 7. Average abundance of northern anchovy eggs versus larvae for each ICHS cruise ($Y=3.51+1.58X$; $r^2=0.84$). The October 1978 data were omitted.

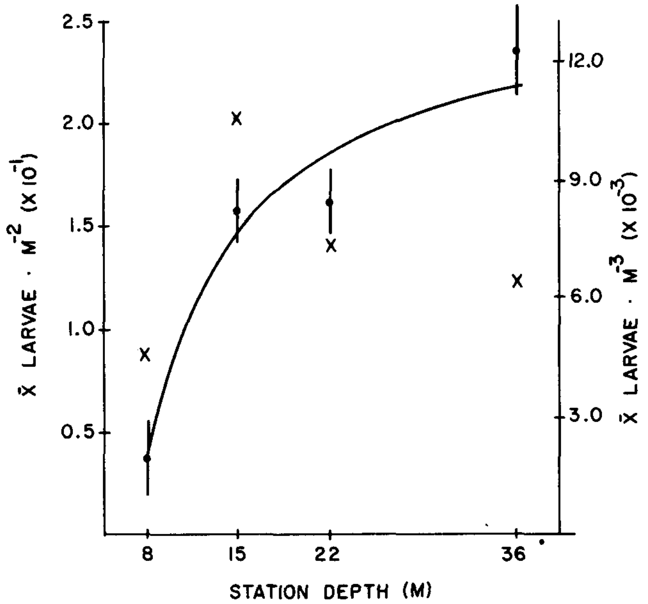

Figure 8. Average abundance per m² and 95 percent confidence intervals of Pacific sardine larvae by station depth within the ICHS region (Y=0.27-1.88/X; r²=0.95). The points and X's represent data from stations as described in Figure 3.

TABLE 8

Transect Data on Pacific Sardine Larvae Abundance along 8-m and 22-m Isobaths within the ICHS Region

	Phase I & II			Phase II		
Transect	# Sta./ positive	x̄ larvae •m⁻²	Std. dev.	#Sta./ positive	x̄ larvae •m⁻²	Std. dev.
80	40/01	0.005	0.034	24/01	0.009	0.04
DR	—	—	—	24/01	0.01	0.05
81.5	40/02	0.01	0.05	24/02	0.02	0.07
RN	—	—	—	24/05	0.07	0.16
83	40/06	0.29	0.98	24/06	0.48	1.24
OB	—	—	—	24/04	0.06	0.17
85	40/03	0.14	0.73	24/02	0.22	0.94
MU	—	—	—	24/07	0.35	0.87
87	38/14	0.44	1.10	24/11	0.65	1.34
RB	—	—	—	24/12	0.55	1.22
PV*	—	—	—	24/12	0.72	1.55
88	40/10	0.85	3.93	24/09	1.40	5.04
BA	—	—	—	24/04	0.09	0.29
90*	40/04	0.04	0.15	24/03	0.05	0.16
SO	—	—	—	24/03	0.05	0.14
91	40/01	0.05	0.34	24/01	0.09	0.44
CD	—	—	—	24/05	0.08	0.18
93	39/05	2.17	12.41	24/03	3.43	15.80
MB	—	—	—	24/06	0.26	0.88
95	40/06	0.16	0.44	24/04	0.15	0.41

*Data from 15-m isobaths substituted for unavailable 8-m data.

station off Del Mar. The Kruskal-Wallis test showed that transect differences were significant ($p<0.01$).

The overall temporal abundance of sardine larvae within the ICHS region is of interest, especially as it compares with the abundance of anchovy eggs and larvae (Figure 9). If one considers the monthly time series during 1979-80, when the frequency of sardine occurrence was relatively high (and if one ignores the one large May 1980 sample), sardine larvae were most abundant during late summer and fall; anchovy were least abundant during this same period. Ahlstrom (1967) showed that (during the 1950s) sardine spawning during the second half of the year was confined to a southern population and to waters off central Baja California. One might speculate that the relatively large occurrence of sardine larvae in the late summer and fall indicated that some southern fish had moved north and contributed to the peak abundance of sardine larvae off southern California. If a similar seasonal spawning cycle persists in subsequent years, CalCOFI surveys conducted during the first half of the year to monitor anchovy spawning may miss peak abundance of sardine larvae off southern California.

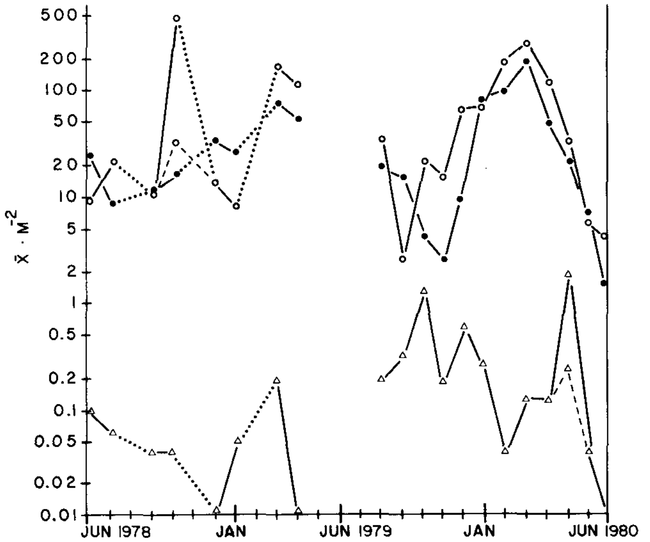

Figure 9. Temporal distribution of northern anchovy eggs (circles), larvae (dots), and Pacific sardine larvae (triangles) within the ICHS region. Dotted lines span months without data. Dashed lines indicate exclusion of unusually large samples from October 1978 transect 83, 36-m isobath (anchovy eggs) and May 1980 transect 93, 22-m isobath (sardine larvae).

DISCUSSION

The spawning habitat of the central subpopulation of northern anchovy extends over 500,000 km² of ocean—roughly between central Baja California and central California—but changing environmental factors apparently restrict the majority of spawning activity to much smaller regions during any one season. Major onshore-offshore and north-south shifts in larval abundance are evident during some years (Hewitt 1981; Smith and Eppley 1981). Broad temporal and spatial variability is a recurring feature of northern anchovy spawning; 20 months of ICHS data spread over 26 months should be interpreted in this context.

Since 1966, the area between Pt. Conception and

San Diego (primarily region 7) has accounted for an average of 64 percent of all larvae from the central subpopulation (Hewitt 1981). Based on the above percentage and the ICHS census estimates, about 2 percent of all anchovy larvae spawned by the central subpopulation were found in the ICHS region. Because densities of anchovy larvae were comparable in concurrent ICHS and CalCOFI cruises, inclusion of ICHS data with existing CalCOFI region 7 data would do little to alter overall abundance estimates used for biomass calculations (Pacific Fishery Management Council 1978). We conclude that the nearshore region off southern California was not a preferred habitat for the adult spawning biomass of northern anchovy during 1978-80. Smith and Duke (1975) reached a similar conclusion on the basis of CalCOFI cruises that sampled nearshore stations during 1964.

Anchovy spawning activity in the ICHS region indicates activity in larger CalCOFI regions. For example, changes in total number of larvae in region 7 were reflected by proportional changes in the ICHS region (Figure 2). Moreover, average density of larvae in ICHS samples during 1979-80 (Phase II) increased 31 percent compared to 1978-79 (Phase I); CalCOFI estimates of larval abundance for the entire central stock increased 36 percent during the same period (Stauffer and Picquelle 1981).

The apparent increase of sardine larvae in nearshore waters is of interest, but data are too infrequent to estimate what proportion of the larvae were spawned in respective ICHS and CalCOFI regions.

A direct relationship is presumed to exist between the abundance of planktonic eggs and larvae of northern anchovy and Pacific sardine and the size of their respective spawning stocks (Smith 1972; Smith and Eppley 1981; Parker 1980). However, numbers of eggs and larvae that survive to recruitment may vary independently of stock size, apparently influenced by environmental factors that are not understood or measured (Lasker and Smith 1977; Lasker 1978; Smith 1978; Bakun and Parrish 1980). The number of larvae that survive to recruitment within the shallow coastal region, i.e., the region's importance as a nursery ground, is not yet clear. Recruitment from any particular region may not be a direct function of the abundance of eggs or young larvae within the area because the environmental factors that favor spawning of adult anchovy (temperatures of 13-18°C and an abundance of available calories, such as large zooplankters) may not coincide with the environmental requirements for larval survival, which include patches of unarmored dinoflagellates or copepod nauplii in a stable ocean, and the absence of predators such as certain large zooplankters and adult anchovy (Hewitt 1982). Currents might transport eggs or young larvae away from spawning grounds to areas favorable or unfavorable for survival (Hunter 1977; Lasker and Smith 1977; Lasker 1978; Hewitt and Methot 1982).

The abundance of eggs and larvae within the ICHS region was consistently greater in certain areas. Transects within the Santa Barbara Channel from Rincon through Ormond Beach were important regions of anchovy spawning, as were transects off Playa Del Rey and Seal Beach. Sardine larvae occurred most frequently at transects throughout Santa Monica Bay and downcoast off Palos Verdes and Seal Beach. Cojo Bay yielded the least anchovy and sardine.

A discussion of environmental features common to the nearshore transects where large numbers of eggs and larvae were found is beyond the scope of this paper; indeed, such a discussion would be premature until we describe how the length-frequencies of the larvae vary between transects; i.e., are large larvae found consistently along certain transects?

Preliminary length-frequency data from ICHS stations show relatively large numbers of 20-30-mm anchovy larvae; larvae in similar size classes are virtually nonexistent in CalCOFI samples (Hewitt, pers. comm.).

We emphasize that the inherent imprecision of sampling fish eggs and larvae over wide areas leads to biases that must be identified and, if possible, quantified before one can understand the relative nursery function of the ICHS nearshore region. For northern anchovy and sardine larvae, these biases may include escapement and extrusion through the meshes of the net and avoidance of the net mouth. These and other factors, such as temperature, that result in sampler catch bias have been discussed by Zweifel and Smith (1981), who offer larval size-specific adjustment factors for correcting raw survey data. Hewitt and Methot (1982) have recently adopted these techniques for 1978 and 1979 CalCOFI data.

If the number of surviving larvae is proportionally greater, relative to numbers of eggs spawned, in the nearshore region versus offshore areas, or between nearshore transects, the techniques of Zweifel and Smith (1981) should be sensitive to such differences. We plan to test these hypotheses in the near future.

ACKNOWLEDGMENTS

We gratefully acknowledge the technical assistance of the ships' crews and laboratory staffs involved with the arduous tasks of collecting, sorting, and identifying ichthyoplankton from CalCOFI and ICHS surveys. Gerald McGowen supervised the sorting and taxonomic standardization of all ICHS samples. We thank Robert Lavenberg for his efforts as coprincipal investigator of the ICHS project.

Donna Cooksey and T.J. Mueller assisted in compiling and summarizing the ICHS data. Richard Charter and Roger Hewitt helped compile the CalCOFI data. We thank an unnamed reviewer for suggestions that improved the original manuscript. The senior author is indebted to Reuben Lasker and other staff at the NMFS Southwest Fisheries Center for providing office space and a stimulating atmosphere in which to work.

The ICHS project was supported by the Southern California Edison Company and by the NOAA Office of Sea Grant, Department of Commerce, under grant numbers 04-8-M-01-186, NA79AA-D-00133, and NA80AA-D-00100.

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DISTRIBUTION OF ICHTHYOPLANKTON IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Larval fish were sampled by oblique 1-meter net and neuston net tows in the Southern California Bight quarterly from 1974 through 1976. The northern anchovy, *Engraulis mordax,* was much more abundant in both types of collections than were all other kinds of larvae combined, but some other fairly common species were found in only one type of tow. Subjective evaluation and analysis of recurrent groups established larval groupings that were distinguished primarily by nearshore versus offshore distribution and summer-fall versus winter-spring occurrence.

RESUMEN

Larvas de peces muestreadas trimestralmente entre 1974 y 1976 en arrastres oblicuos de redes neuston y de 1 metro en la Bahía del Sur de California. En ambos tipos de recoleciones, la anchoveta *Engraulis mordax* era mucho más abundante que todas las otras clases de larvas combinadas, pero otras especies bastante comunes fueron encontradas en sólo un tipo de arrastre. A través de la evaluación subjetiva y el análisis de groups recurrentes se establecieron agrupaciones de larvas que se distinguieron principalmente por su distribución, cerca de la costa o mar afuera, y aperecer durante los periodos de verano-otoño o en invierno-primavera.

INTRODUCTION

In studies of ichthyoplankton off California over the last three decades, the California Cooperative Oceanic Fisheries Investigation (CalCOFI) has emphasized the sampling of eggs and larvae of California Current pelagic species such as the sardine, which declined dramatically in the late 1940s. Recently, importance of recreational fisheries and increased human modification of California's nearshore zone have prompted concern for the fish populations residing there.

The distributions and abundances of some demersal species with pelagic eggs and larvae have been studied in samples from the CalCOFI surveys (Ahlstrom 1965), and many groups of inshore fishes are represented as larvae in CalCOFI collections, but the early surveys did not adequately sample areas close to shore. Depth increases rapidly with distance from shore off southern California, and the spawning of some neritic species is presumably restricted to a narrow band along the coastline and around the channel islands, banks, and seamounts. Pelagic larvae of such species are subject to dispersal by currents and must somehow remain in or return to the coastal zone in sufficient numbers to maintain adult populations (cf. Leis and Miller 1976 for larvae in Hawaiian waters). The larvae of some inshore spawners may develop rapidly enough to maintain their position in the nearshore zone, even though affected by longshore currents; such species would not be well represented in offshore surveys. Many larvae of species with longer larval life must be carried offshore by currents, especially by Ekman drift during periods of upwelling. Shoreward transport of such larvae by subsurface currents generated during upwelling is also possible (Peterson, Miller, and Hutchinson 1979).

The Southern California Bight lies inshore of the southward-flowing California Current. The bight's surface circulation is generally a cyclonic gyre; nearshore currents alternate between flowing south-southwest or north-northwest, though the latter flow dominates (Tsuchiya 1980). This study was carried out to refine the knowledge of seasonal and areal distributions of pelagic larval fish within the Southern California Bight, emphasizing the nearshore zone not sampled by CalCOFI.

METHODS

Southern California Bight Study (SCBS) station positions were chosen to represent quasi-logarithmic distances from the mainland shore (Table 1); SCBS lines 300, 200, and 100 correspond to CalCOFI lines 87, 90, and 93, respectively (for a map, see Eppley et al. 1977, or Eppley, Sapienza, and Renger 1978). SCBS cruises 1 through 9 cover more than two years—from September 1974 through January 1977.

Manuscript received November 14, 1981.

TABLE 1
Depths and Locations of Stations Sampled for Ichthyoplankton in the Southern California Bight Study (SCBS), 1974–77

Station number	Depth (m)	Distance offshore (km)	Position	
301	16	0.9	33°54.3′N	118°25.5′W
302	18	1.9	33°55.1′N	118°27.2′W
303	42	5.6	33°53.8′N	118°28.8′W
304	320	19	33°50.4′N	118°36.2′W
305	920	46	33°45.5′N	118°47.6′W
306	1650	98	33°30.1′N	119°20.0′W
201	36	0.9	33°29.4′N	117°44.9′W
202	54	1.9	33°29.0′N	117°45.5′W
203	90*	5.6	33°28.0′N	117°47.5′W
205	730	52	33°17.3′N	118°10.4′W
206	1240	96	33°07.0′N	118°31.3′W
San Onofre	5	0.5	33°20.1′N	117°30.4′W
101	20	0.9	32°57.4′N	117°16.5′W
102	38	1.9	32°57.3′N	117°17.3′W
103	230*	5.6	32°56.8′N	117°18.9′W
105	1000	41	32°52.2′N	117°37.8′W
106	1850	107	32°31.6′N	118°07.0′W

*Station position and depths of #103 and 203 varied.

Stations were sampled quarterly with the exception of December 1974, when no cruise was undertaken.

Ichthyoplankton was collected with oblique plankton net hauls and surface or neuston net hauls made simultaneously at each station, except at some very shallow stations where only the neuston net was used. Oblique hauls were made with the standard CalCOFI-type net constructed of 505-μm nylon netting with a mouth diameter of one meter and a straining surface-(pore area)-to-mouth-area ratio of approximately five to one. A digital flow meter was centered in the circular mouth opening, attached to the tubular metal frame.

Oblique samples were collected, preserved, and processed following CalCOFI guidelines as described by Kramer et al. (1972). During cruise SCBS 4, the maximum amount of towing wire let out was reduced from 300 to 200 m. In shallow water on all cruises, the depth of tow was adjusted to avoid hitting the bottom.

The neuston frame carried an identical net to that used for oblique hauls, but the mouth of the net was modified from a circle to a rectangle, and for buoyancy, styrofoam floats were placed inside the frame ends (Ahlstrom and Stevens 1976). No flow meter was attached; the neuston net was towed for a minimum of 10 minutes. Neuston collections were preserved and processed similarly to the oblique collections.

All net tows were done during daylight hours, leading to two potential sources of bias. The abundances of those juveniles and late larval stages that are able to see and avoid the net are underestimated. Also, a few species (e.g., *Tarletonbeania crenularis*) would be caught in greater numbers in night hauls because they migrate to the surface waters then.

Most samples were completely sorted for all fish eggs and larvae; for stations 303, 305, 306, 205, and 105 on cruise SCBS-2, only 25 percent of the anchovy larvae were removed and counted, but all other fish larvae were removed from these samples.

Identification of larvae was to species level when possible, but taxonomic difficulties exist in several important groups. The most notable is the rockfish genus *Sebastes,* which includes 48 species known to spawn in the Southern California Bight (Miller and Lea 1972). The genera *Citharichthys* (sand dabs), *Hypsoblennius* (blennies), and *Paralabrax* (basses) each include three local species.

We directly compared the distributional records of different taxa to obtain subjective patterns, at least for the relatively common species. Because the number of samples was fairly large, we also applied a statistical grouping technique—the analysis of recurrent groups—that has previously been applied to communities of adult fish (e.g. Fager and Longhurst 1968), benthos (e.g. Lie and Kelley 1970), and zooplankton (e.g. Fager and McGowan 1963). We chose this approach because of the infrequent occurrence of most species (Table 2), and analyzed data from oblique and neuston tows separately. We tested several levels of affinity at which to form groups, since the level of affinity determines how two species can differ in frequency of occurrence and still be placed in the same group. We also analyzed both the entire set of data and the subset of species occurring at least 5 times; this had relatively little effect on major groupings, though analysis of the complete set resulted in some groups of rare species that were not found in the subset analysis.

The species in the resulting groups are frequent components of each other's biotic environments (or, in the extreme case, the very common species in a group are usual components of the environment of the group's very rare species), both seasonally and geographically, though our method of sampling precludes detecting differences in vertical distributions of species in the same group (see below). Although the members of a group necessarily have similar patterns of occurrence, they need not have similar patterns of abundance. The latter relation was tested for the major groups defined from oblique hauls by calculating a coefficient of rank correlation (Tate and Clelland 1957) between the abundances of species in each possible pairing for those samples in which the entire group occurred, and establishing a matrix of correlation coefficients for all pairs within the group.

TABLE 2

Taxa That Occurred in at Least 5 Oblique or Neuston Tows in the Southern California Bight, Ranked in Order of Decreasing Numerical Abundance in Oblique Tows

	Zone	Spawning type	Mean larvae/10 m^2	% of total larvae for oblique hauls	Mean larvae/10 m^2 in positive hauls	No. of occurrences	% of occurrences in 112 oblique hauls	Rank by occurrence in oblique hauls	% of occurrences in 127 neuston hauls
1. *Engraulis mordax*	C	P	733.2	82.83	774.8	106	94.6	1.0	57.4
2. *Sebastes* spp.	C	O	36.5	4.12	52.4	78	69.6	2.0	19.7
3. *Leuroglossus stilbius*	O	P	33.0	3.72	82.0	45	40.2	5.0	
4. *Stenobrachius leucopsarus*	O	P	19.5	2.20	42.0	52	46.4	4.0	
5. *Genyonemus lineatus*	C	P	15.0	1.70	44.3	38	33.9	7.0	14.2
6. *Merluccius productus*	O	P	14.4	1.63	59.7	27	24.1	12.0	
7. *Citharichthys* spp.	C	P	5.0	0.68	22.0	60	53.5	3.0	3.9
8. *Bathylagus ochotensis*	O	P	3.9	0.44	15.6	28	25.0	10.0	
9. *Paralichthys californicus*	I	P	3.0	0.34	8.6	39	34.8	6.0	
10. *Hypsoblennius* spp.	I	D	2.2	0.25	12.8	19	17.0	15.5	18.1
11. *Pleuronichthys verticalis*	I	P	2.1	0.24	8.4	28	25.0	10.0	
12. *Seriphus politus*	I	P	1.9	0.22	12.0	18	16.1	17.5	5.5
13. *Paralabrax* spp.	I	P	1.8	0.20	7.7	26	23.2	13.0	
14. *Peprilus simillimus*	C	P	1.6	0.18	9.7	18	16.1	17.5	
15. *Triphoturus mexicanus*	O	P	1.3	0.15	6.3	23	20.5	14.0	
16. Gobiidae	C	D	1.2	0.14	4.8	29	25.9	8.0	
17. *Argyropelecus* spp.	O	P	1.1	0.12	4.4	28	25.0	10.0	
18. *Sardinops caeruleus*	C	P	1.0	0.11	15.6	7	6.3	29.0	
19. *Pleuronichthys ritteri*	I	P	0.5	0.06	9.8	6	5.4	32.0	
20. *Parophrys vetulus*	I	P	0.5	0.05	5.4	10	8.9	24.0	
21. *Hypsopsetta guttulata*	I	P	0.5	0.05	4.8	11	9.8	22.0	
22. *Tarletonbeania crenularis*	O	P	0.5	0.06	3.2	19	17.0	15.5	
23. *Argentina sialis*	O	P	0.4	0.05	9.2	5	4.5	36.5	
24. *Oxyjulis californica*	I	P	0.4	0.05	4.9	10	8.9	24.0	
25. *Trachurus symmetricus*	O	P	0.4	0.05	4.2	12	10.7	20.5	6.3
26. *Lampanyctus* spp.	O	P	0.4	0.05	2.8	16	14.3	19.0	
27. *Lyopsetta exilis*	C	P	0.3	0.04	7.2	5	4.5	36.5	
28. *Bathylagus pacificus*	O	P	0.3	0.04	5.3	7	6.3	29.0	
29. Blennioidei	C	D	0.3	0.03	4.2	7	6.3	29.0	
30. *Hippoglossina stomata*	I	P	0.3	0.03	3.8	8	7.1	26.5	
31. *Danaphos oculatus*	O	P	0.3	0.03	3.6	8	7.1	26.5	
32. *Protomyctophom crockeri*	O	P	0.3	0.03	2.7	12	10.7	20.5	
33. *Diogenichthys laternatus*	O	P	0.2	0.03	5.5	5	4.5	36.5	
34. *Bathylagus wesethi*	O	P	0.2	0.02	4.0	6	5.4	32.0	
35. *Stomias atriventer*	O	P	0.2	0.02	3.5	5	4.5	36.5	
36. Clinidae	I	D	0.2	0.02	2.5	10	8.9	24.0	
37. *Tetragonurus cuvieri*	O	P	0.1	0.01	2.8	5	4.5	36.5	
38. *Diaphus theta*	O	P	0.1	0.01	2.0	5	4.5	36.5	
39. *Chromis punctipinnis*	C	D	0.1	0.01	1.9	6	5.4	32.0	
Atherinidae	I	S							24.4
Cololabis saira	C	S							22.8
Exocotidae	C	S							5.5
Medialuna californiensis	C	P							4.7
Girella nigricans	I	P							4.7
Scorpaenichthys marmoratus	C	D							3.9
Hexagrammos decagrammus	C	D							3.9

In cases of ties, the taxon with the greatest abundance in those samples in which it occurred (positive hauls) is ranked first. Unranked taxa occurred at least 5 times only in neuston tows. For "zone", I is inshore, O is offshore, C is inshore and offshore. For "spawning type", P is pelagic oviparous, D is demersal oviparous, O is ovoviviparous, S is a special case. S for Atherinidae indicates demersal in beach sand or floating attached egg mass; S for *Cololabis* and Exocoetidae indicates floating attached egg mass.

RESULTS

Abundances of Taxonomic Categories

Thirty-nine families of larval fish were found in oblique and neuston collections; of these, Engraulidae, Scorpaenidae, Bathylagidae, Myctophidae, Sciaenidae, Bothidae, Merlucciidae, and Pleuronectidae were responsible for over 98 percent of all larvae enumerated in the oblique hauls.

The abundances and/or frequencies of all taxa of larvae that occurred in at least five oblique or five neuston hauls are given in Table 2.

The northern anchovy, *Engraulis mordax,* (the only engraulid sampled) occurred in 95 percent of all oblique hauls (Table 2) and accounted for 83 percent of all larvae enumerated. It also was the most frequent (73 occurrences in 127 hauls) in neuston tows, where anchovy eggs were 15 times more abundant than all other fish eggs.

As expected, the neuston tows gave a somewhat different picture of the relative importance of taxa, though comparisons of absolute abundances are not possible since the volume filtered was not measured. Only 34 kinds of larvae were caught compared to 71 kinds in oblique tows. Atherinids (predominantly the grunion *Leuresthes tenuis*) occurred only twice in oblique tows but were found in almost 25 percent of the neuston tows and were particularly abundant in June 1975 at the shallowest station (San Onofre). The saury, *Cololabis saira,* occurred in 23 percent of the neuston tows and not at all in the oblique tows. The other groups occurring in over 10 percent of the neuston tows were *Genyonemus lineatus* (white croaker), *Sebastes* spp., and *Hypsoblennius* spp., all of which were also frequent in oblique tows. Flying fish (Exocoetidae) and *Hexagrammos decagrammus* (kelp greenling) were never taken in oblique tows, but occurred 7 and 5 times, respectively, in neuston tows.

Conversely, several types of larvae encountered frequently in the oblique tows were found in fewer than 5 neuston tows (*Leuroglossus stilbius, Stenobrachius leucopsarus, Merluccius productus, Paralichthys californicus, Pleuronichthys verticalis, Paralabrax* spp., *Peprilus simillimus, Bathylagus ochotensis, Triphoturus mexicanus, Argyropelecus* spp., and Gobiidae).

Geographical and Seasonal Patterns of Taxa and of Recurrent Groups

General zones of occurrence for larvae, based on cumulative records from both CalCOFI and SCBS cruises, are included in Table 2; Table 3 shows seasonal and inshore/offshore distributional patterns for some important larvae on SCBS cruises. Stations were arbitrarily categorized (see Table 3) with regard to depth and distance from the mainland as "nearshore," "intermediate," or "offshore."

Several kinds of larvae, especially from taxa whose adults are mesopelagic, were found primarily at offshore stations (Table 3A). Larvae of *Leuroglossus stilbius, Bathylagus ochotensis, Argyropelecus* spp. (hatchetfish), and *Merluccius productus* (Pacific hake) occur in greatest abundance below the upper mixed layer (Ahlstrom 1959), and adults of the myctophids *Stenobrachius leucopsarus, Triphoturus mexicanus, Protomyctophum crockeri,* and *Tarletonbeania crenularis* are known to inhabit fairly deep water. Larvae of *Trachurus symmetricus* (jack mackerel) are known to be most abundant in offshore waters (Ahlstrom and Ball 1954; Ahlstrom 1969). Most of the larvae in Table 3A were rarely taken in the inshore zone (except *S. leucopsarus),* but most were well represented in the intermediate zone, and *S. leucopsarus* was most abundant there.

Some larval taxa occurred primarily inshore, though most were also represented in the intermediate zone (Table 3B). The bothid flatfish *Paralichthys californicus* (California halibut) and the pleuronectid flatfish *Pleuronichthys verticalis* (hornyhead turbot) occurred at very few offshore stations, and both early and late larval stages were collected at inshore stations. CalCOFI data from 1955 through 1960 also establish these larvae as being most abundant inshore (Ahlstrom and Moser 1975). Adults of *Hypsoblennius* spp. are restricted to shallow water and spawn demersal eggs, and greatest abundances of larvae on SCBS cruises were in the inshore and intermediate zones. The sardine *Sardinops caeruleus* is included in the inshore group even though earlier CalCOFI data show it occurring both inshore and offshore (Ahlstrom 1959a). Based on the neuston tows, the Atherinidae (grunion) also belong to the inshore group.

Cosmopolitan taxa occurred regularly in all three zones (Table 3C), as did the anchovy (below). *Sebastes* spp. and the bothid flatfishes *Citharichthys* spp. generally exhibited higher concentrations of larvae at offshore and intermediate stations than at inshore stations. Gobies and the Pacific pompano, *Peprilus simillimus,* also occurred in all zones, but numbers of larvae represented were moderate. Larval saury occurred in both nearshore and offshore neuston tows, though they were somewhat more frequent in the latter.

Engraulis mordax exhibits the widest areal and temporal distribution of any larvae sampled, occurring not only on every cruise but at most stations as well. Greatest abundances of larvae appeared in March and June. CalCOFI data show abundance of larvae to be greatest from January through June (Kramer and Ahlstrom 1968). Other kinds of larvae occurring throughout the year in SCBS samples include *Sebastes* spp., *Citharichthys* spp., *Argyropelecus* spp., *Paralichthys californicus,* Atherinidae, and the gobies.

Larvae that occurred most often in June and September were *Hypsoblennius* spp., *Paralabrax* spp., *Sphyraenna argentea* (Pacific barracuda), *Oxyjulis californica* (señorita), *Peprilus simillimus, Trachurus*

TABLE 3
Geographical and Seasonal Distributions of Selected Taxa, Given as Numbers of Larvae per 10m² Sea Surface in Oblique Tows

Season	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore
A. Taxa with offshore larvae									
	Stenobrachius leucopsarus			*Leuroglossus stilbius*			*Bathylagus ochotensis*		
Sept.-Oct.	0	0	0.3	0	0	0	0	0	0.1
Dec.-Jan.	4.5	4.8	18.3	0.1	65.3	125.7	0	5.2	24.7
Feb.-Mar.	20.3	161.5	70.3	0.3	43.8	133.2	0.4	5.4	6.1
June	0	3.6	3.3	0	3.1	2.0	0	0.8	0.9
	Merluccius productus			*Trachurus symmetricus*			*Triphoturus mexicanus*		
Sept.-Oct.	0	0	0.2	0	1.7	2.3	0.6	5.7	6.0
Dec.-Jan.	0.7	4.6	74.2	0	0	0	0	0	0
Feb.-Mar.	0	13.8	51.6	0	0	0	0	0	0
June	0	0	0	0.5	0	0.6	0.6	0.8	1.5
	Argyropelecus spp.			*Protomyctophom crockeri*			*Tarletonbeania crenularis*		
Sept.-Oct.	0	0.5	1.9	0	0.5	1.0	0	0.2	1.2
Dec.-Jan.	0	1.0	2.7	0	0	0.5	0.2	0.7	1.8
Feb.-Mar.	0	1.5	3.3	0	0	1.3	0	0.9	0.5
June	0	1.6	0.3	0	0	0.5	0	0	0.5
B. Taxa with nearshore larvae									
	Genyonemus lineatus			*Paralichthys californicus*			*Sardinops caeruleus*		
Sept.-Oct.	0.6	0	0	8.7	2.1	0.5	6.9	0.5	0
Dec.-Jan.	25.6	36.7	0.5	4.1	1.4	0	0.1	0	0
Feb.-Mar.	102.5	62.7	10.8	5.5	5.2	0.5	0.2	0	0
June	0	0.8	0	2.1	1.6	0.3	0	0	0
	Hypsoblennius spp.			*Paralabrax* spp.			*Seriphus politus*		
Sept.-Oct.	13.1	1.2	0.3	2.9	12.5	2.1	6.5	1.2	0
Dec.-Jan.	0.2	0	0	0	0	0	0.2	0	0
Feb.-Mar.	0	0	0	0.2	0	0	0	0	0
June	2.5	3.0	0.3	4.4	2.4	0.1	11.6	3.5	0
	Pleuronichthys ritteri			*Pleuronichthys verticalis*					
Sept.-Oct.	2.6	0	0	2.1	1.9	0			
Dec.-Jan.	0.7	0	0	1.3	0	0			
Feb.-Mar.	0.3	1.9	0	7.2	7.6	1.9			
June	0	0	0	4.9	3.2	0			
C. Taxa with cosmopolitan larvae									
	Engraulis mordax			*Sebastes* spp.			*Citharichthys* spp.		
Sept.-Oct.	41.0	118.5	73.0	1.6	11.7	2.9	3.0	17.9	5.9
Dec.-Jan.	840.0	214.1	238.4	21.3	29.3	104.6	2.9	3.7	13.8
Feb.-Mar.	490.0	1,567.8	3,074.4	7.0	196.4	94.8	0.6	8.7	3.7
June	1,191.1	1,343.7	167.5	0.4	7.5	7.7	1.4	2.8	1.2
	Gobiidae			*Peprilus simillimus*					
Sept.-Oct.	1.0	1.3	0.5	1.0	2.5	1.1			
Dec.-Jan.	4.7	0.4	0.5	0	0	0			
Feb.-Mar.	0.7	0.5	1.2	0	0	0			
June	0.8	1.2	1.0	8.1	4.6	4.3			

Each seasonal grouping is based on two or three different cruises. The geographical grouping "nearshore" includes the 44 samples from all X01 and X02 stations, 303, and San Onofre (see Table 1); "intermediate" includes the 20 samples from stations 103, 203, and 304; and "offshore" includes the 48 samples from all X05 and X06 stations.

symmetricus, and *Triphoturus mexicanus.* Larval saury were found in every season except winter.

Some of the larvae could be placed into recurrent groups. For the data from neuston tows, we chose an affinity level of ≥ 0.3 as the criteron for grouping. Group N1 (Figure 1) occurred, as a group, in winter and spring primarily at nearshore stations, in spite of the fact that *Engraulis* and the *Sebastes* spp. category were cosmopolitan in distribution (Table 3). Somewhat surprisingly, the three affiliated categories, though themselves of nearshore origin, had higher affinities with the cosmopolites than with *Genyonemus.* Group N2 occurred only six times, in summer and fall, most often at offshore stations; larval saury *(Cololabis)* were found in spring as well.

Taxa from the oblique tows were grouped using an affinity level of ≥ 0.5. Group O1 (Figure 2) included two offshore larvae (Table 3) and two cosmopolites, and the 34 occurrences as a group were mainly at offshore stations in winter, spring, and summer (Figure 3). Within these 34 occurrences, all of the six possible correlations in abundance were positive, and five were significantly so ($p < 0.05$), which means that the populations constituting the group were cohesive; the times and places that were "best" or "worst" (in terms of abundance) for one population

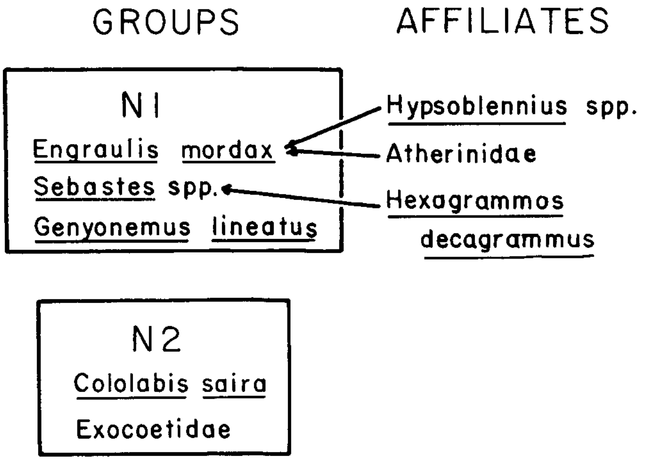

Figure 1. Recurrent groups of larval fish in neuston tows in the Southern California Bight. An affinity index of ≥0.3 is the criterion for grouping. "Affiliates" are those categories having significant affinity with some but not all members of a group, as indicated by arrows.

tended also to be best or worst for all other members of the group. The cosmopolitan flatfish *Citharichthys* was affiliated with the cosmopolitan members of the group, as was the offshore *Bathylagus* with the offshore members.

Group O2 was found exclusively at nearshore stations, and occurred as a group only in summer and fall (Figure 3); this group seems superficially similar to Group O3 in geographic distribution, and the two complete groups occurred together in four of ten possible cases. The members of Group O2 were not particularly coherent in abundance, since there were a positive, a negative, and a zero correlation between the pairs at the ten stations where the group occurred.

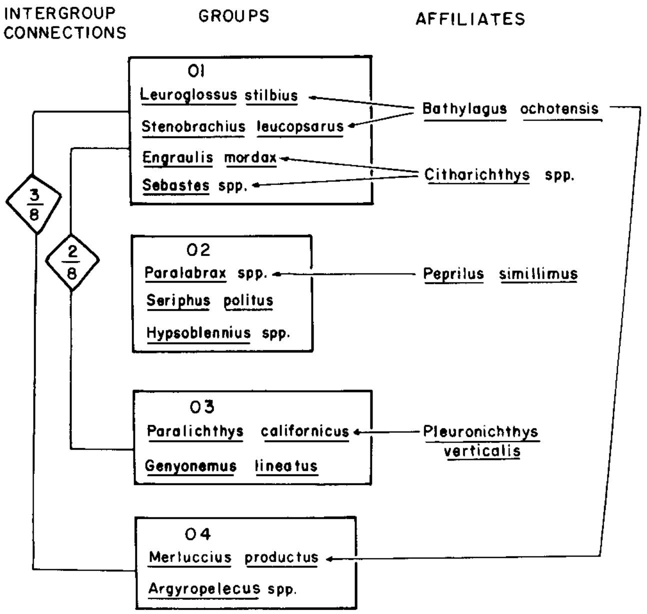

Figure 2. Recurrent groups of larval fish in oblique tows in the Southern California Bight. An affinity index of ≥0.5 is the criterion for grouping. "Intergroup connections" indicates the proportion of all possible affinities (the denominator) that were actually realized (the numerator) between pairs of categories whose members were in different groups. "Affiliates" are those categories having significant affinity with some but not all members of a group, as indicated by arrows.

The principal difference between Group O2 and Group O3 was seasonal: the latter group was found in winter and spring as well as fall (Figure 3), and occurred only once (out of 27 times) in summer. The abundances of its two members were positively correlated in the 27 occurrences, but not significantly so.

Group O4 was found offshore, and in fact was combined with Group O1 when an affinity level of 0.4 was used for grouping. It was even more strictly offshore than was Group O1, and only one of 17 occurrences as a group was outside the period between January and March. Its two members had significant, positive correlations in abundances in the 17 occurrences of the group.

When recurrent groups were established with an affinity level of 0.4 as the criterion, an additional

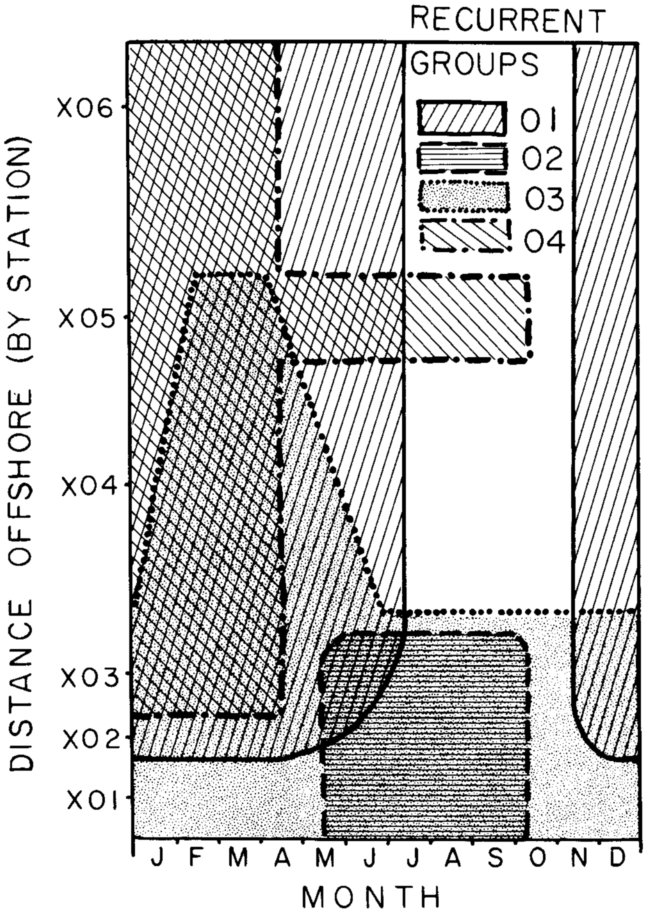

Figure 3. Areal and seasonal distributions of the recurrent groups in oblique tows (see Figure 2). Contour lines enclose all stations at which the entire group occurred. "X" on the ordinate equals 1, 2, or 3; see Table 1 for locations and depths of stations. The 300-m contour and 10-km distance offshore both occur between X03 and X04.

offshore, summer-fall group consisting of *Trachurus symmetricus* and *Triphoturus mexicanus* was found. A second group—*Lyopsetta exilis* (slender sole) and *Parophrys vetulus* (English sole)—was found only in March and at stations an intermediate distance from shore.

DISCUSSION

We have expressed results of oblique tows as catch per 10 m^2 sea surface; this rests on the assumption that the full depth range for fish eggs and larvae was sampled. Studies in the California Current region indicate that most fish eggs and larvae are distributed within the upper mixed layer or in the upper portion of the thermocline, between the surface and approximately 125 m, even in daytime (Ahlstrom 1959). Since most deep hauls averaged 210 m deep, the depth range for most eggs and larvae offshore was sampled. However, the interpretation of results from shallow stations is less sure, since the depth range for larvae and eggs has not been established and since the area on and just above the bottom was not sampled by our oblique hauls. It is likely (Brewer, Lavenberg, and McGowen, unpublished) that we would have found greater abundances of several nearshore larvae had we used an epibenthic net.

The question of vertical distribution also affects the interpretation of the recurrent groups. As mentioned earlier, a recurrent group consists of organisms that are frequently found in the same samples. Since our net tows integrated from the surface to 210 m at the offshore stations, it is possible that members of the same recurrent group have only minor ecological interactions, because they live at different depths. For example, larval *Engraulis, Sebastes* spp., *Citharichthys* spp., and *Stenobrachius* (formerly *Lampanyctus leucopsarus)* occur primarily in the mixed layer near the surface, while *Bathylagus, Leuroglossus,* and *Merluccius* occur below the thermocline (Ahlstrom 1959). Hence a recurrent grouping based on vertical distributions probably would separate *Leuroglossus* from the other members of Group O1.

Brewer, Lavenberg, and McGowen (unpublished) sampled the inshore waters of the Southern California Bight in spring and fall of 1978. The most significant faunal difference between their results and those reported here was the occurrence of large numbers of larval chub mackerel *(Scomber japonicus),* rivaling *Engraulis* for dominance, in June of 1978.

The analysis of the recurrent groups in the oblique tows amplified the tabulation of geographic distributions (Table 3) by indicating subgroups within the basic distinction between nearshore and offshore occurrences. Differences in season of occurrence separated groups that seemed geographically similar, and there was no specifically cosmopolitan group.

A recent study off the coast of Oregon (Richardson and Pearcy 1977) demonstrated clear division of larval fish into an inshore group (the shoreward 28 km, water 100 m deep or less) and an offshore group (37-111 km, water >100 m), with a transition zone where larval fish were rare. Very few species were cosmopolites, and this is perhaps not surprising in view of the relatively simple bathymetry and predominantly longshore transport along the Oregon coast. In the Southern California Bight a complex gyral circulation and a series of deep basins between the coast and the chain of offshore islands and banks make patterns of distribution less clear.

The anchovy *Engraulis* occurred in the offshore assemblage of Oregon and was not as abundant as *Sebastes* spp. and the myctophids *Stenobrachius leucopsarus* and *Tarletonbeania crenularis.* Also, larval anchovy were very seasonal in occurrence off Oregon (June-August), unlike the situation in the Southern California Bight. As in the SCBS collections, *Sebastes* and *Stenobrachius* were found off Oregon in most months, but the season of greatest abundance was the late spring rather than winter and early spring.

A further study off the Oregon coast, based on many transects in the springs of four years, revealed a persistent pattern of two or three coastal assemblages, a transitional assemblage, and one or two offshore assemblages, with the coastal/offshore separation generally paralleling the shelf/slope break (Richardson, Laroche, and Richardson 1980). Minor variations from year to year in the locations of these assemblages may have been related to variations in the strength and direction of coastal winds. An important finding was that the geographical pattern of assemblages was relatively constant in spite of month-to-month and year-to-year variations in the abundances of the species dominating each assemblage, especially near the coast. These variations were not well correlated between species, so that a particular geographically defined assemblage might be dominated by different species in different months or years.

There are some ecological advantages for larvae that develop in the inshore zone. Recently, it has been demonstrated that first-feeding larval *Engraulis mordax* must occur with high concentrations of particles in the size range of large dinoflagellates in order to feed adequately (Lasker 1975). Characteristically, these regions exist close to shore off southern California, and relatively steep inshore-offshore gradients in planktonic stocks (as chlorophyll, primarily production, particulate organic carbon, etc.) have already been reported (Eppley, Sapienza, and Renger 1978).

Sardinops caeruleus, the Pacific sardine, occurred only near shore on SCBS cruises. Eggs and larvae of this species used to be taken over wide areas both inshore and offshore (Ahlstrom 1959a), but occurrence has changed primarily to inshore zones. It is likely that when breeding stocks were reduced, the remaining population tended to spawn selectively in areas of high productivity, where survival of larvae is enhanced. Thus, the inshore zone could be important for the recovery of certain overfished or otherwise depleted stocks, including the anchovy if its population were ever drastically reduced. It is important to verify the relation between depleted stocks and the productive inshore zone, since this zone is the most likely to be affected by anthropogenic perturbations.

ACKNOWLEDGMENTS

Members of the Food Chain Research Group and officers and crew of the R/V *Ellen B. Scripps* assisted in collecting samples, and Richard W. Eppley instigated the research. Much help with the identification of larvae was given by Elaine Sandknop. Reuben Lasker and H. Goeffrey Moser gave useful advice, and Dr. Moser provided helpful comments on the manuscript, as did Jay Quast and an anonymous referee. Elaine Brooks and Elizabeth Stewart assisted with data processing and statistics, and Doris Osborn typed the manuscript.

This research was supported by ERDA and DOE grants AT (11-1) GEN 10 PA 20, EY-76-C-03-0010PA20, 79EV70010 (1974-1977) and by a contribution from Scripps Institution of Oceanography.

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MARINE FARMING THE COASTAL ZONE: CHEMICAL AND HYDROGRAPHIC CONSIDERATIONS

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ABSTRACT

Hydrographic and marine chemical observations are reported in the vicinity of a pilot-scale kelp farm (0.1 hectare) that depends on artificial upwelling of nutrients in the Southern California Bight. Measurements of temperature, salinity, dissolved oxygen, phosphate, nitrate, silicate, and trace metals (Cu and Ni) were made from January 1979 to June 1980 as close as practicable to the facility moored near the 500-m isobath about 10 km SSW of Corona del Mar, California.

The hydrographic results complemented the historical record of conditions in the bight and disclosed several aspects of concern to coastal marine farming projects. The facility depended on nutrients artificially upwelled from a depth of 450 m. Nitrate and phosphate are critical nutrients for giant kelp *(Macrocystis pyrifera)* culture. They were found in abundant supply, averaging 35.3 and 3.00 μM, respectively, during the study period. Though not critical for kelp nutrition, silicate and oxygen concentrations were the most variable parameters in the deep water. Significant fluctuations in nutrient concentration were noted throughout the water column during upwelling events.

Profiles of total copper suggest that surface gyre circulation coupled with anthropogenic pollution in the Southern California Bight cause copper levels 2-5 times higher than those observed at offshore stations in the California Current by previous workers. Our observations confirm existing concepts of metal enrichment in nearshore marine environments relative to oceanic conditions, with implications for mariculture in the coastal zone.

RESUMEN

Observaciones hidrográficas y químicas marinas han sido reportadas en la vecindad de una granja experimental de algas (0.1 hectárea) en la Bahía del Sur de California que depende de la surgencia artificial de nutrientes. Medidas de temperatura, salinidad, oxígeno disuelto, fosfato, nitrato, silicato, y metales de bajas concentraciones (Cu y Ni) fueron hechas desde enero de 1979 hasta junio de 1980, lo más cerca posible a la instalación anclada cerca de la isóbata de 500 m localizada a una distancia aproximada de 10 km al sur-sudoeste de Corona del Mar, California.

Los resultados hidrográficos complementaron el registro histórico de condiciones en el área y revelaron varios aspectos de importancia para proyectos de granjas marinas costeras. La instalación dependía de nutrientes surgidos artificialmente desde una profundidad de 450 m. Nitratos y fosfatos son nutrientes absolutamente necesarios para el cultivo de *Macrocystis pyrifera*. Estos fueron encontrados en abundancia durante el estudio, con promedios respectivos de 35.3 y 3.00 μM. Aunque las concentraciones de silicato y oxígeno no son críticos para la nutrición de algas, dichas concentraciones fueron los parámetros más variables en la zona profunda. Se observaron fluctuaciones significativas en la concentración de nutrientes por toda la columna de agua durante la surgencia.

Los perfiles de cobre total sugieren que la circulación del giro superficial junto con la contaminación antropogénica en la Bahía del Sur de California aumenta los niveles de cobre de 2 a 5 veces más que en las estaciones de fuera de la costa en la Corriente de California observados por otros investigadores. Nuestras observaciones confirman los conceptos existentes acerca del enriquecimiento por metales en medio ambientes marinos cercanos a la costa relativo a condiciones oceánicas, con implicaciones para la maricultura en la zona costera.

INTRODUCTION

Increasing scarcity of critical natural resources has focused attention on developing the fertile coastal zone.

Marine scientists of diverse specializations are greatly concerned with the impacts of use and management of these areas. Coastal developments for mineral extraction, ocean-thermal energy conversion, desalination, fisheries management, or marine farming operations have recently progressed beyond planning to preliminary or pilot-plant stages. Site surveys utilizing the historical data base provide valuable information for initial designs. However, there are few

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[Manuscript received November 23, 1981.]

coastal zones for which an adequate site-specific literature exists. The dynamics of the coastal environment, human population influence, proximity to shore installations, environmental impact, and the particular needs of a project are interrelated factors that must be considered for optimum site selection. The situation is further complicated for marine farming ventures because nutritional requirements are of paramount importance.

This study details chemical and hydrographic conditions in the vicinity of a pilot-scale marine kelp farm supported by artificial upwelling of deep nutrient-rich water in the Southern California Bight. Serial on-site monitoring of oceanographic conditions disclosed unique aspects of the region that were not evident from the past literature.

The giant kelp, *Macrocystis pyrifera,* is a brown alga with potential for large-scale nearshore farming to provide chemicals or energy via anaerobic digestion of its biomass. Kelp harvesting has been practiced for nearly 70 years in the natural beds off the California coast, and even longer elsewhere (Chapman 1970). Recently, the potential of kelp tissues as an alternative energy source has been investigated in a program known as the Marine Biomass Project. Field observations and experiments with juvenile plants and gametophytes have established minimum nutrient requirements for growth. Nitrogen appears to be the most critical nutrient (North 1980), and levels below 3 μM may be suboptimal. Availability of nutrient-rich deep water, together with logistic constraints, resulted in the choice of a site for a pilot-scale marine farm as noted in Figure 1.

The range of field conditions (temperature, nitrate-ammonia, phosphate, etc.) that are associated with a "healthy" status among coastal kelp beds is fairly well defined. Relations between many of these physical-chemical parameters and kelp growth have been studied in the laboratory. Because oceanic surface waters are typically low in N and P, it is clear that plants on a marine farm would have to be fertilized. The need for maintaining a positive energy balance dictates that only artificially upwelled deep water can be used for fertilizing marine farms. Cost considerations indicated that an experimental farm moored in water several hundred meters deep would be the cheapest method of obtaining the large volumes of deep water needed.

The present study deals primarily with chemical micronutrient and trace element distributions in the vicinity of a marine farm moored at the 500-m isobath off the coast of southern California. This study assessed the available nutrient supply via artificial upwelling, emphasizing extreme conditions that might be obstacles to year-round farming. Results are presented so as to complement the historical data base, focusing on actual site conditions as contrasted to regional averages.

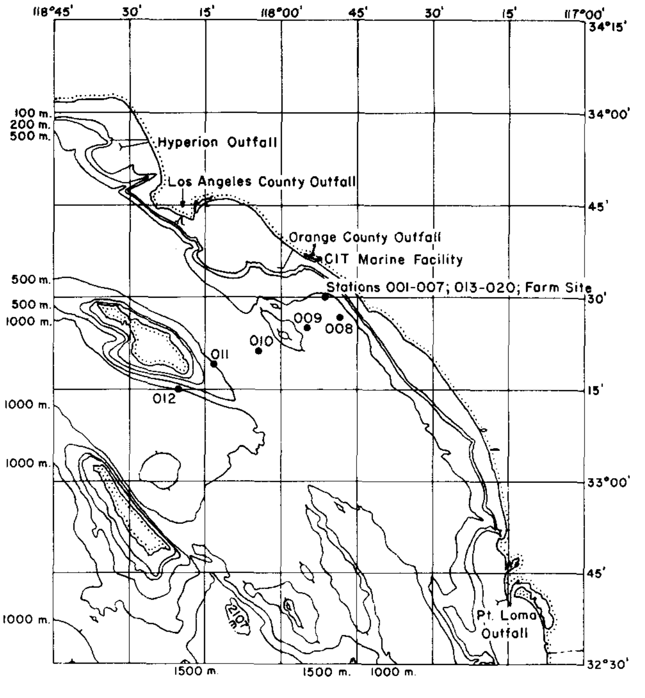

Figure 1. Locations of transect stations and of the moored test farm.

MATERIALS AND METHODS

The study involved standard oceanographic techniques; unless otherwise indicated, guidelines of the U.S. Naval Oceanographic Office (1968) were followed for each station. Fifteen serial hydrographic stations were occupied at the farm site (Figure 1) between January 1979 and June 1980. Station locations were as near as practicable to the moored facility, between the 500-m and 600-m isobaths at the head of the San Diego Trough. The location was semiprotected by offshore islands. The late summer movement of the California Undercurrent has been tracked along the continental margin as far north as Oceanside, California (Tsuchiya 1976). A SW-NE transect of the area was therefore conducted in September 1979 to determine if such deepwater movements materially affected hydrographic conditions at the study site. Five stations were occupied on this transect. The geostrophic approximation was made to calculate the current regime using the computer program OCLDAT4 (NOAA, Ocean Chemistry Laboratory 1979). The deepest common depth between the stations (500 m) was chosen as the level of no-motion.

Acid-washed PVC "go-flo" Niskin bottles of 5-l capacity were used for water sampling. Salinity, dissolved oxygen, reactive phosphate, and silicate were determined within 48 hours on subsamples stored at 4°C. Analytical procedures and observed precision limits are shown in Table 1. Copper and nickel were determined in acid-preserved subsamples collected with rigorous precautions against contamination. These subsamples were taken from each Niskin bottle immediately after oxygen samples were drawn. Shipboard metal sampling procedures included rinsing the sampling valve with Milli-Q water, flushing the polyethylene transfer line (leading to a lucite-supported glove bag) with at least one liter of sample, rinsing the 250-ml polyethylene sampling bottle and cap (within the glove bag) twice, and finally taking the sample and adding 500 μl of G.F. Smith redistilled HC1 to preserve it for analysis. Analyses used a modification of the cobalt-APDC coprecipitation method described by Boyle (1976).

All subsequent sample transfers and digestions were conducted in a clean hood flushed with HEPA-filtered laboratory air. Possible contamination from the hydrowire was checked by taking surface samples from a rubber raft at least 100 m upswell from the research vessel in carefully cleaned one-liter polyethylene bottles. Samples were split for duplicate determinations by the technique described above. Flameless atomic absorption measurements were made on digested concentrates using a Varian AA-6 instrument with graphite furnace atomization capability. Oxygen-free filtered nitrogen or argon provided an inert atmosphere for the dry, char, and atomization steps. Instrument settings used to optimize sensitivity differed little from those reported by Boyle (1976), Boyle et al. (1977), and other workers (Bruland et al. 1979).

TABLE 1
Analytical/Sampling Errors of Hydrographic Parameters

Parameter (method)	Symbol	(N)*	Mean ± 2 (standard deviations)	Percent deviation
Salinity (A)	S^0/oo	(170)	34.922 ± 0.004	0.01
Temperature	T (°C)		(Traceable to NBS standard thermometers, reading error ±0.05C°)	
Oxygen (B)	O_2 (mL/L)	(85)	2.50 ± 0.03	1.2
Phosphate (C)	PO_4 (μM)	(40)	1.60 ± 0.16	10
Silicate (D)	$Si(OH)_4^{=}$ (μM)	(40)	50.0 ± 0.75	1.5
Nitrate (E)	NO_3^- (μM)	(40)	20.0 ± 0.8	4
Nickel (F)	Ni (nM)	(13)	5.0 ± 0.61	12.2
Copper (F)	Cu (nM)	(11)	7.5 ± 0.79	10.5

*N = Number of duplicate standards run during the project period. Methodology covered in *Hydro-Lab Procedure Manual* of the Kelp Habitat Improvement Project.

A —High-precision induction salinometry, Beckman RS-7C.
B —Iodometric titration, Carpenter modification (1965).
C,E —Strickland and Parsons (1972) 2nd edition.
D —Fanning and Pilson (1973).
F —Boyle (1976).

Sampling was performed from the R/V *Osprey* and R/V *Ms. Acrylic* of the California Institute of Technology. Several stations were occupied from the R/V *Westwind*, a commercial vessel.

RESULTS AND DISCUSSION

Hydrography of the Farm Site

Hydrographic results (Figures 2 and 3) for the eighteen-month period from January 1979 to June 1980 included monthly data for stations CIT-001→007 and 013→020. Average oceanographic conditions at the site were similar to those previously reported (Reid et al. 1958). Holm-Hansen et al. (1966) have fully discussed biological implications of these chemical distributions for a station off the California coast. Seasonal variations in the thermohaline properties of the water column were considerable. Upwelling is a regular occurrence off the west coast of the Americas and is most intense in the Southern California Bight in the spring. It was observed to compress the base of the shallow thermocline from 100 to 40 meters and increased the slope (C°•m^{-1}) from −0.06 to −0.25.

Apart from upwelling events, temperature and salinity distributions at the site were similar to "California shelf" water described by Emery (1960). This

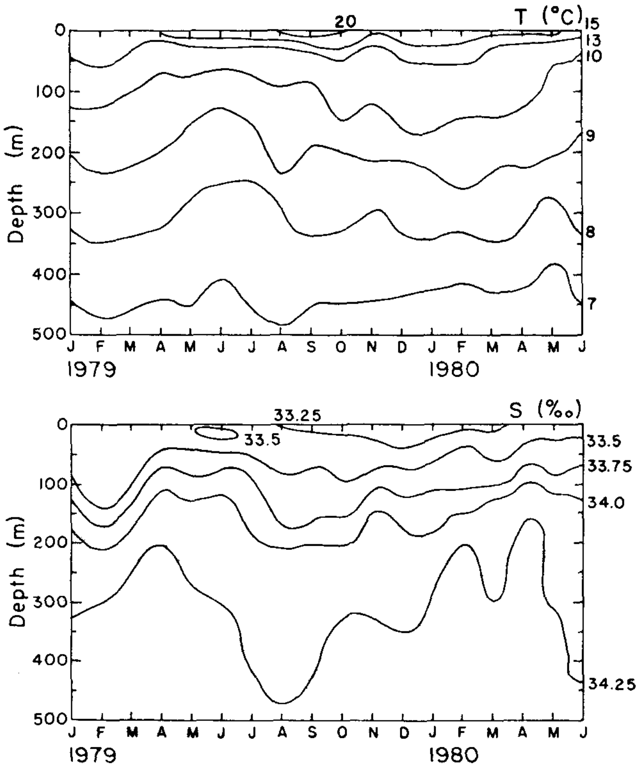

Figure 2. Annual distributions of temperature (T, °C) and salinity (S, ‰) in the water column at the study site.

water type results from mixing of Subarctic and Equatorial water masses carried into the area by the California Current from the north and subsurface countercurrents from the south (Reid et al. 1958). Analysis of the historical record (CalCOFI cruise reports 1963-1971) and the records of the National Oceanographic Data Center from 1970 to 1978 (NODC 1978) revealed that all our temperature and salinity profiles fell within two standard deviations of the historical means.

Nitrate, dissolved oxygen, reactive silicate, and phosphate distributions showed considerable variability induced by coastal upwelling events in the spring (Figure 3). The well-oxygenated surface waters were generally depleted of nitrate (<10 μM) and phosphate (<1 μM) despite the 50-100-m rise of the deep water isopleths during upwelling. Upwelling is primarily an inshore phenomenon in the region, and little increase in surface values was expected at the offshore farm site. Nitrate, a critical nutrient below 3 μM (North 1980), dipped to a winter minimum at 450 m of 31.5 μM in 1980. Within the analytical uncertainty of ±0.8 μM, the minimum available supply of nitrate in the upwelled water seems more than adequate. No significant nitrite (NO_2^-) was observed at any time during the study period.

Similarly, deep phosphate levels fluctuated very little (<5 percent as compared to the analytical uncertainty of ±10 percent), and the supply seems sufficient for good kelp growth (North 1980). Salinity and temperature showed seasonal changes related to upwelling events, as mentioned above. The calculated density at 450 meters deviated only ±0.14 percent from the mean value of 1.02694 kg$\bullet$l^{-1}.

The dissolved oxygen distribution varied significantly during the study period. The lack of a defined oxygen minimum below the photic zone was due presumably to mixing in the nearshore waters.

Oxygen and silicate levels in the deep water showed variability that may be related to an intermittent influx of intermediate or bottom water. Samples low in oxygen and high in silicate were encountered during the first half of 1979, extending beyond the spring upwelling event. In 1980, however, values near the 18-month mean were observed during the first half of the year; after upwelling the silicate levels fell as oxygen levels increased. Upwelling combined with variable wind force and direction may contribute to nearshore

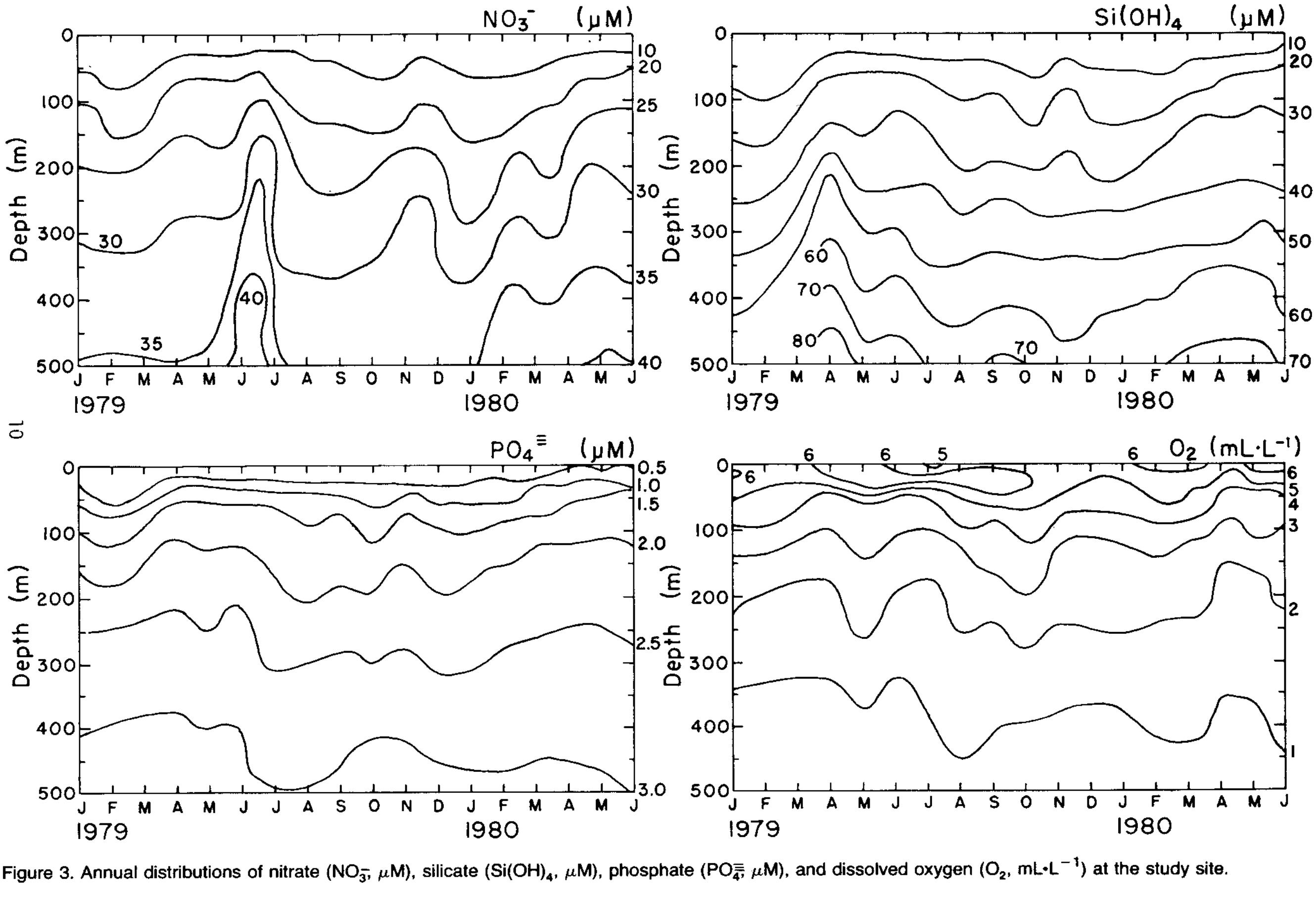

Figure 3. Annual distributions of nitrate (NO_3^-, μM), silicate ($Si(OH)_4$, μM), phosphate ($PO_4^{\equiv}$, μM), and dissolved oxygen (O_2, mL$\bullet$L^{-1}) at the study site.

surface current reversals, incomplete mixing, and an unstable water column. Temperature inversions were frequently noted throughout the water column in biweekly XBT traces during this period. The apparent instabilities occurred well into midsummer. Our sampling frequency makes further comment speculative.

Nearshore Circulation

A five-station transect was executed during late summer 1979 in order to define regional transport better. The northward movement of the California Undercurrent, a warm nutrient-rich flow, was of particular interest. This feature is best developed near shore during August and September (Tsuchiya 1976). Hydrographic characteristics of the undercurrent were quite similar to those encountered at the farm site. There were no obvious offshore trends evident in the subthermocline chemical distributions. Results of the geostrophic flow calculations are shown in Figure 4 as flow contours along the ENE-WSW transect line. Results for the 011-012 station pair were questionable because of the proximity of the Catalina Island landmass. However, the results from these stations have been included in the contours for the sake of completeness. The general flow regime agrees quite well with previous results representative of this time of year (Reid et al. 1958; Hendricks 1977). The inshore surface flow bears NNW at 10-15 cm•sec^{-1}, while the offshore southerly California Current flows at somewhat greater speeds—~20 cm•sec^{-1}. This is manifest evidence of a counterclockwise eddy in the Southern California Bight, which tends to restrict exchange and extends the residence time of its waters. Subsurface geostrophic flows were very weak (at or below the noise level) at the inshore stations, and there is little evidence of northward countercurrent flow of equatorial water at the core depth range of 200-300 meters (Tsuchiya 1976). Absence of a high salinity bulge (>34.30 ⁰/₀₀) in the dashed region of the temperature-salinity plot (Figure 5) further supports this conclusion (Wooster and Jones 1970).

Much of the recent literature deals with circulation as it affects the mixing and residence time of municipal sewage effluents in shelf waters. Hendricks (1977) has pointed out that coherency in shallow, subthermocline motions can occur at distances of <35 km from shallow water outfalls. Directions of these currents frequently oppose those of surface water motions at speeds averaging 3 cm•sec^{-1}. Hendricks observed longshore and offshore components that mix effluents with deeper waters, aided by bottom currents with speeds up to 20 cm/sec. Because the study site lay less than 15 km from the Orange County Sanitation District sewage outfall and heavily trafficked Newport Harbor, pollutant transport to the farm site had to be considered. In fact, the farm was at the deep end of the Newport Submarine Canyon. When the dominant surface flow is to the NNW, one would expect some return flow along the canyon's contours in the direc-

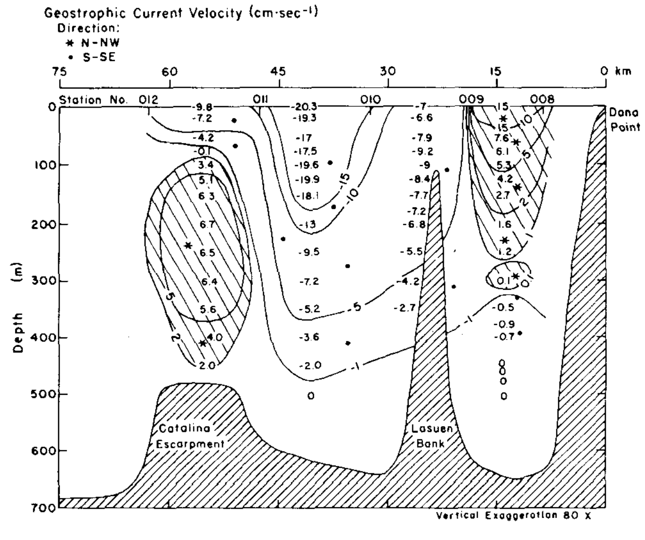

Figure 4. Geostrophic currents calculated from hydrographic observations on east-west transect of study region (CIT stations 008-012, September 1979).

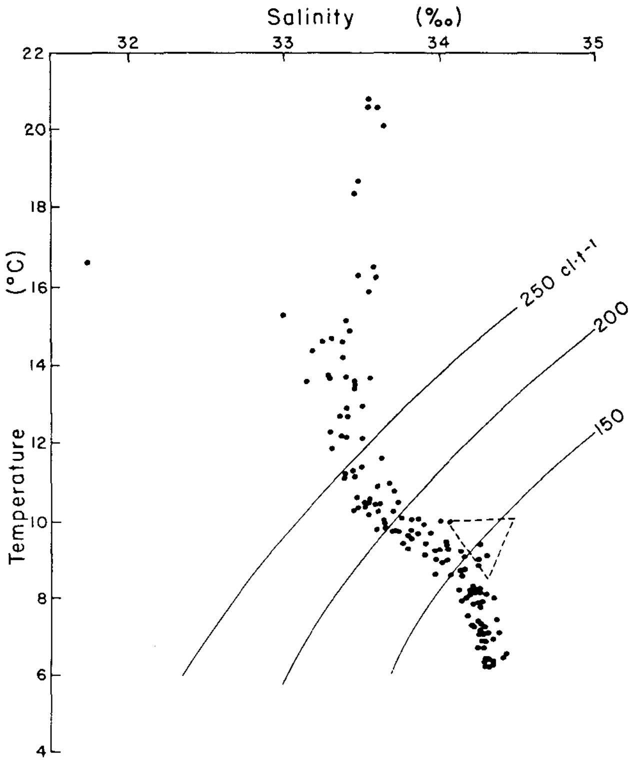

Figure 5. Temperature-salinity diagram for sixteen serial stations occupied at the study site. Values of the isanosteric anomaly are contoured in 50 cl•t^{-1} increments. The triangular region denotes zone of T-S properties indicative of countercurrent water.

tion of the farm. Bascom et al. (1978) noted "changed" sediment conditions judging from a sediment "Infaunal Trophic Index" over an 11-12-km^2 area near the sewage outfall. Patches of "changed" conditions were reported to the SSW near Newport Harbor and Dana Point. The potential for impact at the moored farm and the elevated water column levels of copper near the site prompted closer examination of anthropogenic influences.

Copper and Nickel Distributions in the Study Area

The trace metal data show an influence of human activities on the marine chemistry of the bight. Figure 6 depicts the hydrographic profiles of copper and nickel for five stations taken at the site from April 27, 1979, to August 13, 1979. The data show significant variability over the four-month period of intense upwelling. Copper was found to vary from 3.2-15.6 nM in the upper 100 m. Surface and subthermocline data sets were not significantly different at the 90 percent confidence level. Thus the possibilities of controlling atmospheric or sediment-related inputs were discounted. The variability for nickel was somewhat less than copper and agreed generally with the data of Boyle (1976) and Bruland et al. (1979).

Overall copper levels were 2-5 times higher than those at similar depths reported by the above workers for stations considerably more distant (>90 km) from shore. They observed total copper levels ranging from 2-4 nM using essentially identical analytical methods. In Figure 7, the envelope of our data set is compared with the profiles of previous workers. The nearshore levels were clearly elevated over their results. Further, our surface values were also higher than those reported by Windom and Smith (1979) for samples off the southeastern coast of the United States. Circulation in the Southern California Bight is characterized by a counterclockwise eddy, which tends to limit communication with open ocean waters. Thus it was necessary to examine the available trace-metal data for inshore stations near the study area.

Young's results (1979) are most comparable to our data, because his sampling and analytical methods were nearly identical to ours. He observed copper levels in Newport Harbor ranging from 139-35 nM. His surface value at the offshore station (9.4 nM) shows excellent agreement with our observed mean surface value of 8.98 ± 3.51 nM (N = 15), with a range of 5.01-18.6 nM. Results from Zirino et al. (1978), though not strictly comparable because they

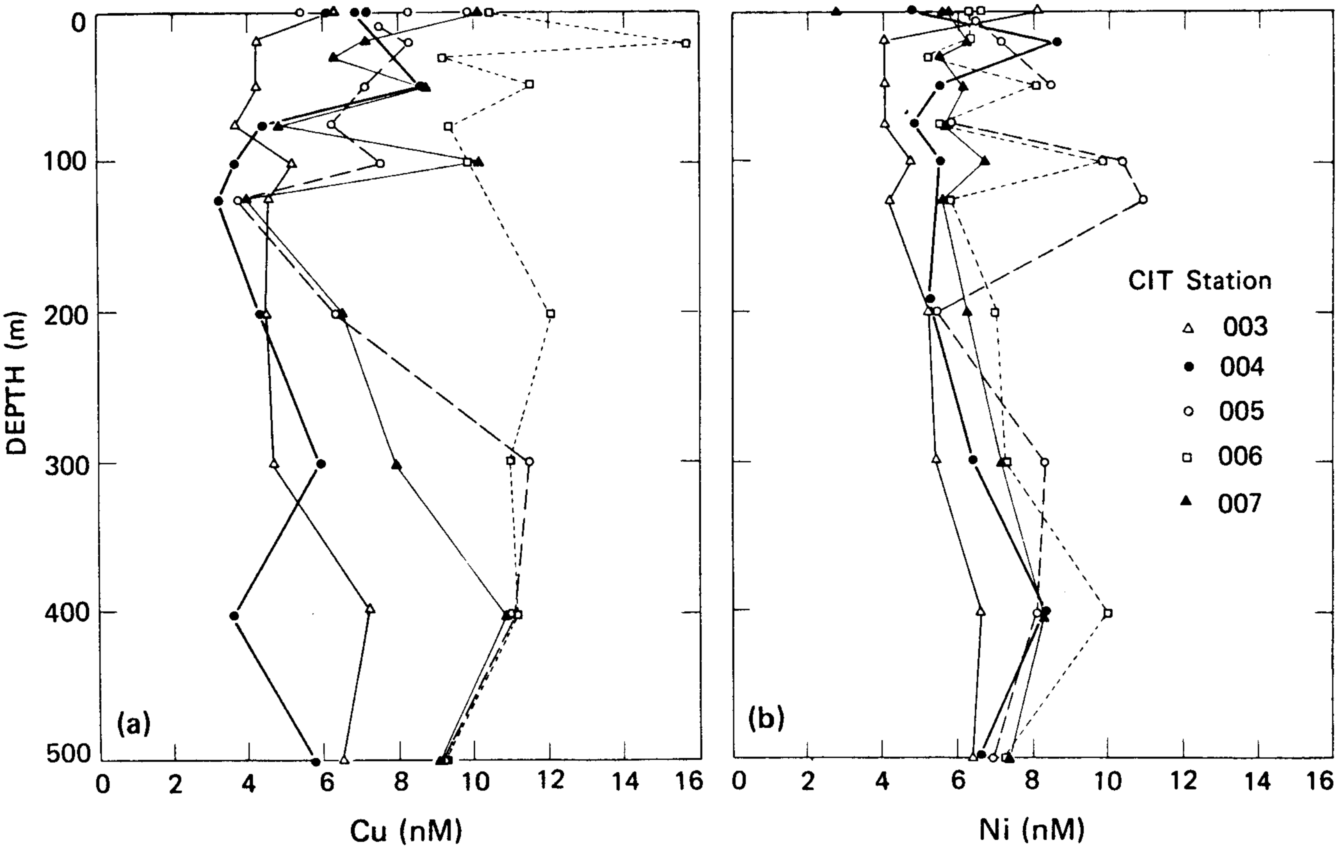

Figure 6. Hydrographic profiles of total copper and nickel with depth at the study site.

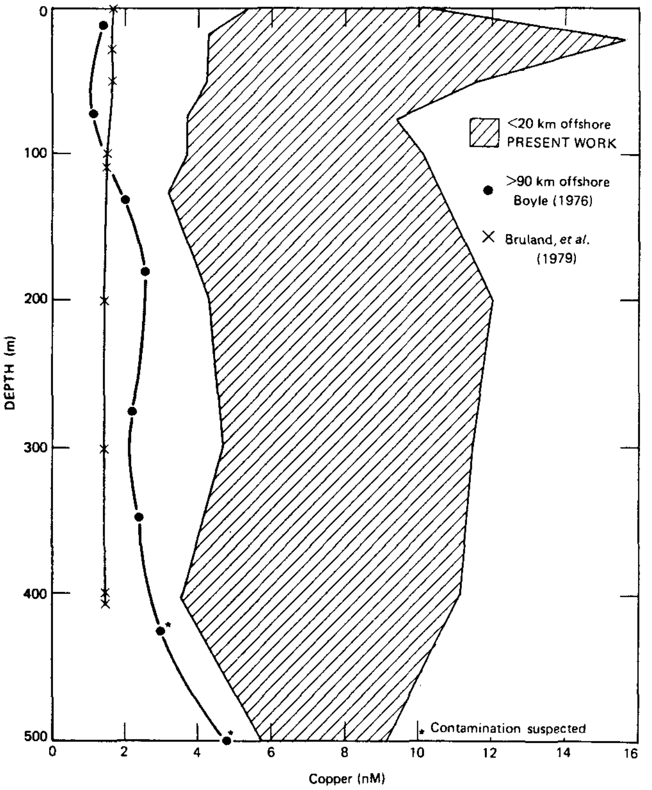

Figure 7. Envelope of nearshore total copper levels versus depth contrasted with offshore results.

used electrochemical techniques, were of the same order of magnitude (10-39 nM-Cu) and demonstrated the strong tidal variations noted in copper levels in the harbors.

The highly industrialized, densely populated southern California coast provides numerous pollutants to the coastal waters. The study site lay within 125 km of three major sewer outfalls discharging more than $3 \times 10^9 l \cdot day^{-1}$ of primary and secondary treated effluent (Schafer 1978). Copper, nickel, chromium, and lead are important toxic metals identified in these discharges. In coastal areas of restricted circulation, total metal levels probably reflect the influence of all sources.

The history of trace-metal inputs to the coastal zone has been studied in the sedimentary record by Bruland et al. (1974) and Bertine and Goldberg (1977). These authors demonstrated recent enrichment of several trace metals in the coastal basins within 30 km of the shore. Bruland et al. (1974) further pointed out that about 1.9 percent of the discharged copper associated with wastewater alone could account for its observed enrichment in nearshore sediments. Thus, a substantial fraction of the total copper discharged remains available for transport in coastal waters. Estimates were made of the annual inputs of copper from various sources in the immediate vicinity (<30 km) of the site (SCCWRP 1978; and Schafer 1978). These inputs are shown in Table 2 for various source categories. Sewage discharge is clearly the dominant anthropogenic input. Correcting the annual copper input for a 0.1-1 percent loss from rapidly settling particles (Herring and Abati 1978), and using a water residence time of 3-4 months, we find it conceivable that a 2-5 nM increase in total copper in the nearshore water column could occur. Such an increase would be sufficient to account for the high total copper levels observed in this study.

TABLE 2
Estimated Copper Inputs to the Study Area

Activity	Mass input rate (metric tons/yr) Cu
Discharge of municipal waste waters (Orange County)	87
Boat maintenance (Newport Bay)	40
Storm runoff (Santa Ana River, San Diego Creek)	1.8
Aerial deposition	1.6
Dredging (slip maintenance)	1.3
Discharge of power plant cooling waters	0.44
Total estimated annual input	132.0

Sources: SCCWRP 1978; Schafer 1978.

Our investigation suggests the potential for anthropogenic impact at an offshore farm site. Observed copper levels were elevated over oceanic conditions. A severe impact on kelp plants is not expected because natural inshore beds flourish close to significant sources of the metal; examples are the Point Loma beds near the San Diego municipal discharge and those at Palos Verdes near the Los Angeles County outfall.

North (1980) observed little enrichment of copper in kelp tissue at dissolved copper levels below 50 nM under batch culture conditions where media were renewed every other day. Slight reduction of specific growth rate first occurred at copper supplements of 100 μM, where 400 μM additions led to strong growth inhibition and greening of blade tissues within a few days. Considerably lower copper concentrations would be required under flowing conditions to achieve comparable adverse effects. Probably continuous exposure to 10 μM copper alone would not damage *Macrocystis*. Problems might appear at 20 to 30 μM.

One should also be aware of the potential impact of chronic plant exposure to various metals at "low" concentrations. Though no single metal may be present at "toxic" levels, the combination of nickel, lead, and copper exposures, for example, could prove stressful to the organisms. Any kelp farming operation, coastal or oceanic, should avoid sites lying immediately downcurrent from major sources of toxic elements.

SUMMARY AND CONCLUSIONS

Eighteen months of hydrographic measurements at an offshore (~8 km) 0.1-hectare marine farm have delineated the variability in certain chemical factors related to mariculture of the giant kelp, *Macrocystis pyrifera*. The results complement the historical record and demonstrate the variability of deep water (450 m) available for artificial upwelling. Nutrient supplies of nitrate and phosphate were more than adequate for kelp production within the prototype design limitations. Estimates of current flow using the geostrophic approximation agree with reports of average conditions within the Southern California Bight.

The facility's proximity to coastal sources of pollution led to total copper levels intermediate between typical values for inshore kelp beds and oceanic levels. Such exposures are not expected to affect growth of kelp. Future developers of marine mariculture in the nearshore waters must consider the influence of coastal pollution.

ACKNOWLEDGMENTS

The authors would like to acknowledge the contributions of Drs. Valrie Gerard and George Jackson for advice during varying stages of the work, Thomas Stephan and Randall Berthold for ship operations, and B. Barth, P.C. Beavers, and Larry Jones for help in preparing the manuscript.

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TEMPORAL AND SPATIAL VARIABILITY OF TEMPERATURE IN TWO COASTAL LAGOONS

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ABSTRACT

With *in situ* continuous recording thermographs, year-long surface-temperature time series were generated at four points in San Quintin Bay and at three points in Estero de Punta Banda. During spring and summer, upwelling events were clearly detected at the mouth of San Quintin Bay. Upwelled waters propagate throughout San Quintin Bay by tidal currents. In both coastal lagoons, temperature increases, in general, from the mouth to the interiors, except during some winter periods when the gradient reverses. The time series have in general a semidiurnal behavior, with high temperatures corresponding with low tides and vice versa. Water residence time in the lagoons is minimal with spring tides and strong currents parallel to the coast in the adjacent oceanic area.

The Estero de Punta Banda waters are warmer than those of San Quintin Bay during summer; during winter they have similar temperatures. Time series from Estero de Punta Banda indicate that upwelling water from the area off Todos Santos Bay is being carried by coastal currents to the estero. At the mouth of San Quintin Bay, minimum temperature for the year was registered during summer and was clearly associated with an upwelling event. In both lagoons, maximum temperatures were registered at the end of September.

RESUMEN

Termógrafos colocados en cuatro lugares en Bahía San Quintín y en tres en el Estero de Punta Banda han proporcionado durante un año completo, series continuas de la temperatura del agua de superficie. En la Bahía San Quintín se aprecia claramente que en primavera y verano se producen una serie de fenómenos de surgencia, y las corrientes de marea propagan estas aguas de surgencia por todo el interior de la bahía. En estas bahias la temperatura aumenta en general, de la boca hacia el interior, excepto durante algunos períodos en invierno, cuando el gradiente se invierte. Se observa que el ciclo de la temperatura es en general semidiurno, de acuerdo con las mareas, correspondiendo temperaturas altas con mareas bajas y viceversa. La permanencia del agua en las bahías es de corta duración en períodos de mareas vivas y de corrientes fuertes paralelas a la costa en la zona oceánica adyacente. En verano, las aguas del Estero de Punta Banda son más cálidas que las de San Quintín, y en invierno ambas zonas presentan una temperatura similar. Los termogramas indican que aguas de surgencia de la zona fuera de la Bahía Todos los Santos son arrastradas hacia el estero por las corrientes costeras. En la boca de la Bahía San Quintín, la temperatura mínima se observó en verano y parecía evidentemente asociada con fenómenos de surgencia. En ambas bahías las temperaturas máximas se registraron hacia finales de septiembre.

INTRODUCTION

Since the beginning of the 1970s, there has been an increasing interest in developing aquaculture in coastal lagoons of Baja California. The main interest has been concentrated on oyster culture. Very successful experiments with *Crassostrea gigas,* the Japanese oyster, and *Ostrea edulis,* the European oyster, have been carried out in most of the coastal lagoons of the peninsula's Pacific coast (Islas-Olivares 1975; Islas-Olivares, et al. 1978). Most of the coastal lagoons are still very much in their natural state in Baja California, though very few, if any, remain unaltered by human activities in southern California. As development goes on from the two ends of the Baja California peninsula, human activities will begin to make an impact upon the ecology of the lagoons. Basic ecological studies can give the background against which future situations may be compared. Also, studies can be designed to gain useful information that might be applied to make rational decisions as mariculture is developed. For example, it is important to know the spatial and temporal ranges of such important variables as temperature and salinity, the relative food availability in different lagoons, the mechanisms responsible for greater or lesser fertility of some lagoons with respect to others and with respect to the open ocean, and the water exchange rate between the lagoons and the adjacent ocean (Lara-Lara et al. 1980).

The objectives of the work reported herein were to describe the temperature variability throughout a year

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[Manuscript received March 1, 1982.]

in San Quintin Bay and Estero de Punta Banda—two coastal lagoons of northwestern Baja California; to describe associations between seawater temperature changes and oceanic and atmospheric processes in these lagoons; to study the penetration of upwelled waters into these two coastal lagoons; and to qualitatively study the variation of residence times in both lagoons. To do this, we generated one-year-long surface-water temperature time series at various locations in these lagoons.

San Quintin Bay is located between 30°24′-30°30′N, and 115°57′-116°01′W on the Pacific coast of Baja California (Figure 1a). The bay is 300 km south of the Mexico-U.S. border. It is Y-shaped, with a single permanent entrance at the foot of the Y. It has a general north-south orientation, and an area of about 41.6 km². The lagoon is extremely shallow, and at lower low tide some portions of the bottom are exposed. There are narrow channels that rarely exceed 8 m in depth.

Estero de Punta Banda is located between 31°42′-31°47′N, and 116°37′-116°40′W, on the Pacific coast of Baja California, at the southeastern extreme of Todos Santos Bay, 13 km south from Ensenada (Figure 1b). It is L-shaped, with a single permanent entrance at the end of the longest arm. There is one channel along the main arm. Depth in this channel decreases nonuniformly from the lagoon's mouth towards the interior, from 8 to 1 m. The estero has an area of about 11.6 km².

San Quintin Bay and Estero de Punta Banda have water densities equal or almost equal to those of the open sea, and water movement is mostly caused by tides and wind. Tidal ranges are about 2.5 m during spring tides. There are no streams flowing into these lagoons: they are evaporation basins. However, with winter rains, sometimes there are significant inflows of fresh water. This happened with the high precipitation of the winters of 1978 through 1980.

METHODS

Identifying and interpreting the characteristic frequencies or periodicities of the ecosystems' variables should be one of the central goals of the discipline of ecology (Platt and Denman 1975). Since the work of Acosta-Ruiz and Alvarez-Borrego (1974), time series have been generated to study the variability of water properties in these two coastal lagoons. These time

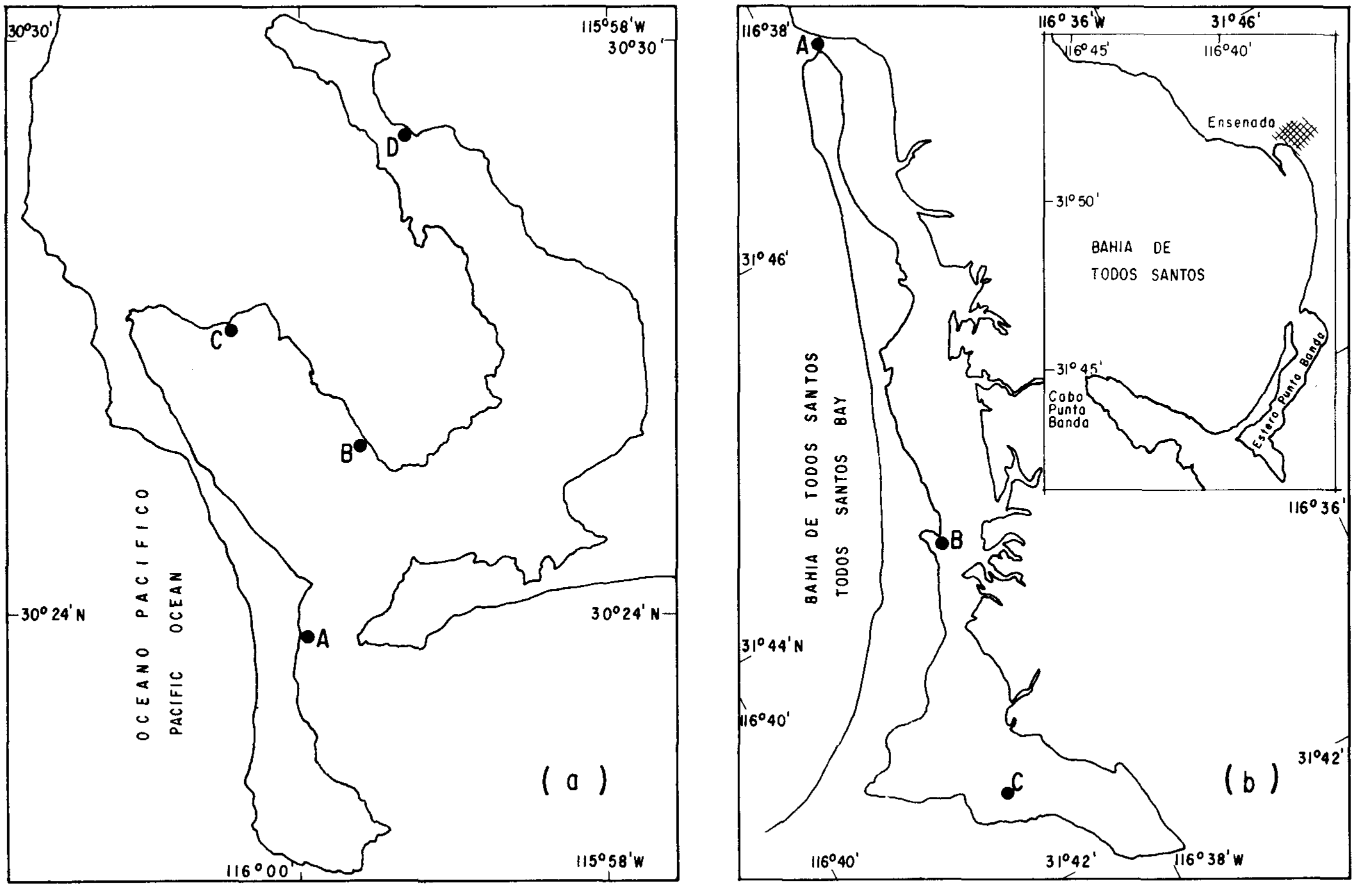


Figure 1. Location of sampling points in San Quintin Bay *(a)* and Estero de Punta Banda *(b)*.

series had been generally too short, of the order of tens of hours. Lara-Lara, Alvarez-Borrego, and Small (1980) generated 17-day time series, with sampling every hour. Ideally, time series should be at least one year long, to roughly describe seasonal changes. Usually this is not possible, because an enormous amount of samples has to be collected and analyzed manually. With relatively cheap and reliable thermographs able to automatically generate time series, it is possible to study the natural phenomena that cause temperature changes.

Temperature was measured *in situ* with Peabody Ryan thermographs, which produce an analog record on paper. The thermographs were situated at four locations in San Quintin Bay, and at three in Estero de Punta Banda (Figure 1a and b). They were located deep enough to remain under water even at the lowest spring tides. They can register without attention for as long as three months. Precision for temperature is ±0.5°C, and the maximum error in time was half an hour for a three-month period. Data were digitized manually, with readings every hour, by two independent readers. Data were then input to a Prime-400 computer.

In order to study the relationship between the factors that affect temperature in different locations, a lagged cross-correlation technique was applied to the temperature time series, and to temperature and tide series, through application of a standard algorithm (Jenkins and Watts 1968). Spectral analysis of the temperature time series was also performed. Spectral analysis of a series of data may be regarded as an analysis of variance in which the total variance of a property fluctuation is partitioned into contributions arising from processes with different characteristic time scales (Platt and Denman 1975). The spectral estimate presented here was computed with a fast Fourier transform algorithm (Jenkins and Watts 1968).

We also obtained estimates of coherence and phase spectra of the different temperature series, and between them and tide series. Coherence gives an estimate of the relationship between components of one series with those of another, and the phase spectrum gives the angular time lapse between two components of the same frequency. However, we consider that these estimations did not provide significant additional information. This type of estimate would have been more informative if we had time series of air temperature, solar irradiance, tidal currents, winds, etc.

RESULTS

San Quintin Bay

The temperature time series for San Quintin Bay were located at four points, with point A at the mouth of the bay and point D nearest the head of the bay. The time series for each point was as follows:

Point A	May 17, 1979, through May 13, 1980
B	July 6, 1979, through May 13, 1980
C	May 17, 1979, through May 13, 1980
D	May 17, 1979, through May 13, 1980

Upwelling occurs in the open ocean immediately off the mouth of the bay during spring and summer (Dawson 1951). Bakun (1973) calculated upwelling indices for the west coast of North America, and these calculations show favorable upwelling conditions throughout the year for latitudes 27°N to 33°N, with the maximum upwelling indices from March to June. Upwelling intensification events are clearly shown from the end of spring through the end of summer at point A, the mouth of the bay. These events are also evident at the other data stations because of tidal currents, but are attenuated. Upwelling intensification periods were from a week to ten days.

The temperature minimum, maximum, and yearly mean are shown below:

Location	Minimum		Maximum		Yearly
	Date	°C	Date	°C	mean (°C)
A	12 July	11.0	19 Sept.	21.5	15.2
B	22 Nov.	12.9	20 Sept.	23.5	16.7
C	24 Dec.	13.3	20 Sept.	25.3	18.4
D	23 Nov.	13.0	19 Sept.	27.3	19.0

All stations show a semidiurnal behavior in relationship to the tides, with the highest amplitudes at point A. Flash floods at point B caused the thermograph to be buried in sediments from January 8-27. This burial acted as a physical filter for the high-frequency temperature changes. Spring and neap tides are clearly evident at each station.

During spring, summer, and the beginning of fall, the short-period temperature variability was smaller at points C and D than at points A and B (Figures 2-5). However, towards the end of fall and during winter, there was a greater low-frequency variability (periods of one to two weeks) in points C and D than in A and B. This was possibly due to changes of atmospheric temperature, solar irradiance, and winds during the rainy winter season. These atmospheric changes have more effect on the waters at points C and D because of their shallow depth.

Estero de Punta Banda

The temperature time series for Estero de Punta Banda were located at three points, with point A at the mouth of the estero and point C near its head. The time series for each point was as follows:

Point A May 29, 1979, through Dec. 12, 1979

FIGURE 2 - POINT A

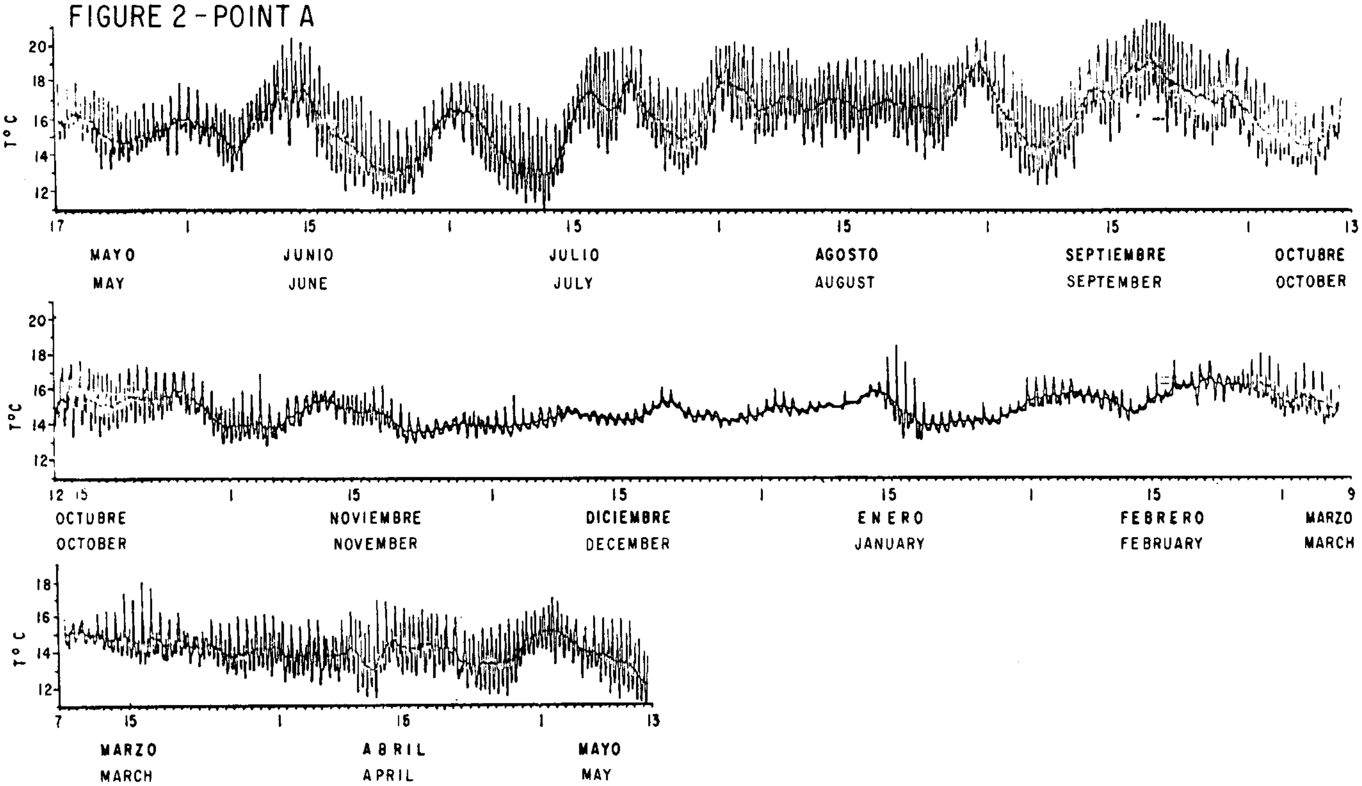
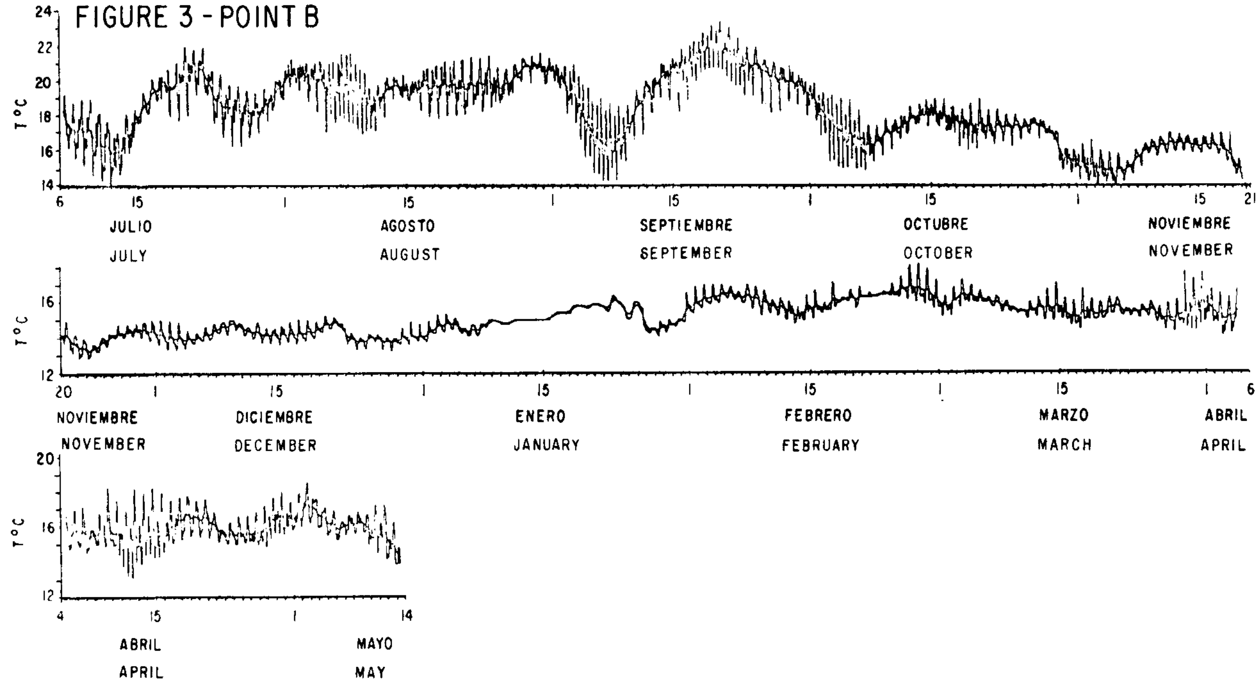


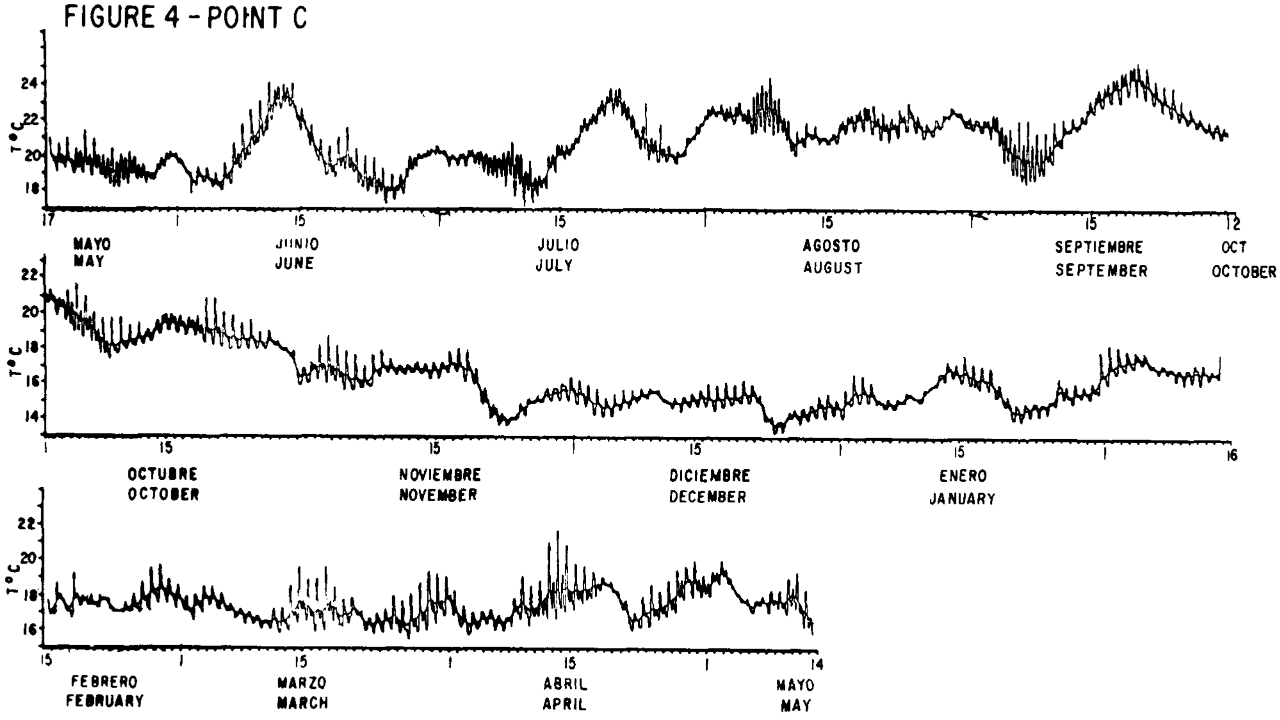
FIGURE 3 - POINT B

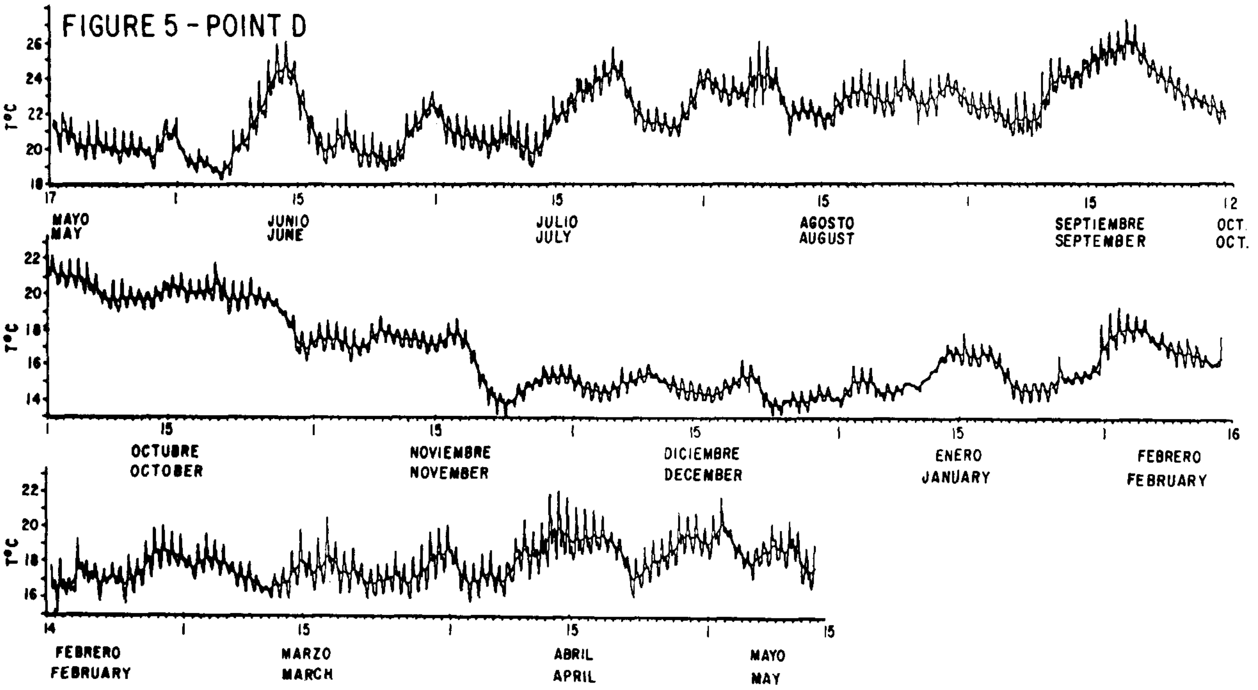


Figures 2 and 3. Thermograms from points A and B of San Quintin Bay. Marks on the horizontal axis are midnights. Numbers are dates.

Apr. 16, 1980, through May 20, 1980
B May 29, 1979, through Oct. 1, 1979
Oct. 16, 1979, through Oct. 28, 1979
Dec. 14, 1979, through Mar. 6, 1980
C May 29, 1979, through May 20, 1980

The interruption at point A was caused by the loss of the thermograph during strong winter rains. At point B the thermograph was inoperative during several periods; thus it was necessary to make three separate time series.





Figures 4 and 5. Thermograms from points C and D of San Quintin Bay. Marks on the horizontal axis are midnights. Numbers are dates.

The temperature minimum, maximum, and yearly mean are shown below:

Location	Minimum		Maximum		Yearly
	Date	°C	Date	°C	mean (°C)
A	8 Dec.	12.7	23 Sept.	25.3	19.2
B	11 Feb.	14.1	16 Sept.	26.4	19.8
C	21 Nov.	12.1	9 Aug. 16 Aug. 19 Sept.	28.0 28.0 28.0	19.7

An almost constant temperature was recorded during nine days at the beginning of the series at all three stations. This was possibly due to the combination of neap tides and a horizontal surface temperature gradient of almost zero. Between May 29 and June 2, temperature in the estero showed a horizontal gradient, with values increasing from the mouth (18-19°C) towards the extreme (20-21°C), but the following four days all the estero showed the same temperature of 19°C, which is exceptional.

In the estero, the sequence of spring and neap tides is also clearly shown in the diurnal temperature ranges at all three sampling points (Figures 6-8). Temperature semidiurnal variability in the estero was in general greater during spring, summer, and beginning of fall than during the end of fall and winter, with rare exceptions such as that registered at the end of May and beginning of June 1979. This greater semidiurnal variability is due to greater horizontal temperature gradients during spring, summer, and beginning of fall than during the rest of the year.

At the end of spring and during summer, the temperature time series from point B and the estero's entrance had a similar behavior. Some colleagues have indicated (pers. comm.) that a possible explanation for the low-frequency temperature fluctuations is that they are due to the sequence of spring and neap tides. With spring tides, greater turbulence and mixing would produce lower surface temperatures, and vice versa with neap tides. However, in the series from point B, it is interesting to notice that greater diurnal temperature ranges, corresponding to spring tides, were presented with both valleys and crests of the temperature low-frequency fluctuations. This can be seen in the other time series also, but it is particularly clear in this one.

From January 8 through 13, another case of very low diurnal variability was evident. This was also shown in the series from point C (Figures 7 and 8), and it was possibly due to a horizontal temperature gradient near zero in the estero. The difference from the May-June case, mentioned above, was that in January there was a gradual temperature increase throughout the estero. This was possibly due to more intense solar radiation, with a sequence of clear days, and with relatively high water residence time. During several days after January 13, spring tides increased the diurnal temperature ranges, but the general warming tendency continued until January 16 at both points, B and C (Figures 7 and 8).

In general, the temperature behavior at point C was very similar to that at point B (Figures 7 and 8), except during the second half of winter, when there was a greater variability. At both sampling points there was a clear low-frequency fluctuation (with a period of about two weeks) towards the end of fall and during winter. This was possibly due to the incidence of atmospheric events. Air temperature and solar radiation changes have a strong effect on the estero's shallow waters. Again, it is interesting to notice that at point C spring tides coincided sometimes with higher water temperatures.

During summer, temperature was significantly greater at the estero's entrance than at the mouth of San Quintin Bay. During winter these two places had similar temperatures (Figures 2 and 6).

During spring and summer, low-frequency temperature fluctuations in Estero de Punta Banda are similar to those of San Quintin Bay, especially with regard to low temperatures between July 11 and 15, between September 7 and 12, and around April 25 (Figures 2 and 6). The strongest upwelling event registered at the mouth of San Quintin Bay had a minimum temperature on July 12. On that same date, the summer's minimum temperature at the estero's entrance was registered. This indicates that upwelled water from outside Todos Santos Bay was being carried to the lagoon by coastal currents.

Cross correlation and spectral analysis of time series

Table 1 shows the maximum cross-correlation coefficients and the lags in hours. These are for the different temperature time series, and between them and the tide series. Summer and winter data are separated to deal with the upwelling season separately. The highest cross-correlation coefficients were those for thermograms from points C and D of San Quintin Bay (0.91 for summer and 9.95 for winter, with zero lag). This indicates the similarity of physical phenomena acting on both extremes of the bay. Cross-correlation coefficients for the San Quintin mouth series with those from points C and D were lower for summer than for winter, because of upwelling events during summer. Cross-correlations between the mouth's and the interior's temperature series of Estero de Punta Banda were higher than those for San Quintin Bay. This was due to the smaller influence of oceanic events on the entrance to the estero, because it is inside Todos Santos Bay. The negative lag of the cross-correlation between points A and D of San Quintin Bay in summer (−12 hr) may be due to the occurrence of spring tides before an upwelling event, which happened on several occasions (cross-correlation coefficients were significantly lower for lags between −11 and +12, at the 95% confidence limit). For example, at the beginning of July, temperature started to decrease in point D (Figure 5) because of the effect of spring tides currents that were carrying colder water from the area near the bay's entrance to point D. At point A, the temperature started to decrease on July 5 because of an upwelling event (Figure 2).

FIGURE 6 - POINT A

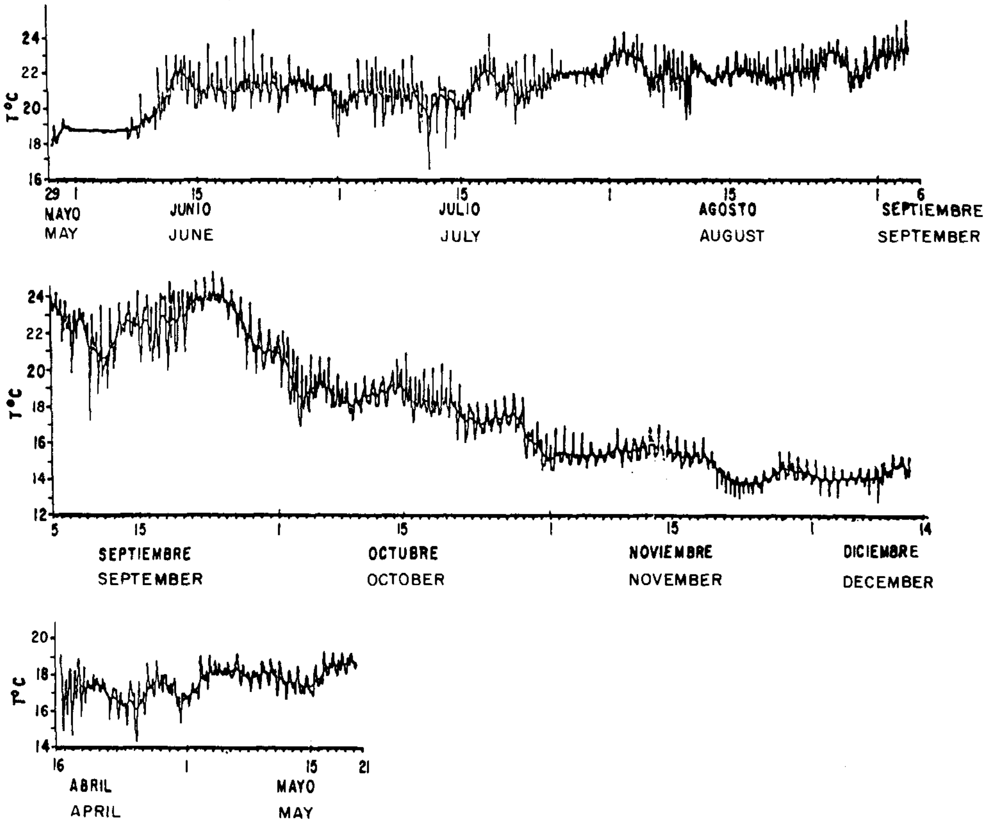
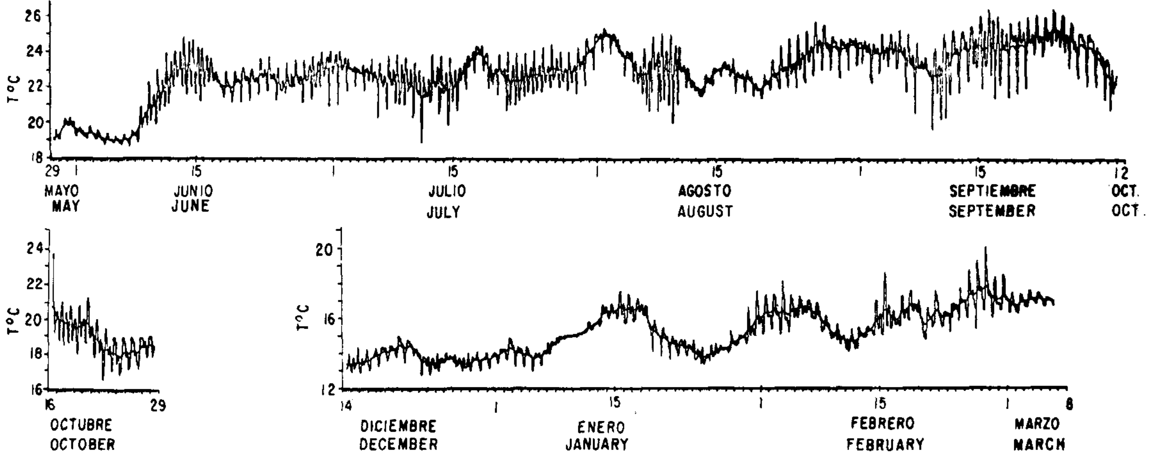


FIGURE 7 - POINT B



Figures 6 and 7. Thermograms from points A and B of Estero de Punta Banda. Marks on the horizontal axis are midnights. Numbers are dates.

Cross-correlation coefficients were low for temperature and tide series, both for San Quintin Bay and Estero de Punta Banda. Oceanic and atmospheric events, such as upwelling, and seasonal changes of air temperature and solar irradiance were responsible for most of the water temperature variance. This is indicated by the high low-frequency component of the variance spectrum (Figure 9).

We illustrate only one variance spectrum because differences between spectra from the seven sampling points are not statistically significant (Figure 9). Spectral analysis shows that temperature variance generally decreased with frequency. Seasonal temperature changes caused a greater variance than that due to processes of intermediate frequency (~0.0025 cph), such as the sequence of spring and neap tides,

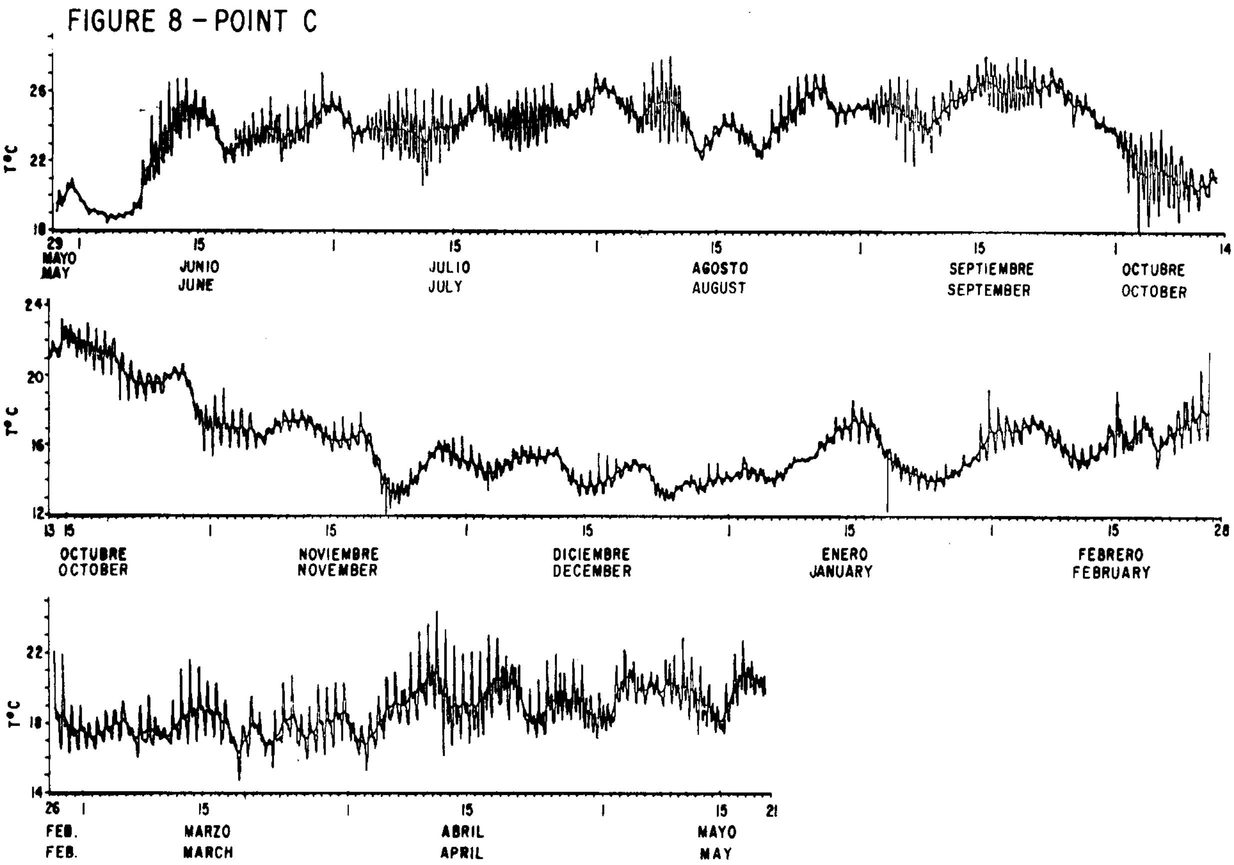


Figure 8. Thermogram from point C of Estero de Punta Banda. Marks on the horizontal axis are midnights. Numbers are dates.

the sequence of upwelling events, or the incidence of winter storms. The spectrum shows distinct peaks at the diurnal and semidiurnal periods (0.04 and 0.08 cph frequencies, respectively), indicating the effect of tidal currents on temperature. As is to be expected from this, coherence between temperature and tide was high for the diurnal and semidiurnal periods (not illustrated).

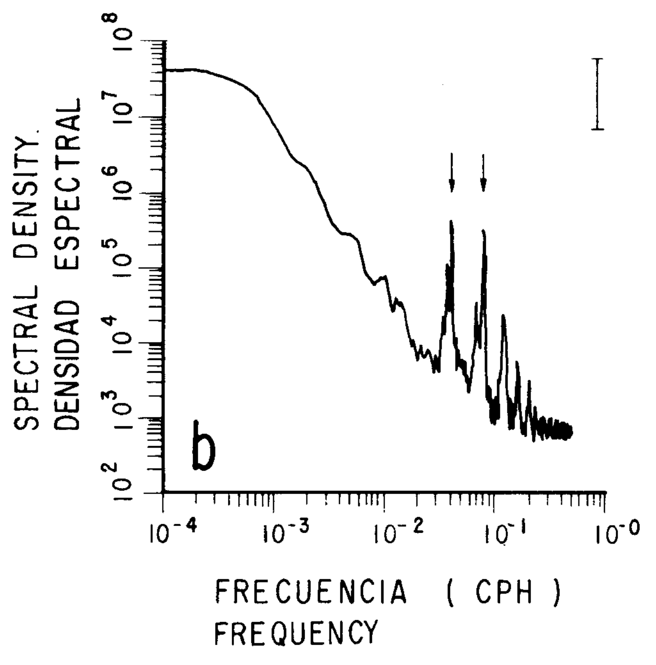


Figure 9. Spectral density of thermograms from San Quintin Bay and Estero de Punta Banda. Differences between spectra of the different time series were not significant, at the 95% confidence level. The bar at right shows the 95% confidence interval, with 36 degrees of freedom. CPH means cycles per hour. Arrows mark the diurnal and semidiurnal frequencies.

DISCUSSION

When sampling seawater temperature at a fixed point, one finds that the short period variations (smaller than diurnal) are mainly caused by tidal currents and horizontal temperature gradients. In general, temperature increases from the mouths of San Quintin Bay and the Estero de Punta Banda to the extremes, with some exceptions during winter, when low air temperatures invert the surface seawater temperature gradients. Therefore, temperature generally increases with ebb flow, at a fixed point, and vice versa. Very short period temperature variations (on the order of a few hours) are mainly due to the irregular bathymetry of these coastal lagoons. This bathymetry causes an irregular warming of the water by solar radiation, or

TABLE 1

Maximum Cross-Correlation Coefficients (R) between the Thermograms (Represented by Letters) from the Different Sampling Points, and between the Thermograms and Tides in San Quintin Bay and Estero de Punta Banda.

	DATES	SERIES	R	LAG
BAHIA DE SAN QUINTIN	MAY 17 TO AUGUST 5	A - C	0.70 ± 0.03	+ 1
		A - D	0.64 ± 0.03	−12
		C - D	0.91 ± 0.01	0
		A - TIDE	−0.47 ± 0.03	− 2
		D - TIDE	−0.21 ± 0.04	− 1
	DECEMBER 22 TO FEBRUARY 29	A - B	0.62 ± 0.03	+ 2
		A - C	0.80 ± 0.02	+ 2
		A - D	0.76 ± 0.02	+ 2
		B - C	0.80 ± 0.02	0
		B - D	0.84 ± 0.01	0
		C - D	0.95 ± 0.01	0
		A - TIDE	−0.32 ± 0.04	− 1
		D - TIDE	−0.18 ± 0.05	− 1
ESTERO DE PUNTA BANDA	MAY 29 TO AUGUST 5	A - B	0.86 ± 0.02	+ 2
		A - C	0.80 ± 0.02	+ 1
		B - C	0.93 ± 0.01	0
		A - TIDE	0.29 ± 0.05	+ 7
		C - TIDE	0.30 ± 0.05	+ 4
	NOVEMBER 12 TO DECEMBER 12	A - C	0.85 ± 0.01	0
		A - TIDE	0.17 ± 0.06	+13
		C - TIDE	−0.14 ± 0.06	− 1

Lag is the number of hours that the series represented by the letter at the left has to move to the right to obtain the maximum R. Intervals are at the 95% confidence level.

cooling by evaporation and low air temperature. It also causes irregular mixing processes by tidal currents and winds. During summer, water is generally warmer in shallow areas than in channels. Atmospheric temperature, solar input, and winds affect the interiors of these lagoons more than the areas near the entrances, because of shallow depths and greater residence times in the interiors. Long period temperature variations (one week or more) are caused by phenomena that change the temperature throughout the whole lagoon and adjacent oceanic area in a similar fashion. Examples of these phenomena are the sequence of upwelling events during spring and summer; a sequence of clear, warm days; the incidence of winter storms; the seasonal change of atmospheric temperature and solar irradiance; or a combination.

During summer, temperature variations at a given location in these coastal lagoons are related to changes of the water residence time for that location. With low residence times causing high water renewal, temperatures tend to be lower, and vice versa. Residence times in these coastal lagoons do not depend only on their geometry and the spring-neap tide sequence. They also depend strongly on the adjacent ocean dynamics. During summer, at the mouth of San Quintin Bay upwelling causes surface water temperatures sometimes lower than 12°C, with dissolved oxygen saturation of about 60%. This low oxygen saturation shows that the low-temperature water is the result of upwelling and not, for example, the result of mesoscale structure of advection off the bay. During summer, low water temperatures generally correspond with high salinities, low dissolved oxygen, high nutrient concentrations, relatively low chlorophyll concentrations, and low phytoplankton productivity, and vice versa (Lara-Lara et al. 1980). In general, all year round, there are horizontal salinity and temperature gradients, with values increasing from the mouth to the extremes of the lagoon (Chavez de Nishikawa and Alvarez-Borrego 1974; Alvarez-Borrego et al. 1975). The entrance to Estero de Punta Banda is some 14 km from the upwelling area outside Todos Santos Bay. In general, all year round there are horizontal salinity and temperature gradients, with values increasing from the mouth to the extreme of the estero (Acosta-Ruiz and Alvarez-Borrego 1974; Celis-Ceseña and Alvarez-Borrego 1975).

During periods with weak coastal currents in the adjacent oceanic area, water leaving the lagoon during ebb flow returns in high proportion with flood flow, causing a high residence time in the lagoon. With strong currents parallel to the coast, water leaving the lagoon during ebb flow is carried away from the area near the entrance, and during flood flow "new" water enters the lagoon, causing a low residence time. The thermograms show that if spring tides occur simultaneously with the attenuation of coastal currents, high temperatures are produced, indicating high residence times. On the other hand, if neap tides occur simultaneously with strong coastal currents, water temperatures are relatively low, indicating low residence times. This happened in June 1979 in the Estero de Punta Banda (Figure 6). Around June 15, with spring tides, greater temperatures were registered than during the first days of that month, with neap tides. Contreras-Rivas (1973) detected a northward current parallel to the coast, off the estero's entrance, on July 30, 1972. Alvarez-Sanchez (pers. comm.) has measured these currents using drifting buoys. Maximum measured surface velocity is 30 cm sec^{-1}. Velocity changes of these currents are not adequately known yet, but there is evidence they are associated strongly with the wind regime. Alvarez-Borrego, Acosta-Ruiz, and Lara-Lara (1977) indicated that abrupt temperature and salinity decreases, detected sometimes at the estero's entrance at the beginning of flood flow, were caused by currents parallel to the coast. Lowest residence times in these lagoons occur with spring tides coinciding with strong coastal currents.

Lara-Lara, Alvarez-Borrego, and Small (1980) showed that with an upwelling event off San Quintin Bay's mouth, water residence time in the bay decreased greatly, whereas during relaxation periods residence time increased.

Some researchers (pers. comm.) have indicated that low-frequency temperature changes in San Quintin Bay's mouth (periods of 10 to 15 days) during spring and summer could be due to the sequence of spring and neap tides and not to upwelling events. However, minimum winter temperature was 13.5°C and occurred during spring tides (Figure 2); it was 2.5°C greater than minimum summer temperature. Besides, the maximum temperature of the year occurred during spring tides in September. This indicates that the sequence of upwelling events causes most of the low-frequency temperature changes during spring and summer. Also, as indicated above, in the estero spring tides coincided indistinctly with crests and valleys of low-frequency temperature variations.

Both at San Quintin Bay and Estero de Punta Banda temperature maxima for the year were registered at the end of September. This may be due to the attenuation of upwelling events at a time when solar radiation is still high. According to Bakun (1973), in September the upwelling index is about half of the year's maximum, although its value may vary from year to year.

Low temperatures registered in Estero de Punta Banda in June, July, September, and April (Figures 6 and 7) possibly correspond to upwelling waters carried from the oceanic area adjacent to Punta Banda and Todos Santos Island, by coastal currents like those mentioned above. These waters are warmed in the trajectory to the estero's entrance. The temperature time series from San Quintin Bay's mouth (Figure 2) shows an upwelling intensification event occurring from August 31 through September 8, 1979. Millan-Nuñez, Ortiz-Cortez, and Alvarez-Borrego (1981) generated nutrients, chlorophyll and phytoplankton abundance time series from September 1-11, 1979, at the estero's mouth. Their results show high chlorophyll-a concentrations and phytoplankton abundances during the last four sampling days, up to 12 mg m^{-3} and 10^6 cells per liter, respectively. These high values indicate the presence of upwelled waters that after a few days have been "conditioned" in the sense of Barber and Ryther (1969); that is, certain unavailable micronutrients in the freshly upwelled water became available through chelation as the water aged, and phytoplankton populations responded by growing rapidly.

ACKNOWLEDGMENTS

We thank A. Granados-Guzman for his help with the field work. We also thank L. Brambila, A Montiel, and E. E. Millan-De-Alvarez for their patient and generous help with reading the thermograms. A larger version of this work was presented by Josue as a B.S. thesis to the University of Baja California. This represents a segment of a long-term project by the Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. A small grant for this work was received from the National Council of Science and Technology of Mexico through project PCMABNA-005324.

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THRESHOLDS FOR FILTER FEEDING IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

The density threshold for the onset of filter feeding in adult anchovy *(Engraulis mordax)* fell between 5 and 18 *Artemia salina* nauplii/l, between 1 and 2 anchovy eggs/1, and between 151 and 328 *Gymnodinium splendens* cells/l. Observations of the incidence of filtering schools indicate that behavioral changes occurred at lower food densities. These observations also indicate that the intensity of filtering by anchovy schools may be a function of the biomass of filterable foods. Filtering persisted long after the density in the tank was reduced below that required for the initiation of filter feeding.

RESUMEN

La densidad mínima para el comienzo de alimentación por filtrado en adultos de *Engraulis mordax* disminuyó entre 5 y 18 nauplios de *Artemia salina* por litro, entre 1 y 2 huevos de anchoveta por litro, y entre 151 y 328 células de *Gymnodinium splendens* por litro. Observaciones sobre la incidencia de cardúmenes en proceso de actividad filtradora indican que se producen cambios en su comportamiento cuando el alimento aparece en densidades bajas. Estas observaciones también indican que la intensidad de filtrado en los cardúmenes de anchoveta puede estar determinada por la biomasa de alimento filtrable. Este tipo de alimentación aún persistió mucho después de que disminuyera la densidad en el tanque, alcanzando valores por debajo del umbral que marca el comienzo del proceso de alimentación por filtrado.

INTRODUCTION

Northern anchovy are facultative filter-feeding planktivores. They change from filter feeding to particulate feeding on the basis of prey size; they filter small prey, such as *Artemia salina* nauplii, and bite larger ones, such as *Artemia* adults (Leong and O'Connell 1969). A significant proportion of the natural mortality of northern anchovy eggs can be attributed to adult anchovy filtering their eggs (Hunter and Kimbrell 1980; MacCall 1980), but the extent to which eggs are filtered selectively or taken inadvertently while filtering other prey is not known. Selective filtering requires that the density of prey be sufficient to cause the school to filter intensively within an aggregation of a particular prey. Thus, the prey density thresholds for filter feeding are important in modeling effects of egg cannibalism as well as in understanding the ecology of anchovy feeding. The densities of prey used by Leong and O'Connell (1969) to estimate maximum filtering rates of anchovy (292-1,120 *Artemia* nauplii/l) are far above the threshold. The objective of this study was to estimate the prey density threshold for filtering in northern anchovy. Three prey types are used: *Artemia* nauplii (0.433 mm x 0.236 mm; 1.70 μg dry weight); northern anchovy eggs (1.34 mm x 0.66 mm; 30.1 μg dry weight); and the dinoflagellate *Gymnodinium splendens* (40 μm dia; 0.0117 μg dry weight).

METHODS

Schools of 56-596 northern anchovy (6.4-10.2 cm standard length) were maintained in a tank (3-m dia.; water depth 0.6 m) with continuous flowing seawater of ambient temperature (14.3-21.6°C). Seawater was filtered continuously through a sand-and-gravel filter and subsequently was irradiated with ultraviolet light. The tank was dimly lit from above by a 40-W incandescent lamp for 12 h per day and was dark for 12 h. Fish were fed trout food (Oregon Moist Pellets)[1] and frozen adult *Artemia salina* (brine shrimp). Schools were deprived of food for 48 h prior to an experiment, and a few hours before a test the tank was cleaned and the seawater shut off. Numbers of anchovy in schools varied (Table 1), and the tank was completely restocked 11 times over the 2 years that experiments were conducted. Partial restocking and some mortality account for the variability in school size.

At the onset of an experiment the tank was stirred vigorously with a large dip net (60-cm dia); the school recovered from this disturbance in 1-2 min. Immediately after stirring, the incidence of filtering behavior was recorded for 9 min. Food was then added and the tank stirred again while water samples were taken to estimate the density of food in the tank. After the tank was stirred for the second time, behavior ob-

[Manuscript received November 24, 1981.]

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[1] Use of a trade name does not imply endorsement by the National Marine Fisheries Service.

TABLE 1

Effect of Prey Density and Prey Type on Filter Feeding in Northern Anchovy, *Engraulis mordax*, Schools

Food type			Incidence of filter feeding			
Initial density n/l	Final[1] density n/l	Significance of density change[2]	Before food added[3]	After food added[3]	Significance of change[4]	School Size n
Artemia nauplii						
0.87	0.76	0	0	1.2	0	430
2.81	2.84	0	7.6	7.9	0	430
3.27	2.22	0	0.6	4.3	+	357
4.59	4.46	0	2.0	3.9	0	300
5.51	2.59	+	14.5	43.7	+	318
5.96	1.68	+	3.3	12.0	+	256
6.71	4.33	0	1.2	7.0	0	300
8.77	8.47	0	0.2	20.0	+	567
9.03	4.60	0	1.6	10.4	+	567
9.13	6.90	0	0.1	0.3	0	357
13.10	11.40	0	1.6	5.4	+	357
13.62	9.62	+	2.1	26.8	+	318
16.05	10.14	0	0	25.5	+	357
18.04	8.74	+	12.6	36.1	+	430
18.79	10.71	+	3.6	49.7	+	300
20.46	9.44	+	2.1	57.4	+	430
23.96	9.17	+	8.6	47.5	+	430
26.64	12.85	+	10.8	70.7	+	430
114	—	—	—	57.8	—	438
190	—	—	—	53.4	—	569
285	—	—	—	86.0	—	596
378	—	—	—	71.9	—	167
386	—	—	—	81.8	—	374
Anchovy eggs						
0.26	0.15	0	3.9	20.5	+	106
0.32	0.37	0	0.2	7.6	+	75
1.11	1.52	0	1.8	22.7	+	300
1.50	0.46	+	4.1	59.5	+	116
3.32	1.70	+	2.1	45.8	+	131
4.14	1.21	+	5.0	63.2	+	357
4.76	0.84	+	3.9	80.1	+	300
5.34	0.73	+	5.1	58.6	+	256
10.50	2.90	+	1.6	79.8	+	126
Gymnodinium cells						
151	104	+	0.2	7.8	+	—
161	104	0	2.1	31.2	+	—
259	200	+	0.4	9.3	+	56
328	358	0	0.6	3.2	+	67

[1] Measured 9 min after food introduction in *Artemia* and egg experiments, and after 18 min in *Gymnodinium* experiments; five highest *Artemia* densities were preliminary experiments, and no final density was recorded.
[2] Comparison of initial and final density using t-test; + = $P < 0.05$ and 0 = $P > 0.05$ (2 tail).
[3] Average for 9-min test period.
[4] Comparison of mean incidence of filtering before and after food added using t-test when + = $P < 0.05$ and 0 = $P < 0.05$ (2 tail).

servations were resumed for 9 min, then the tank was stirred for the third time while another set of water samples was taken. In the *Gymnodinium* experiments the final set of water samples was not taken until 18 min after the introduction of food, in order to increase the probability of detecting a change in food density, since the filtering response was weak even at the highest density.

Methods for estimating food density in the tank varied. When the density was about four prey per liter or less we took seven 12-liter samples; at higher densities we took 12-15 one-liter samples. Water in each sample was filtered, prey were counted, and a mean density was calculated. The t-test (2 tail) was used to compare initial to final food densities.

Filtering behavior was recorded by three to five observers stationed around the tank. Each observer watched a single anchovy for 2 sec. If the operculum was fully extended during any part of the 2-sec period, the observer recorded a filtering act. After recording on push-button counters whether or not a filtering act had occurred, the observer randomly selected another fish and continued to accumulate 2-sec observations of individual fish over a 2-min period. After 2 min each observer had accumulated a set of about 60 observations of 60 fish; the proportion of these observations in which filtering occurred was transcribed and another 2-min observation period begun. In the 9-min test period, each observer made four sets of cumulative observations, and the number of sets per test period ranged from 12 to 20, depending on the number of observers. Each set was considered as an estimate of the incidence of filtering behavior in the school. The sets taken by all observers during a test period were combined, and a mean and variance were estimated assuming each set to be an independent observation. We used the t-test (2 tail) to determine if sets of observations taken before and after the addition of food differed from each other.

RESULTS

The density threshold for the onset of filtering of *Artemia* nauplii fell between 5 and 18 nauplii/l when a significant difference ($P<0.05$) between initial and final density was the criterion (Table 1). No significant changes occurred at densities less than 5 nauplii/l, and initial and final densities were consistently different above 17 nauplii/1. Significant changes in the density of anchovy eggs occurred consistently at densities greater than two eggs/l, indicating that the threshold for the onset of filtering may occur between 1 and 2 eggs/l. The density of *Gymnodinium* changed significantly in two of the four experiments, indicating that a 50 percent threshold for filtering this dinoflagellate may fall between 151 and 328 cells/l.

Even when no food has been present for some time, usually a few fish, typically about 2 percent, execute filtering movements. The frequency of such acts is low and their duration short: they may serve in early detection of food or may have some other function. At high food densities, similar to those used by Leong and O'Connell (1969), nearly all fish in a school filter, and filtering bouts are nearly continuous. At such densities, about 70-80 percent of the fish filter during any 2-sec period. At lower food densities, the frequency of filtering bouts and their duration decreases, and the time between bouts increases until, at the lowest densities, the behavior approaches that of fish without food.

The percentage of fish filtering usually increased when food was added, even at the lowest densities. Thus, significant changes in filtering behavior occurred at lower densities than those at which we were able to detect a change in food concentration caused by filtering (Table 1). The proportion of fish filtering increased with the initial food density but differed among food types (Figure 1). For a given density, the incidence of filtering was highest for anchovy eggs and intermediate for *Artemia* nauplii; only a small portion of the fish filtered *Gymnodinium* at densities as high as 328 cells/l. A strong response (filtering fish >50 percent) occurred at food densities of 4 eggs/l and 20 *Artemia* nauplii/l; above these densities the incidence of filtering increased gradually with food density, reaching a maximum of about 80 percent.

The behavior data shown in Figure 1 were combined by expressing the initial food density in terms of dry weight per liter instead of numbers per liter. Con-

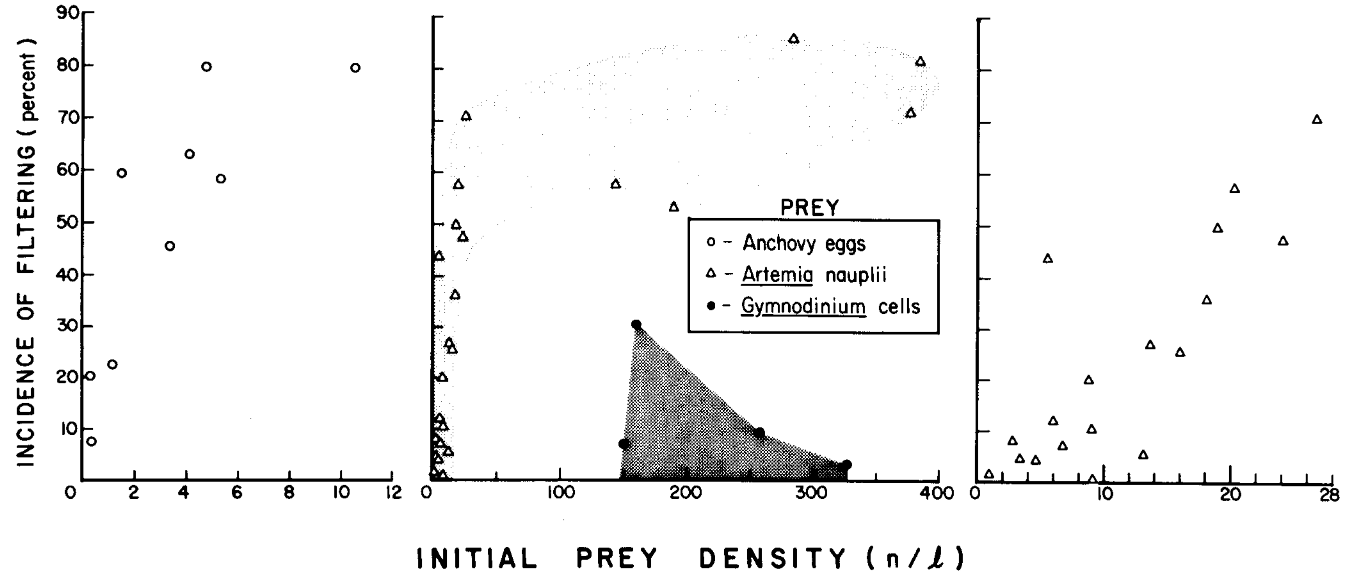

Figure 1. Mean incidence of filter feeding in northern anchovy schools during initial 9 min of feeding as a function of initial prey density in numbers per liter. *Left*, filtering incidence as a function of anchovy egg density; *center*, filtering incidence as a function of density of *Artemia* nauplii (lightly shaded) and *Gymnodinium* cells (darkly shaded); *right*, enlargement of *Artemia* nauplii data for densities of 1-27/1.

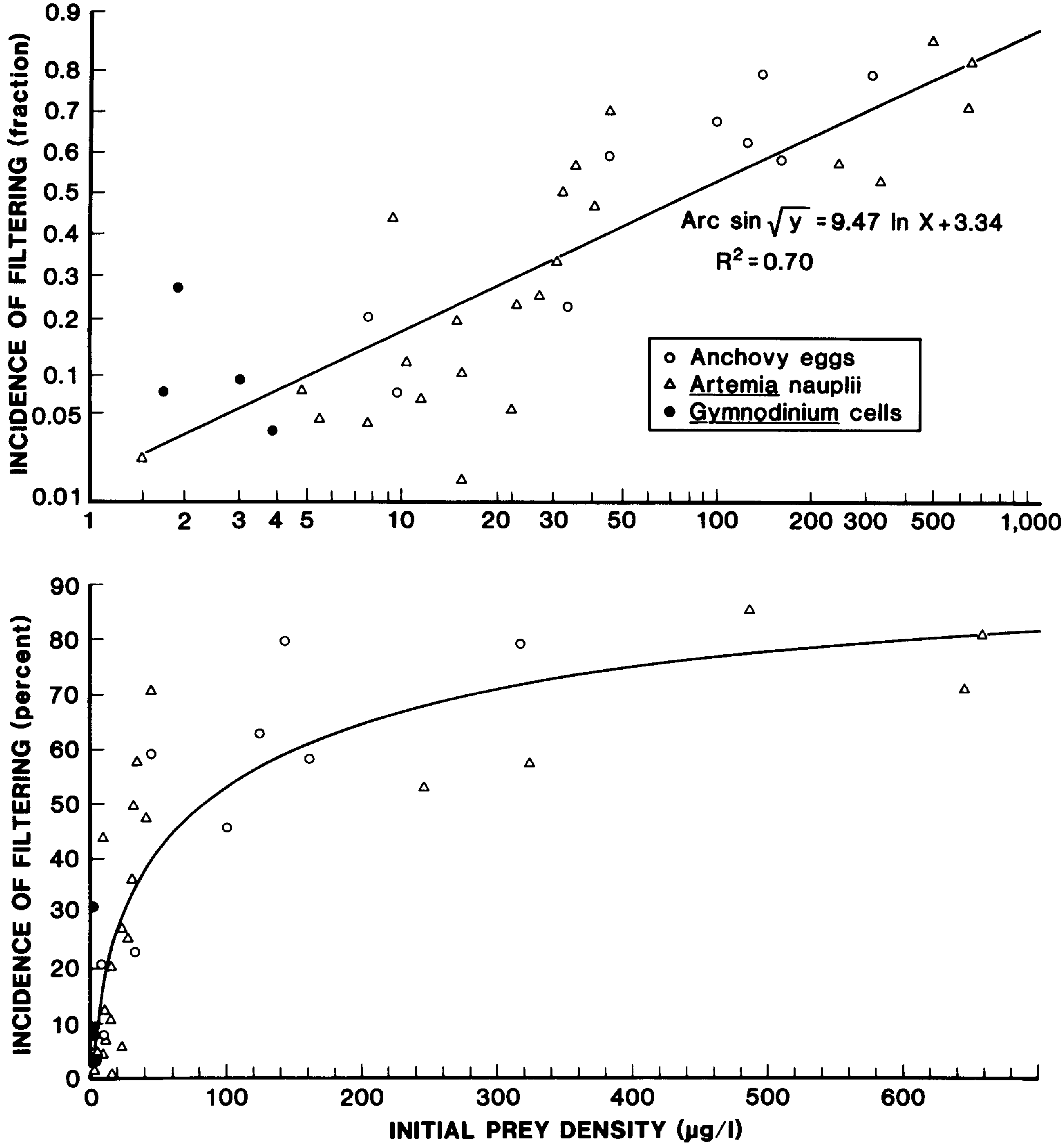

Figure 2. Mean incidence of filter feeding in northern anchovy schools during initial 9 min of feeding as a function of initial prey density in dry weight per liter. Data in Figure 1 have been converted from numbers per liter to dry weight per liter using the conversions, anchovy egg = 30.1 μg; *Artemia* nauplius = 1.70 μg; and *Gymnodinium* cell = 0.0117 μg. *Upper panel,* incidence of filter feeding plotted on arcsine transformed scale (arcsin $\sqrt{y}$) and dry weight per liter on $\log_e$ scale; *lower panel,* both parameters plotted on arithmetic scales, line from equation in upper panel.

version to dry weight brought together the behavior observations made on the three foods even though they were taken at widely different particle densities (Figure 2, upper panel). Because many of the percentages of fish filtering were near the extremes (<30 percent or >70 percent), we used the arcsine transformation of the fraction of fish filtering (Sokal and Rohlf 1969) and regressed the transformed fractions on the $\log_e$ dry weight of prey per liter. The form of the relation between incidence of filtering and dry weight of food per liter (Figure 2, lower panel), resembles the type II predator response of Holling (1965), i.e., a negatively accelerated rise to a plateau. Because of variability in our data, we cannot distinguish statistically between a type II and a type I predator response, which is characterized by a linear rise to a plateau.

The intensity of filtering in anchovy schools may be a function of the density of filterable biomass. Figure 2 indicates that similar responses to different foods occurred at the same density of biomass but not at the same particle density. Because we used only three foods, the results could also be attributed to specific food preferences, the prey weight proportionality being chance. On the other hand, *Artemia* might be expected to be the preferred prey because *Artemia* adults were a routine part of the laboratory diet, but the school responded much more strongly to eggs than to *Artemia* at low prey densities. We conclude that the density of biomass, regardless of prey type, is probably an important factor regulating the intensity of filter feeding in anchovy schools.

In contrast, the lowest concentrations of prey that stimulated filter feeding were inversely related to particle size or mass. A higher concentration of biomass per liter was required to elicit filtering of anchovy eggs than of *Artemia* nauplii, and a higher concentration of biomass was required to stimulate filtering of *Artemia* nauplii than was required for the much smaller particle *Gymnodinium* (Table 2). Threshold prey concentrations for initiating filter feeding are also inversely related to particle size in menhaden (Durbin and Durbin 1975). Thus the intensity of filtering by anchovy schools was proportional to the density of biomass in the water, whereas the threshold concentrations required to initiate filtering were inversely related to biomass. These findings may be explained in the following way. A higher concentration of biomass may be required for initiation of egg filtration than for filtration of *Gymnodinium* cells because at lower egg concentrations it is probably more efficient to bite rather than to filter eggs, whereas it is never efficient to bite an individual *Gymnodinium* cell. In other words, the threshold density for initiation of filtering a particular prey may be a function of the cost of filtering relative to biting the prey, as well as of its mass; this would elevate the filtration threshold for larger filterable prey such as anchovy eggs, which may be profitably eaten either way.

TABLE 2

Density Threshold Range for the Onset of Filter Feeding in Northern Anchovy

	Particle size		Threshold for onset filter feeding	
Food type	Dimensions µm	Dry weight µg	No/l	Dry wt (µg)/l
Anchovy eggs	1340 x 660	30.1	1-2	30-60
Artemia nauplii	433 x 236	1.7	5-18	8.5-31
Gymnodinium	40 x 40	.0117	151-328	1.8-3.8

In five preliminary experiments anchovy schools were given a high initial density of *Artemia* nauplii (29-322 nauplii/l), and the school was permitted to graze the food to low levels over an extended period. The incidence of filtering and the density of *Artemia* nauplii were recorded at intervals over the feeding period. In these experiments filtering activity remained at a high level even when the density in the tank was reduced below that required for the initiation of feeding. The average incidence of filtering at the end of the feeding period was 32 percent, by which time the density of *Artemia* had dropped to an average of 2 nauplii/l (Table 3). In contrast, the incidence of filtering was close to zero when nauplii at densities of 2-4/1 were initially offered (see Figure 1, right panel). We observed the same behavior in anchovy that were fed eggs. The tendency for high levels of filtering to persist after nearly all food has been removed seems to be a common characteristic in filter-feeding clupeoids, for similar behavior has been observed in Atlantic menhaden (Durbin and Durbin 1975). Thus, anchovy schools that encounter a dense patch of prey may reduce the density below the threshold for initiation of feeding and consequently have a greater impact on the prey than indicated by filter-feeding thresholds.

DISCUSSION

A strong filtering response to eggs occurred at densities above five eggs/l, and the threshold for the onset of filtering (based on a detectable change in egg density) was between 1 and 2 eggs/l. The density of anchovy eggs in the sea, estimated from horizontal

TABLE 3

Persistence of High Levels of Filtering of Northern Anchovy Schools Fed on Initially High Food Density

Initial density *Artemia* nauplii (n/l)	Initial incidence of filtering[1] (percent)	Duration of feeding (min)	Final density *Artemia* nauplii (n/l)	Final incidence of filtering[2] (percent)	School size (numbers of fish)
322	89	29	3.1	33	488
58	31	27	1.3	42	424
53	57	29	1.4	30	418
39	35	30	3.8	29	486
29	30	28	0.6	27	498
Mean 100	48	29	2.0	32	463

[1] Measured over initial 9 min of feeding.
[2] Measured over last 2 min of experiment.

plankton tows, is typically two or more orders of magnitude below this filtering threshold. On the other hand, very high egg densities are occasionally recorded. The highest density of anchovy eggs taken in a neuston net was 31/1, corresponding to a density of 46,000 eggs/10 m^2 of sea surface, which compares with the upper 5 percent of all anchovy egg samples (ranked by density) taken in oblique tows (nylon nets) by the California Cooperative Oceanic Fisheries Investigations ichthyoplankton surveys (unpublished data Southwest Fisheries Center, La Jolla, California).

The integrating characteristic of plankton tows doubtless underestimates to some extent the peak densities of anchovy eggs actually encountered by an anchovy school. Further, the threshold based on density changes in our tank probably underestimates possible effects, because behavior observations indicated that at least some of the fish are stimulated to filter eggs at densities as low as 0.26 eggs/l. Finally, that as many as 730 eggs have been taken from a single anchovy stomach indicates that at times eggs are highly concentrated in the sea (Hunter and Kimbrell 1980). All of these factors point to the conclusion that at least occasionally anchovy egg densities are sufficiently high in the sea to stimulate filter feeding directly, but that eggs are probably also taken when fish are stimulated to filter by concentrations of other prey. It will require more accurate measurements of egg density in the sea to determine the extent of selective feeding on eggs.

Measurement of the size structure of zooplankton assemblages in front of and behind northern anchovy schools indicates that anchovy feed selectively by consuming relatively more of the larger prey and less of the smaller ones in an assemblage (Koslow 1981). The size of zooplankters selected by anchovy in Koslow's study were frequently less than 1 mm. Adult northern anchovy filter eggs (ca. 1.3 mm x 0.6 mm) and smaller particles, whereas they bite anchovy larvae in the yolk-sac stage (ca. 2.8-4.0 mm) and *Artemia* adults (5-10 mm); (Leong and O'Connell 1969). Since the transition from filtering to biting probably occurs at a prey size between 1 and 3 mm, Koslow's data indicate that selectivity results from filter feeding as well as biting.

At least three mechanisms could cause selectivity in filter feeding: selective ingestion, selective gaping, and selective orientation. Selective ingestion, retention on the gill rakers, and ingestion of a preferred prey might occur, but no evidence exists. On the other hand, the fineness and structure of the gill rakers establishes the minimum size of filterable prey; in a limited sense this could be considered selectivity.

Selective gaping was documented in this paper. Our experiments indicated that the frequency or duration of filtering acts increased with the density of biomass (our behavioral observation methods do not distinguish between increases in frequency or duration of filtering acts, but they appear to covary). Thus, preferred prey can be selected by varying the intensity of filtration, and preferences appear to exist for large filterable prey or for smaller ones at an equivalent density of biomass. In addition, filtering persisted long after the density of prey was reduced to subthreshold levels. This factor amplifies the effect of selective gaping.

Selective orientation of a school to patches of prey can also cause selectivity in filter feeding. When food (*Artemia* nauplii or anchovy eggs) was added to a small area in our test tank the anchovy would interrupt their circuit of the tank when they encountered the patch; at first the school would be disorganized, with individuals independently swimming rapidly in small elliptical orbits while filtering intensively in the area of the food patch. Soon this behavior would become synchronized, with the entire school swimming in a larger elliptical orbit through the food patch while continually filtering. Chemical stimuli alone are sufficient to elicit the first stages of this behavior (change in school direction with individuals swimming independently in small elliptical orbits), but filtering and formation of a well-organized school in the patch require the presence of food (C. Barnett, pers. comm.). Thus, food preferences based on chemical stimuli may cause changes in the direction of school movement that could lead to selective filter feeding.

In conclusion, northern anchovy schools may regulate filtering intensity in accordance with the concentration of filterable biomass in the water, and this probably results in selection of the larger prey in an assemblage. Selectivity also may be accomplished by the school's orientation to chemicals produced by a patch of prey. Since anchovy eggs are large relative to many planktonic foods and occur in dense patches, selective gaping and orientation probably occur. It would be of interest, in this regard, to determine if the intensity of filtering depends upon the largest and most abundant component in an assemblage or on the combined total of all filterable organisms.

ACKNOWLEDGMENTS

We thank C. A. Kimbrell for her assistance in analyzing and tabulating the data, and C. Barnett, A. D. MacCall, A. G. Durbin, and J. A. Koslow for very helpful reviews of the manuscript. The list of those who helped record behavior observations resembles a roster of the laboratory staff over the last years; we express our thanks to all.

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AN *IN SITU* DEVICE FOR SENSING AND COLLECTING MICROPLANKTON

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ABSTRACT

This report describes a simple system that was developed to search for and collect "patches" of microzooplankton at sea. It consists of a shipboard diaphragm pump, 50 meters of vacuum hose, and an *in situ* particle sensor attached to the influent end of the hose. This system was used to collect water at discrete depths while the particle concentration of the water was continuously monitored as it entered the pump hose.

Laboratory tests showed no significant avoidance by live microzooplankton of the particle sensor or the collecting device. There appeared to be no difference in the mortalities of organisms that were pumped through the system compared with those that did not pass through the system. In addition, laboratory tests indicate that small, high-density patches of microzooplankton can be collected with minimal smearing of the sample.

The device was tested in several sea trials off the southern California coast, in the New York Bight, and in the Austnesfjorden near Lofoten, Norway. In Austnesfjorden, a water sample was collected that contained 0.6 micronauplii/ml. This is believed to be the highest concentration of micronauplii ever collected.

RESUMEN

En este trabajo se describe un mecanismo sencillo, ideado para encontrar y recolectar en el mar, concentraciones de micro-zooplancton. Se utiliza a bordo una bomba de diafragma con 50 metros de tubo de vacío y un sensor de partículas *in situ* adaptado a la extremidad del tubo. Este sistema fué usado para recoger agua a ciertas profundidades, controlando continuamente las partículas que entraban con el agua.

Los análisis en el laboratorio no indicaron que los integrantes vivos del micro-zooplancton escapasen al sensor de partículas o al dispositivo de recolección. No se observó diferencia en la mortalidad de organismos obtenidos mediante este sistema y los que no sufrieron la acción del mismo. Los análisis de laboratorio indican además, que los organismos experimentan una fricción mínima al ser obtenidos de pequeñas zonas en el mar donde aparecían con densidad de población elevada.

El dispositivo mencionado se probó repetidas veces en el mar, cerca de la costa sur de California, en la bahía de Nueva York y en Austnesfjorden cerca de Lofoten (Noruega). En Austnesfjorden se tomaron muestras de agua que contenian 0.6 micro-nauplios por ml., y se se considera que esta concentración es la máxima obtenida hasta la fecha.

INTRODUCTION

Although it is widely recognized that the distribution of marine plankton is not random (Boyd 1973), little is known about the microstructure of the upper mixed layer because of the limitations of conventional collecting devices. Plankton nets sample large volumes of water and therefore lack the resolution necessary to detect the small-scale structure of planktonic communities. Fisheries biologists, in particular, need to study the microdistribution of marine plankton because of an apparent contradiction in many investigations of larval fish survival at sea. Several laboratory studies with pelagic fish larvae indicate that the concentration of appropriate food organisms required for moderate growth and survival is generally higher than the density of analogous organisms found in the spawning grounds (May 1974). Most observers agree that this discrepancy results from the inadequacies of conventional plankton-sampling schemes; that is, although plankton nets give mean densities of plankton in a scale of thousands of cubic meters, this information can be misleading because microzooplankton densities can vary by more than 2 or 3 times in a scale of less than a meter (Owen 1981). Since the searching volume of a fish larva is generally less than 100 liters per day (Blaxter 1966; Rosenthal and Hempel 1970; Hunter 1972) it is obvious that a description of plankton distribution on the meter scale or less is necessary to understand the feeding dynamics of fish larvae.

Recently developed *in situ* particle counters can detect the number and sizes of individual plankters with spatial resolution in the scale of centimeters (Boyd and Johnson 1969; Maddux and Kanwisher 1965). Although these instruments are useful for studying the microstructure of planktonic com-

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[Manuscript received January 29, 1982.]

munities, they do not collect discrete samples of monitored water. I found this to be a serious limitation for my work on larval fish survival at sea. Fish larvae are selective predators, and feeding success depends on a number of factors including the type, density, and size of the prey (Lasker 1975; Scura and Jerde 1977). Also the food selected by fish larvae can differ in nutritional value (Lasker et al. 1970; Scura and Jerde 1977). To study these relationships and their effect on larval survival one must collect discrete samples of seawater from various locations within the spawning grounds so that the densities, size frequency distributions, and species of the prey can be determined.

If seawater samples can be collected without injuring the prey or altering their concentration, then feeding experiments can be conducted by introducing laboratory-produced fish larvae into the seawater samples. This technique can be used to determine feeding thresholds and prey preferences of fish larvae at various developmental stages.

Lasker (1975) established feeding criteria for first-feeding anchovy larvae *(Engraulis mordax)* in waters collected from the chlorophyll maximum layers off the southern California coast. He used an *in situ* pump in conjunction with a shipboard fluorometer to find aggregations of the naked dinoflagellate *Gymnodinium splendens* that were rich enough to initiate feeding in early post-yolk-sac anchovy larvae. Although *G. splendens* is a good food for first-feeding anchovy larvae, older larvae require larger particles (e.g., copepod nauplii) to meet their energy needs (Hunter 1972). Lasker was unable to find aggregations of microzooplankton rich enough to support substantial feeding by anchovy larvae because his fluorometric technique was only useful for detecting phytoplankton. Although zooplankton may aggregate in or near chlorophyll maxima (Mullin and Brooks 1972), Lasker had no way of monitoring zooplankton concentrations other than by random discrete sampling, which was found to be ineffective.

In this report I describe a simple system to search for and collect "patches" of microzooplankton. It consists of a shipboard diaphragm pump that samples water from discrete depths and a particle sensor that continuously monitors the particle concentration of the water as it enters the pump hose.

This system has been used in several sea trials off the southern California coast, in the New York Bight, and in the Austnesfjorden in the Lofoten area of Norway.

DESCRIPTION OF THE DEVICE

The system for sensing and collecting microplankton is made up of two components: (1) a shipboard diaphragm pump (Jabsco Model #34600) capable of pumping 25 to 30 liters of water per minute through 50 meters of 2.5-cm. I.D. vacuum hose (Gemline light duty) and (2) a particle-detecting system that consists of an *in situ* continuous-flow particle sensor that independently samples water from a point adjacent to the influent end of the pump hose. The particle sensor is connected to a shipboard Coulter Counter Model A by a shielded cable, which is taped along the length of the pump hose. The Model A was modified by connecting an integrator buffer gain control as illustrated in the circuit diagram in Figure 1. The output from the integrator connects to a multiple-voltage range recorder. The impulses from the particle sensor are integrated so that increases in counting rate (i.e., higher particle concentration) deflect the recorder pen from the baseline. The response is proportional to the counting rate, so knowledge of the flow rate through the particle sensor can be used to calibrate the instrument to give the concentration of particles in the water. However, I did not rely on the instrument for precise particle counts because of the possibility of erroneous counts due to electrical interference, air bubbles, or nonliving particles. This instrument was designed as a searching and collecting device. If the detector response indicated a region with high particle concentration, it was easy to collect the water from the pump effluent for detailed shipboard examination with either a microscope or a Coulter Counter Model T_A, or for preservation for later laboratory analysis.

The particle sensor operates on the Coulter Counter principle. Seawater passes through a 3-mm tube containing two electrodes separated by a 1-mm aperture (Figure 2). The seawater acts as the electrolyte, and a current is induced between the electrodes. As a particle passes through the aperture, the resistance between the electrodes is changed proportionally to the volume and impedance of the particle.

The particle sensor was machined from a 1.9-cm-diameter solid Lexan rod (Figure 2). The electrodes consisted of 2-cm squares of platinum foil that were welded to the leads from the shielded cable. Prior to welding, the leads were passed through the electrode component and out the particle sensor end of the 3-mm passage by way of a small hole drilled in the side of the electrode component (Figure 2). After welding, the foil was rolled into a cylinder and fitted into the 3-mm passage of the electrode component by pulling back on the lead from the shielded cable. The length of exposed lead from the shielded cable to the electrode component was then imbedded in a flexible urethane resin to insulate against electrical leakage. The electrode components were removable so that the sensor could be disassembled in case the aperture became

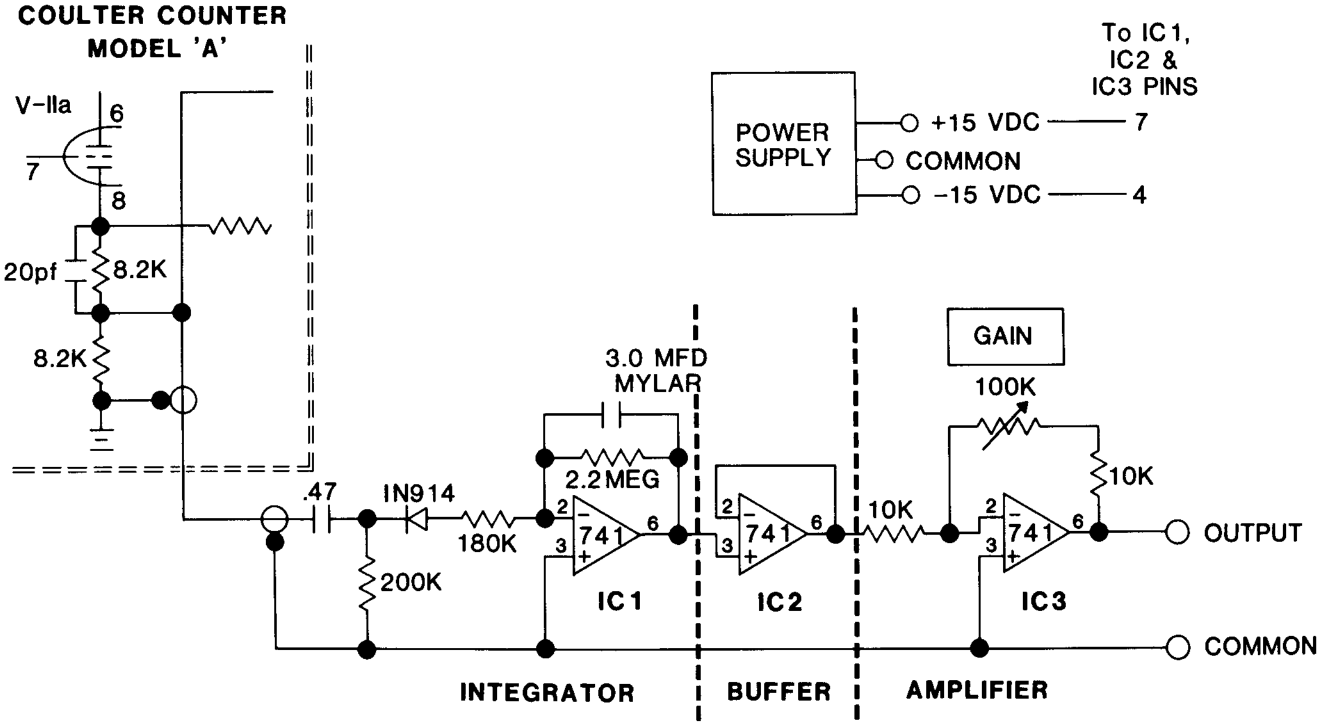
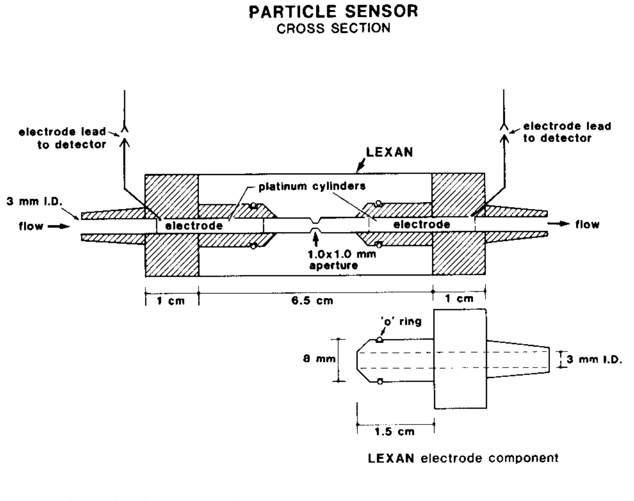


Figure 1. Circuit diagram for modified Coulter Counter Model A particle counter.

clogged (something that has not happened during 45 days of sea trial).

Water is pumped through the sensor at a rate of 200 ± 10 ml/minute by a vacuum created from connecting the effluent end of the particle sensor to the intake of the pump hose as illustrated in Figure 3. This connection was made with a 2-M-by-3-mm I.D. tygon tube to insure that the electrical resistance through the aperture between the electrodes is much less than by any other route. For the same reason, the intake for the particle detector was connected to a 30-cm-by-3-mm I.D. tygon tube. The connections between electrodes and the shielded cable (that transmitted the signal to the ship) were imbedded in a flexible urethane resin to insulate against electrical leakage.



30 cm x 3 mm I.D. tube connected to inlet
2 M x 3mm I.D. tube connected to effluent

Figure 2. Particle sensor.

OPERATION

To operate the system, the sample probe, which consists of the influent end of the pump hose with attached particle sensor, is attached to a weighted (20 kilos) hydrowire and slowly lowered through the water column with the pump and the particle detector in operation. Depths are taken from the winch-metering device and called out to the operator, who records them on the chart paper adjacent to the corresponding response on the recorder. Using this technique, it is possible to get a vertical profile of the particle distribution to a depth of 35 m. Longer lengths of hose could be used to study the particle distribution to greater depths, but it was not needed for our work.

The detector responds to the particle concentration in the water within 2 seconds after the water enters the pump hose; it takes 60 seconds for the water to pass through the hose to the deck of the ship. It is therefore a simple matter for the operator to collect a discrete water sample at the effluent end of the pump system 58 seconds after observing an interesting response on the recorder. Occasionally particle sizes overlap,

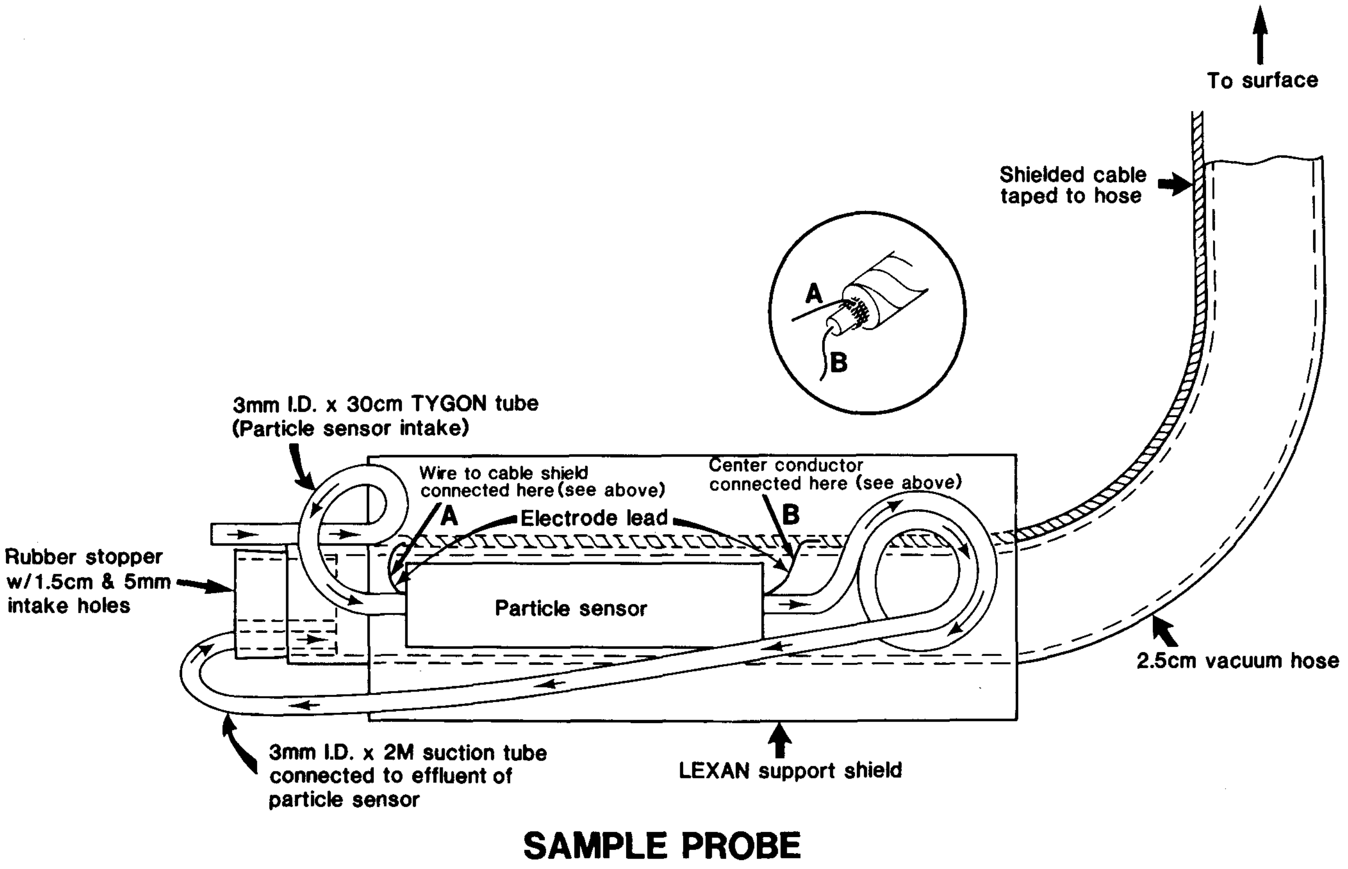


Figure 3.

making it difficult to detect the smaller micronauplii. Such is the case when the concentration of larger phytoplankton (e.g., *Ceratium sp.*) is sufficiently high to mask the presence of the less-concentrated microzooplankton. Careful manipulation of the instrument's threshold adjustment is important at such times.

The particle sensor operates on direct current so that the polarity of the electrodes must be reversed approximately every minute to prevent a change in sensitivity due to plating of the electrodes. This is easily accomplished on the Coulter Counter Model A by tripping the reset switch.

PERFORMANCE

With any plankton-collecting device, there is always the question of avoidance. This system has two separate components that sample plankton. One is the diaphragm pump, which samples at a rate of 25 to 30 l/min through a 1.5-cm orifice; the other is the particle sensor, which samples at a rate of 90 to 210 ml/min through a 3-mm orifice. Although larger zooplankters are likely to avoid such slow influent currents, this system was designed to collect microzooplankton smaller than 600 μm. To test for this, wild plankton were collected off La Jolla, California, in a 42-μm plankton net.

Back in the laboratory, the plankton were filtered through a 560-μm screen and collected on a 64-μm screen. The plankton were allowed to settle for 2 hours to eliminate those killed by handling. Then they were added to a tank containing 400 liters of filtered seawater to make a final concentration of 0.8 ± 0.3 organisms/ml (± 2 S.D.). This concentration was chosen because it is within the range that might be expected in a plankton patch at sea. The particle-pumping system was started in a separate tank containing filtered seawater, and once normal pumping was established, the sample probe was transferred into the tank containing the microplankton. Pumping was resumed for 2 minutes, and after 70 seconds, six 1-liter samples were collected and the plankton concentration determined. If plankton in the 64 to 560-μm size range are capable of avoiding the influent current of the particle-pumping system, then the concentration of particles in the pumped water should have been less than in the tank. The mean ± 2 S.D. for the pumped samples was 0.7 ± 0.3 organisms/ml, which was not significantly different from the water in the tank (0.8 organisms/ml).

To test for microzooplankton's avoidance of the particle sensor, a 3-mm I.D. tube was connected to a peristaltic pump set at a flow rate of 200 ml/min. The influent end of the tube was placed in a 4-liter beaker filled with seawater containing microzooplankton (64-560 μm) at a concentration of 1.5 ± 0.4 organisms/ml (± 2 S.D.). Four 10-ml samples were collected over a 2-minute period, and the particle concentration was determined. The mean ± 2 S.D. for the pumped water was 1.7 ± 0.6 organisms/ml. This test was repeated with seawater containing 0.5 ± 0.2 organisms/ml, and the pumped water contained 0.5 ± 0.1 organisms/ml.

INJURY

If this system is to be used to collect seawater for feeding experiments with fish larvae, it is important that the prey organisms not be injured. A diaphragm pump was selected for this system in the belief that it would be less harmful to plankton than a centrifugal pump. To test for injury to microzooplankton during collection, seawater containing 0.8 organisms/ml (the same organisms that were collected for the avoidance experiments) was pumped through the system and collected in two 2-liter separatory funnels. Identical but unpumped seawater was also collected in two 2-liter separatory funnels. The 4 funnels were left undisturbed for 4 hours in a temperature-controlled room at 17 ± 1°C. Then 25 ml of the seawater were drawn from the bottom and the number of organisms counted. After 24 hours, another 25 ml were collected and counted from the same funnels. There appeared to be no difference in the mortalities of organisms that were pumped through the system compared to those that did not pass through the system (Table 1). The high number of mortalities during the first 4 hours was probably due to injuries resulting from the excessive handling required to capture the zooplankton and separate out the 64-to-560-μm size range.

TABLE 1
Comparison of Microplankton Mortality in Water Passed and Not Passed through a Diaphragm Pump

	Pump Number of organisms/25 ml		*No pump* Number of organisms/25 ml	
	Funnel #1	Funnel #2	Funnel #1	Funnel #2
4 hours	344	295	300	252
24 hours	27	41	35	43

SMEARING

If the distribution of plankton is highly contagious in a region, then the sample probe might quickly pass from high-particle-density seawater to lower density. Depending on the flow characteristics through the hose and pump, the sampled water can smear during the collecting process so that it is difficult to collect seawater with representative plankton concentrations.

To test for smearing, normal pumping was established with the sample probe immersed in a tank of filtered seawater. A 1-liter "square wave" of high-particle-density seawater was introduced into the pumping system with an underwater connection between the sample probe and a 1.5-cm I.D. tube connected to a graduated cylinder containing seawater with 135 rotifers/ml *(Brachionus plicatilis)*. No air bubbles were introduced into the pumping system using this technique. (Air bubbles would disrupt the flow characteristics in the pump and hose.) Normal pumping of the filtered seawater was resumed after the 1 liter of seawater containing the rotifers was introduced. Fifteen 1-liter samples were collected in sequence from the pump effluent starting at 40 seconds after the rotifers were sampled, and the concentration of rotifers in each 1-liter sample was determined. There was minimal smearing: 94 percent of the rotifers introduced in 1 liter were recovered in 3 liters of discharge water.

FIELD TRIALS

The device for sensing and collecting microplankton was tested in several sea trials off the southern California coast, in the New York Bight, and in the Austnesfjorden in the Lofoten area of Norway. The system was tested by comparing the particle concentration in discrete samples of seawater collected from the pump to the corresponding response of the detector. A good correlation was found between the response of the detecting system and the actual concentration of particles in the sampled water as determined by direct microscopic counts.

Figure 4 depicts the chart recordings of the vertical distribution of particles at one station in Austnesfjorden, Norway, on two separate days. Discrete samples were collected from the pump at various depths, and the concentrations of nauplii were determined by microscopic counts. At 2230 hours on May 15, 1977, we found a concentration of 0.6 nauplii/ml near the surface. The mean carapace length of the nauplii was 250 μm S.D. ± 48 μm (n = 50). To our knowledge, this is the highest concentration of micronauplii ever collected at sea. It is interesting to note the contagious nature of the particle distribution. For instance, within 3 meters of the surface, the nauplii concentration had dropped by a factor of ten. Also, on May 10, 1977, the concentration of nauplii at the same station was low.

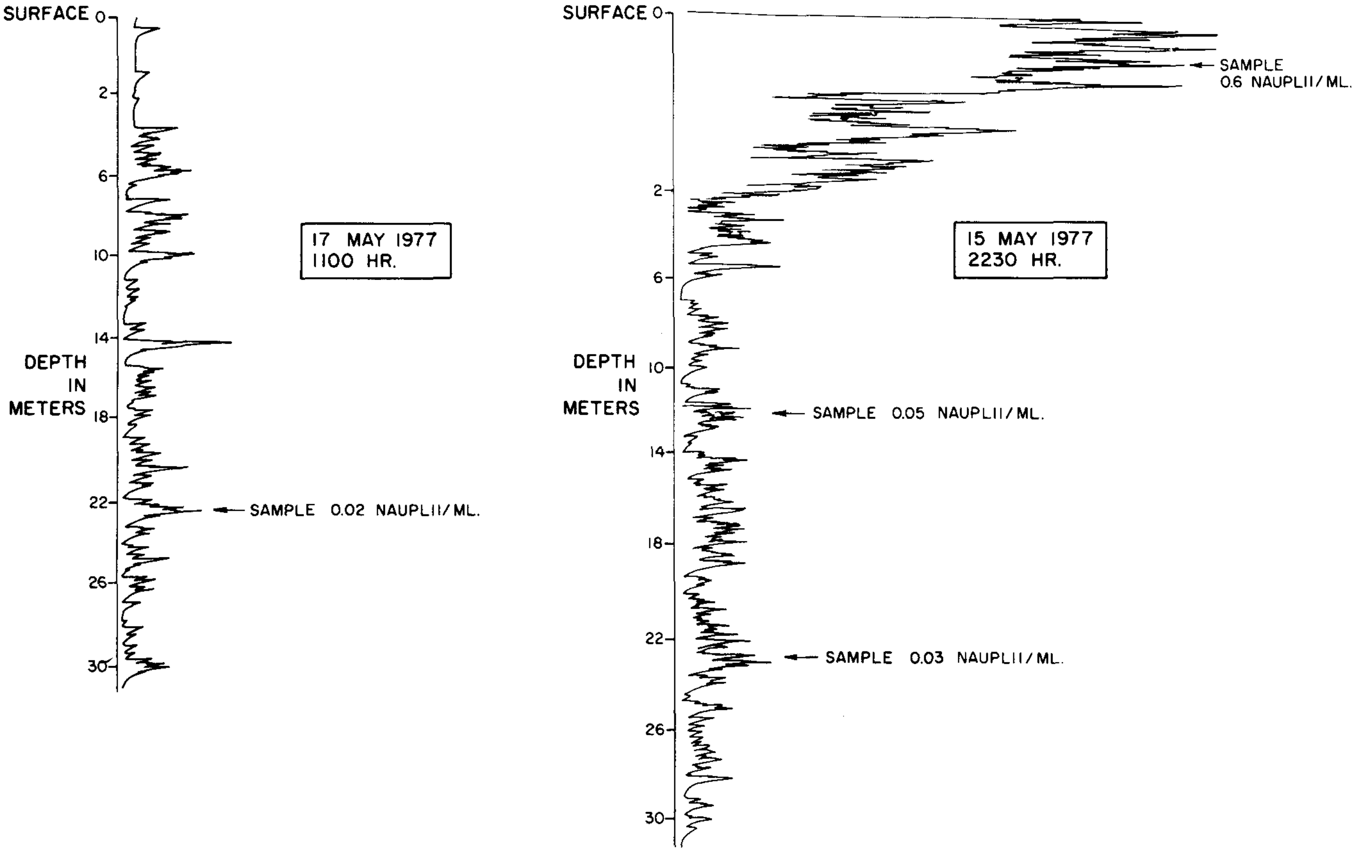


Figure 4. Chart records of vertical distribution of copepod nauplii collected in Austnesfjorden, Norway, by the *in situ* device for sensing and collecting microplankton.

In Austnesfjorden, we found the device to be very effective in identifying and collecting discrete samples of seawater from regions of high plankton density. Seawater collected in this manner was used for bioassay experiments with cod larvae to determine feeding thresholds, rates, and food preferences (Ellertsen et al. 1981).

The effectiveness of this technique depends on local conditions. For instance, during two cruises in the New York Bight, rough weather hampered attempts to identify plankton patches. It is hard to assess how much this was caused by the dispersal of patches due to mixing on the upper layers, and how much was due to the ship's movement, which made it impossible to sample discrete points in the water column.

The effectiveness of the device can also be reduced by interfering particles in the water. During one cruise off the coast of Long Island, New York, high concentrations of a large phytoplankton *(Ceratium tripos)* masked the presence of micronauplii.

SUMMARY

The device for sensing and collecting microplankton was found to be effective during 45 days of sea trials. Effectiveness depends on local conditions such as sea state, weather, and the presence of interfering particles like large phytoplankton or detritus that can mask the presence of micronauplii.

This device has been used successfully to collect discrete samples of seawater from regions of high nauplii density for use in larval fish bioassay experiments. To our knowledge, the highest concentration of nauplii (0.6/ml) ever found at sea was collected with this device.

Laboratory tests indicate that zooplankton nauplii less than approximately 560 μm could not avoid the influent currents of this device. Also, there was no evidence of injury to nauplii during pumping, and smearing of the sample during collection was minimal.

An old Coulter Counter Model A was modified for this application because one happened to be available. However, an inexpensive pulse height analyser could also be used for this purpose.

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CALIFORNIA CURRENT CHLOROPHYLL MEASUREMENTS FROM SATELLITE DATA

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ABSTRACT

A new procedure for rapid quantitative measurement of chlorophyll-like pigment concentrations from data collected by the Coastal Zone Color Scanner on board the Nimbus-7 spacecraft has been implemented. Removal of atmospheric effects revealed ocean features not apparent in the original imagery. Comparison of chlorophyll estimates derived from independent shipboard and satellite data collected concurrently yielded a correlation coefficient of $r = 0.92$.

Satellite chlorophyll images (1260 km on a side) showed a high degree of heterogeneity in the chlorophyll distribution patterns, at all scales. New, recurrent chlorophyll features in the California Current were detected. Comparison of two images collected one month apart showed important changes, both inshore and offshore. Extensive, long-term programs like the California Cooperative Oceanic Fisheries Investigations may largely benefit from the synopticity and repetitive coverage of meaningful satellite observations.

RESUMEN

Ha sido implementado un nuevo procedimiento para la rápida medición cuantitativa de concentraciones de pigmentos clorofílicos utilizando datos obtenidos por el Coastal Zone Color Scanner (Escudriñador en Color de la Zona Costera) a bordo del satélite Nimbus-7. La eliminación de los efectos atmosféricos reveló estructuras oceánicas que no eran visibles en las imágenes originales. La comparación de concentraciones clorofílicas derivadas de los datos adquiridos independientemente, y de manera casi simultánea, por el barco y por el satélite resultó en un coeficiente de correlación de $r = 0.92$.

Las imágenes clorofílicas obtenidas utilizando el satélite (1260 km de lado) mostraron un alto grado de heterogeneidad en los patrones de distribución clorofílica, en todas las escalas. Fueron detectadas estructuras clorofílicas nuevas, de carácter repetitivo, en la Corriente de California. La comparación de dos imágenes obtenidas con un mes de diferencia mostró cambios importantes tanto en la zona costera como en mar abierto. Programas extensivos y a largo plazo, como el California Cooperative Oceanic Fisheries Investigations (CalCOFI), pueden obtener grandes beneficios del carácter sinóptico y repetitivo de observaciones realistas obtenidas desde satélites.

INTRODUCTION

Chlorophyll is an index of phytoplankton abundance (Raymont 1980). Phytoplankton is a major food source in the ocean, at the base of most marine food webs (Ryther 1969). Despite its ecological importance, chlorophyll has been measured in only a few of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises since 1949. Here we show the results of a satellite-related procedure that can repeatedly provide rapid, quantitative measurement of chlorophyll-like pigments over large areas of the ocean. This new approach should allow biological oceanographers to obtain the quantitative chlorophyll field shortly after the fact. It should also permit more efficient interdisciplinary research with other more automated branches of oceanography.

In its 1981 report, the CalCOFI Committee (Reid et al. 1981) discussed the desirability of reducing ship time and the areal scope of ship operations, while trying to preserve the integrity of the CalCOFI time series (at least at the level of resolution of low-frequency, large-scale events). Recently, complementary shipboard and satellite data (Bernstein et al. 1977; Lasker et al. 1981; Smith et al. submitted), and complementary coastal and satellite data (Peláez 1981) have successfully studied oceanographic problems in the California Current region. Results presented here strongly suggest that extensive, long-term programs like CalCOFI may benefit from the synopticity and repetitive coverage of meaningful satellite observations.

In this report we outline a procedure for rapidly obtaining remotely sensed estimates of chlorophyll concentrations. We compare the derived data to shipboard measurements, estimate the accuracy of the method, and show some typical chlorophyll patterns in the California Current.

DATA AND METHODS

Shipboard Data

Shipboard data collected during the May-June 1981 CalCOFI cruises of R/V *David Starr Jordan* and R/V *New Horizon* included a wide variety of oceanographic measurements (temperature, salinity, oxygen,

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[Manuscript received March 19, 1982.]

phosphate, nitrate, nitrite, silicate, chlorophyll-a, primary production, and zooplankton) in the water column of the California Current, at fixed CalCOFI stations from about 28°N to about 38°N. Along ship tracks temperature and salinity were measured with a thermosalinograph. R/V *David Starr Jordan* covered from about 28°N to about 33°N, and also performed continuous underway fluorometric determinations of chlorophyll using a Turner Designs model 10 continuous-flow-through fluorometer. Discrete determinations of the chlorophyll to fluorescence, and of chlorophyll-a to phaeopigments-a ratios (Lorenzen 1966; Strickland and Parsons 1972) were done frequently (about every two hours) with a Turner model 111 fluorometer.

Procedure for Deriving Quantitative Chlorophyll-Like Pigment Estimates from the Satellite Data

The Coastal Zone Color Scanner (CZCS) was designed to measure phytoplankton pigment concentrations in the ocean (Hovis et al. 1980) using narrow (20 nm) spectral bands centered at 443, 520, 550, and 670 nm (the instrument also has two wider bands centered at 750 and 11,500 nm). Satellite determinations of chlorophyll are possible because the upwelled spectral radiance just beneath the sea surface contains valuable information about the constituents of the water. Phytoplankton, which contains the photosynthetically active pigment chlorophyll-a, plays a dominant role in the processes of absorption and scattering of visible light within the water (especially at specific wavelengths), except for unusual ocean regions like land-related discharge areas. At 443 nm, chlorophyll-a absorption is strong, and the solar radiation backscattered out of the ocean decreases rapidly with increasing chlorophyll-a concentrations. At 520 and 550 nm, near the so-called "hinge point" (Duntley et al. 1974), upwelled radiance variations are less dependent on chlorophyll concentrations. Bands available in the CZCS cannot separate chlorophyll-a from phaeopigments-a, a degradation product of chlorophyll-a, because both have almost the same absorption spectrum: hence the term *chlorophyll-like pigments* for the estimations obtained with this sensor. Accessory pigments (chlorophyll-c and carotenoids) may also contribute to total absorption in the 443 nm band. Statistical relationships between chlorophyll-like pigment concentrations (hereafter called simply chlorophyll concentrations), and ratios of upwelled subsurface spectral radiances at various wavelengths have been obtained (Clarke et al. 1970; Arvesen et al. 1973; Hovis and Leung 1977; Morel and Prieur 1977; Gordon and Clark 1980a; Gordon et al. 1980).

The atmosphere between the sea surface and the spacecraft poses an important problem for the quantitative remote sensing of chlorophyll concentrations in the ocean. Atmospheric scattering contributes about 80% of the radiance detected by the satellite sensor, at about 950-km altitude. The main problem in obtaining the desired subsurface signal is the removal of the aerosol scattering component. Aerosols vary considerably in concentration, composition, and size distribution over space and time. We have developed a relatively simple and practical procedure to remove the atmospheric influence on the CZCS imagery without the requirement of shipboard optical measurements (Guan, in preparation). Processing was done on subscenes of about 420 km on a side, and larger coverages were treated subscene by subscene. The spectral information contained in a subscene was split into two components: a fluctuation and a constant background. The fluctuating component included the aerosol and subsurface radiant contributions, and a small variation of the Rayleigh scattering background.[1] This regular variation of the Rayleigh scattering with increasing scan angle was removed by subtracting a sloping gray wedge obtained from the difference in Rayleigh scattering radiance at both sides of each subscene.

The aerosol and the subsurface radiant contributions had different spectral signatures. Aerosol scattering was assumed to change linearly with optical thickness (Gordon and Clark 1980a). Aerosol radiant fluctuations δLa at two wavelengths λ_2 and λ_1 were considered proportional to each other

$$\delta La(\lambda_2) = \Delta(\lambda_2,\lambda_1)\delta La(\lambda_1),$$

where $\Delta(\lambda_2,\lambda_1)$ is the proportionality constant. $\Delta(\lambda_2,\lambda_1)$ was determined by regression analysis of two CZCS spectral images over areas with evident changes in aerosol content. As a first approximation, a linear relationship between the fluctuations of upwelled subsurface radiances at different wavelengths was used. A nonlinear relationship was also considered. Differences in the corrected result between the nonlinear and linear cases were usually small, except under extreme conditions. Therefore, the linear relationship was preferred for this study. Aerosol fluctuations were separated from subsurface fluctuations using this two-dimensional linear model, in an image-element-by-image-element basis. Removal of the atmospheric variations clearly revealed the ocean patterns, although each spectral image still had a constant background corresponding to a clear and even atmosphere. The constant backgrounds were removed

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[1] Larger scan angles and changes in the wind field result in changes in the reflection characteristics of the sea surface. Their effects on the CZCS imagery appeared to be very similar to the aerosol fluctuations, and were mostly eliminated after removal of aerosol scattering from the images.

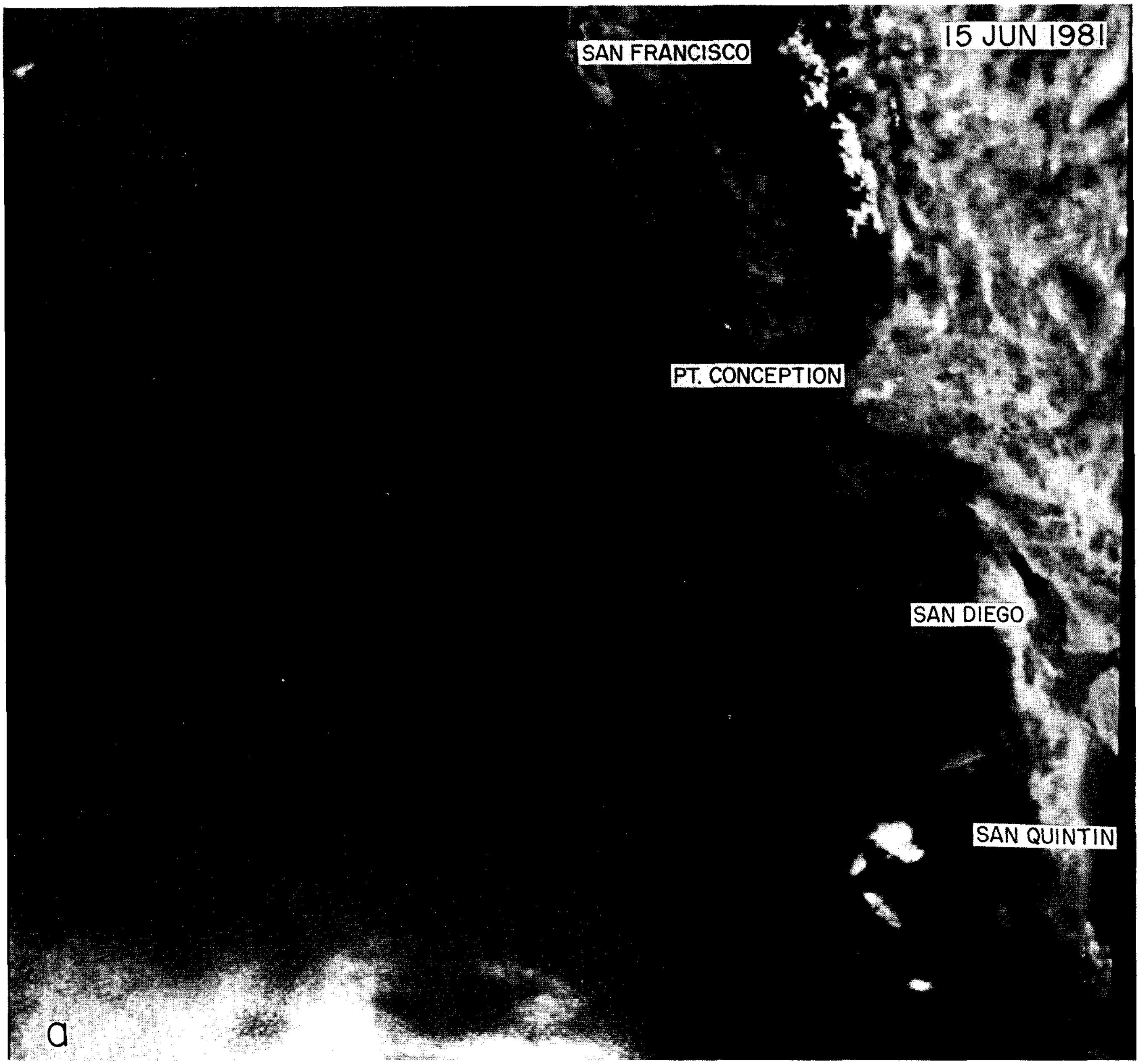

Figure 1a. Comparison of Nimbus-7 CZCS band 1 (443 nm) radiances off the Californias before atmospheric correction. Data-collection time was approximately four minutes near local noon on June 15, 1981. The image is about 1260 km on a side.

by setting appropriate bias values. Bias settings were selected considering the high stability of the spectral reflectance of clear seawater.[2] Sequential analyses of images at the same location under changing atmospheric conditions have shown that the atmospheric correction yields consistent results. Chlorophyll concentrations were estimated from ratios of the corrected upwelled subsurface spectral radiances at various wavelengths (Gordon and Clark 1980a). Using ratios may eliminate the effect of undesired covarying influences in the divided bands. The processed CZCS data are entirely independent of the May-June 1981 CalCOFI shipboard data, which were used only to test the procedure.

Satellite Data

Satellite data from the CZCS on board the Nimbus-7 spacecraft were collected and totally processed at the Remote Sensing Facility of the Scripps Institution of Oceanography. CZCS data ground resolution at nadir is about 0.8 km. Data-collection time by the spacecraft for any of the images presented here

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[2] Locating clear water areas in the imagery has not been a limitation while processing data off California, but in some cases it might require comparison with neighboring subscenes.

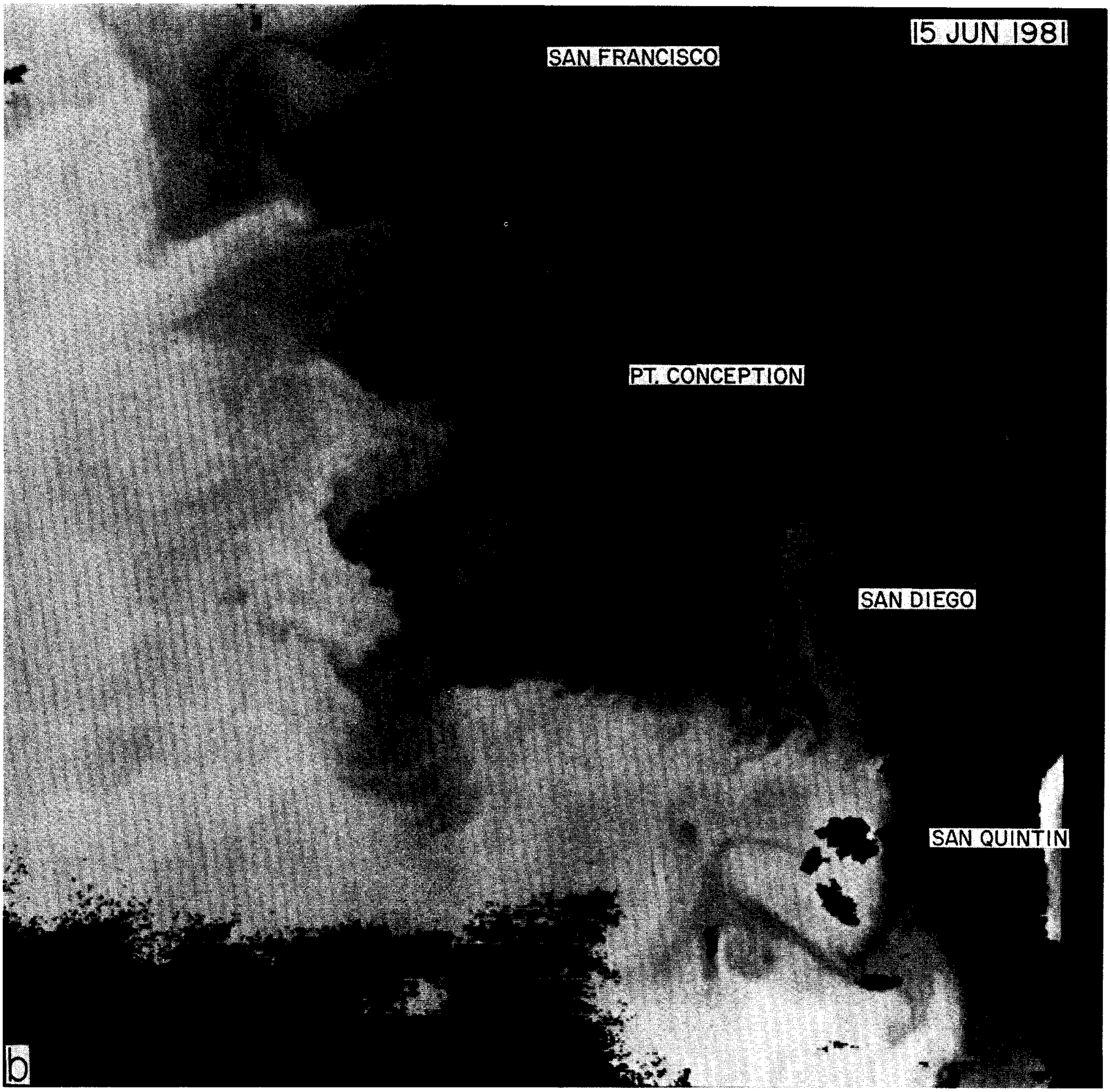

Figure 1b. Same data as in Figure 1a, but after atmospheric correction. The procedure cleaned up haze and revealed ocean features not apparent in the uncorrected image. Land and clouds have been masked in black.

is less than four minutes, at about local noon. A black mask over land and clouds has been applied to all the corrected images (but not to the uncorrected images in Figures 1a and 2a). Lighter gray tones correspond to higher chlorophyll concentrations (except for the absorption images in Figure 1). Some anomalous lighter or darker areas in the vicinity of clouds should be considered cautiously or disregarded since they may be due to cloud structures smaller than an image element (about 0.68 km^2), for which the atmospheric correction may not account.

RESULTS AND DISCUSSION

The Atmospheric Correction

The atmospheric correction procedure was applied to an almost cloud-free image off the Californias from San Francisco to Vizcaíno Bay (about 38°N to about 28°N), on June 15, 1981 (Figures 1 and 2). Images are

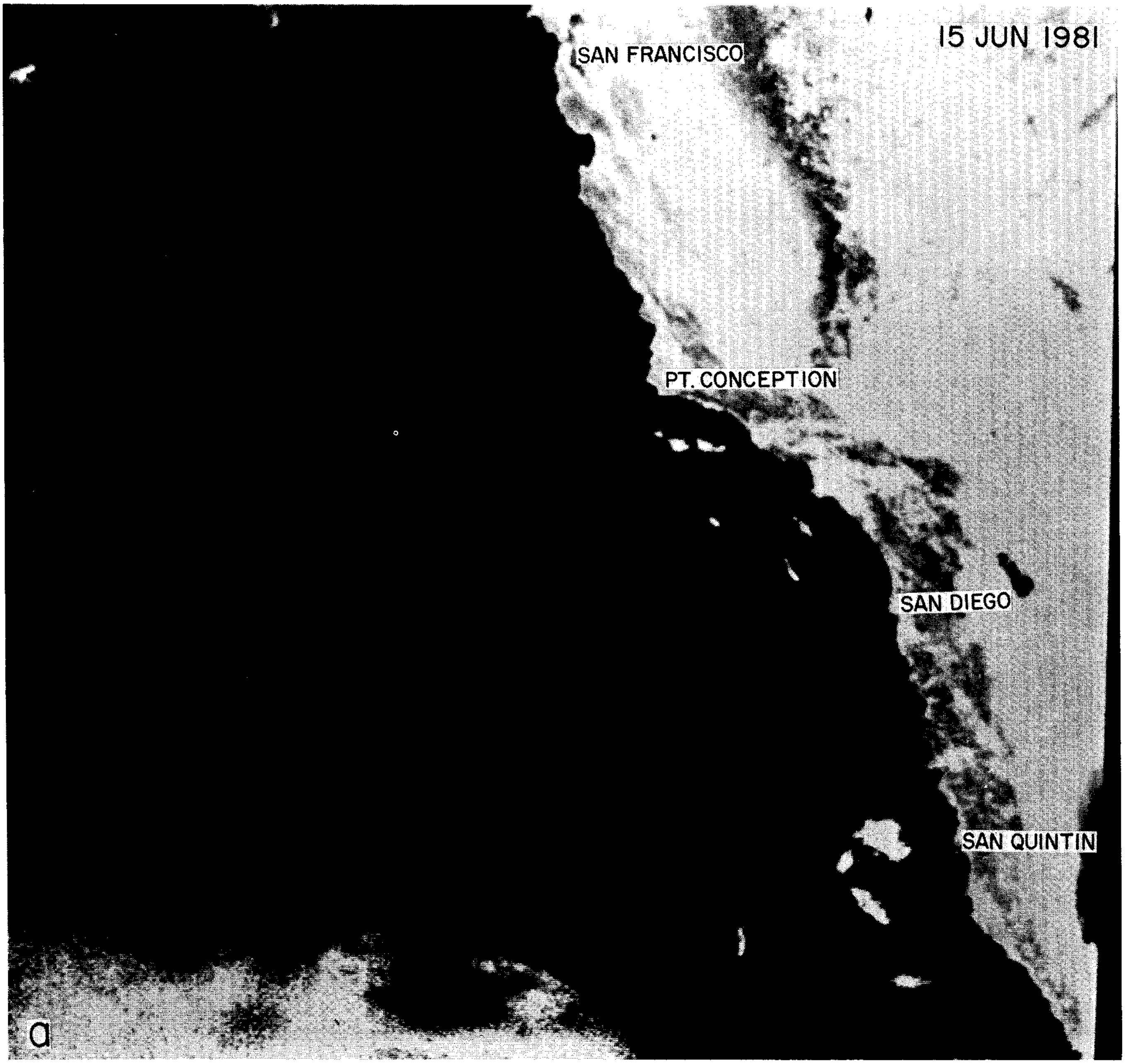

Figure 2a. Nimbus-7 CZCS band 3 (550 nm) radiances before application of the atmospheric correction procedure. Other characteristics are the same as in Figure 1a.

about 1260 km on a side. Images in Figure 1 show CZCS band 1 data (443 nm) before and after application of the correction procedure. Darker gray tones represent stronger absorption areas. The atmospheric correction cleaned up haze and aerosols to reveal ocean features not apparent in the uncorrected image. Figure 2 is the analog of Figure 1, for the CZCS band 3 data (550 nm). Lighter gray tones represent stronger backscattering areas. The corrected image (Figure 2b) shows again a large amount of detail and mesoscale structures that were covered by the overlying atmosphere (Figure 2a). The atmospheric contribution relative to the subsurface contribution is stronger at 550 nm (Figure 2a) than at 443 nm (Figure 1a). This, combined with the coarser onboard digitization scheme for the lower-frequency bands of the CZCS, resulted in less smooth transition from darker to lighter gray tones in the 550-nm corrected image (Figure 2b). More even images can be obtained by applying data-smoothing techniques while applying the atmospheric correction. However, to preserve as much detail as possible, we applied no smoothing.

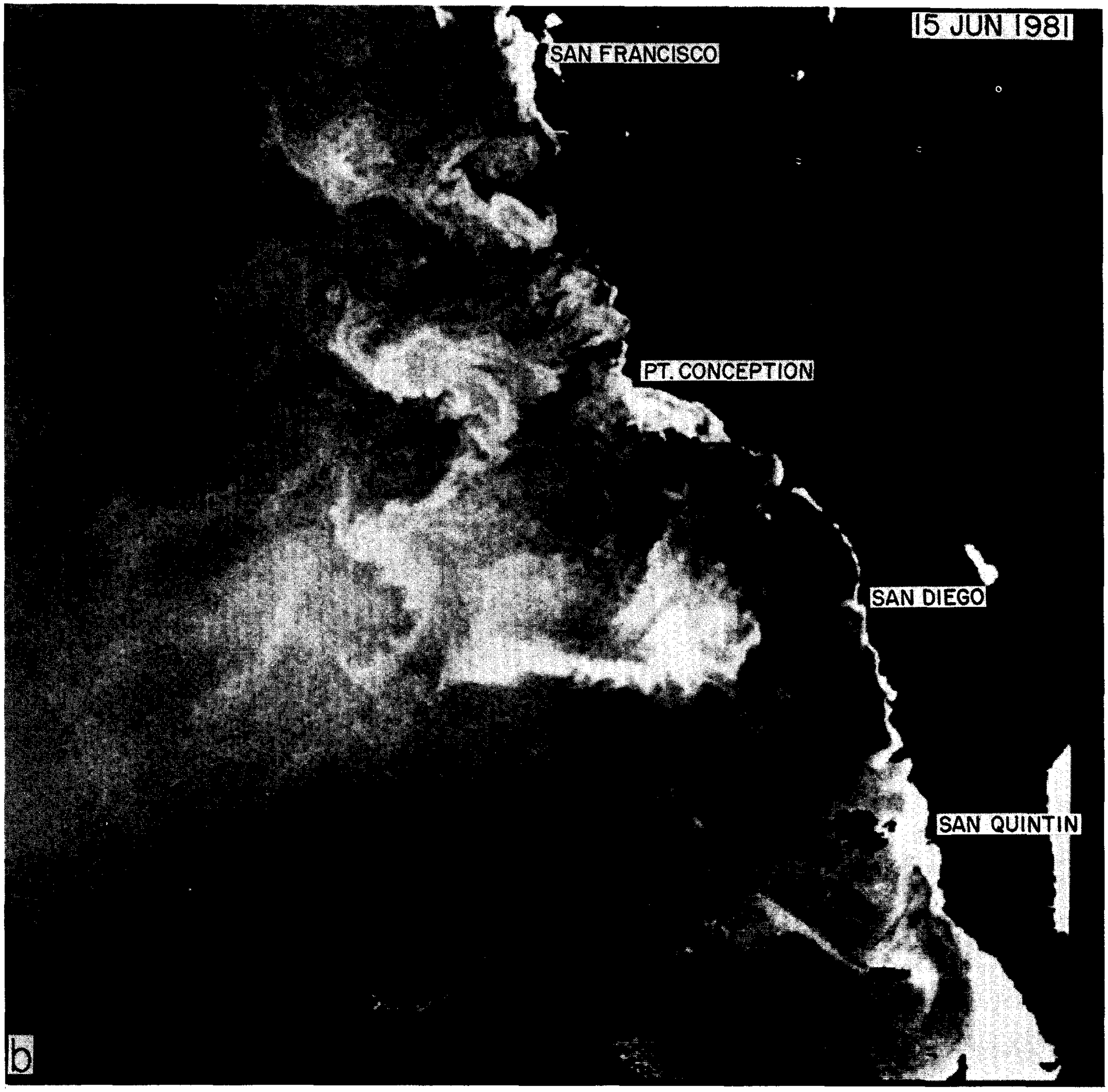

Figure 2b. Same data as in Figure 2a, but after application of the atmospheric correction. The procedure disclosed mesoscale structure and finer details that were concealed by the overlying atmosphere in the uncorrected image.

Comparison of Satellite and Shipboard Chlorophyll Measurements

On June 13, 1981, R/V *David Starr Jordan* steamed from near Guadalupe Island, in Central Baja California, back to San Diego, yielding a fairly long (about 450 km) continuous shipboard transect of underway, calibrated chlorophyll measurements (light track line in Figure 3). A relatively cloud-free CZCS image was collected concurrently. These two data sets allowed us to perform quantitative comparisons between the satellite and the shipboard measurements. The only criterion used to select the June 13 data sets was the availability of concurrent shipboard and satellite measurements over the same cloud-free area. The complete chlorophyll procedure was applied to the June 13, 1981, CZCS data off southern California and northern Baja California (Figure 3) from about 33°N (Del Mar) to about 29°N (northern edge of Guadalupe

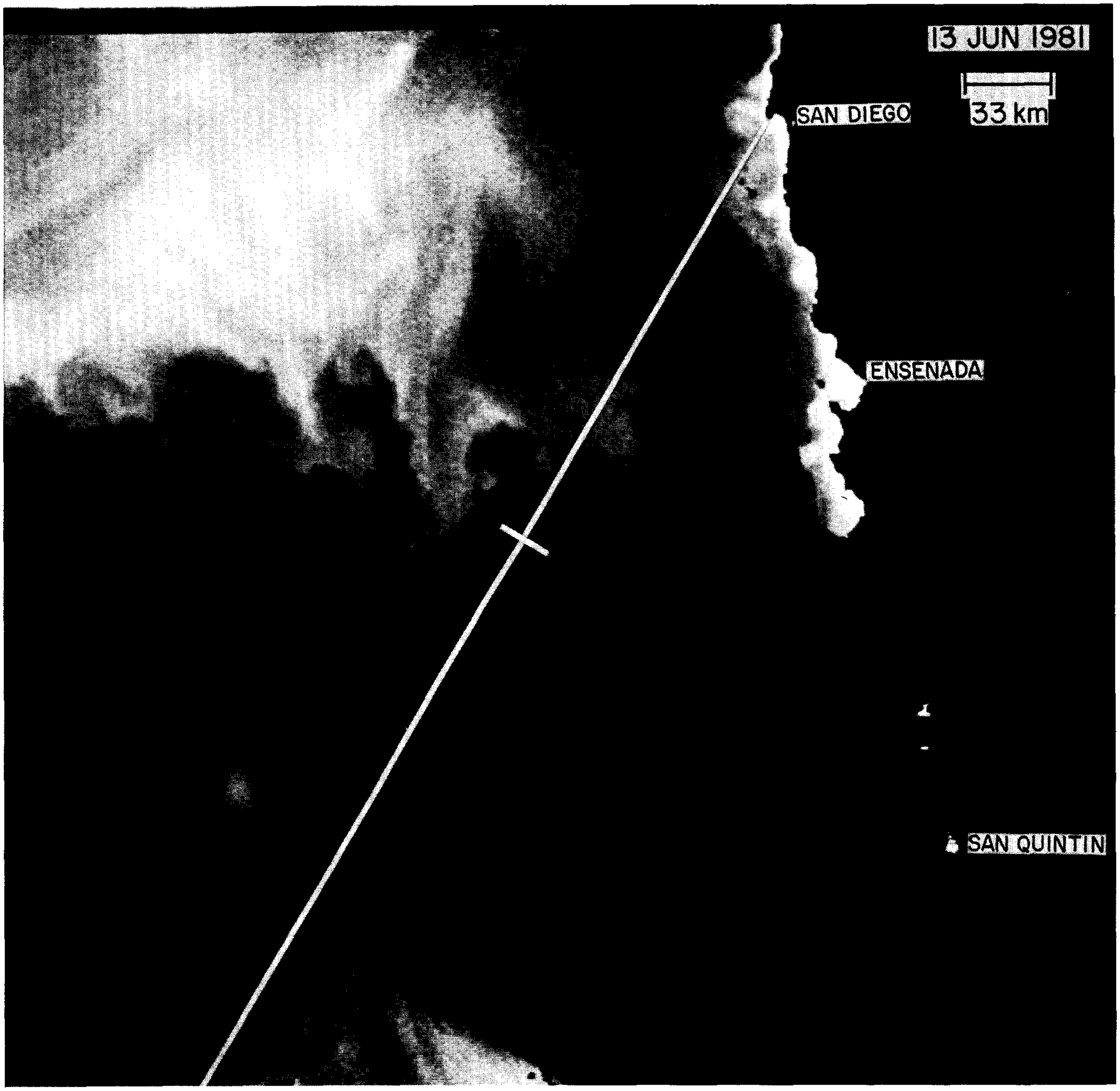

Figure 3. Processed chlorophyll-like pigment image off southern California and Baja California derived from the Nimbus-7 CZCS imagery (ligher gray tones correspond to higher chlorophyll concentrations). The light track line was followed by R/V *David Starr Jordan* on her way back to San Diego, from about 9 p.m. June 12, 1981, to about 7 p.m. June 13, 1981, local times (black area near the end of track line corresponds to a cloud). Data-collection time was less than two minutes, near local noon on June 13, 1981. Image is about 420 km on a side.

Island, in bottom left of Figure 3). The southern part of the ship track showed a flat, monotonous chlorophyll profile, and the same feature was apparent in the satellite profile. Since our main concern was comparing how well the satellite measurements were able to detect changes in the chlorophyll field in relation to the shipboard measurements, we discarded most of the flat part of the profiles. The light track line between the tick mark and San Diego in Figure 3 shows the approximately 190-km ship track used for the quantitative comparison between shipboard and satellite chlorophyll concentrations. Individual image elements of the satellite chlorophyll data were sampled at maximum resolution. Every other image element was compared to the corresponding value of the shipboard transect. Therefore, no smoothing or averaging was applied to the data.

Superimposed ship and satellite transects (Figure 4)

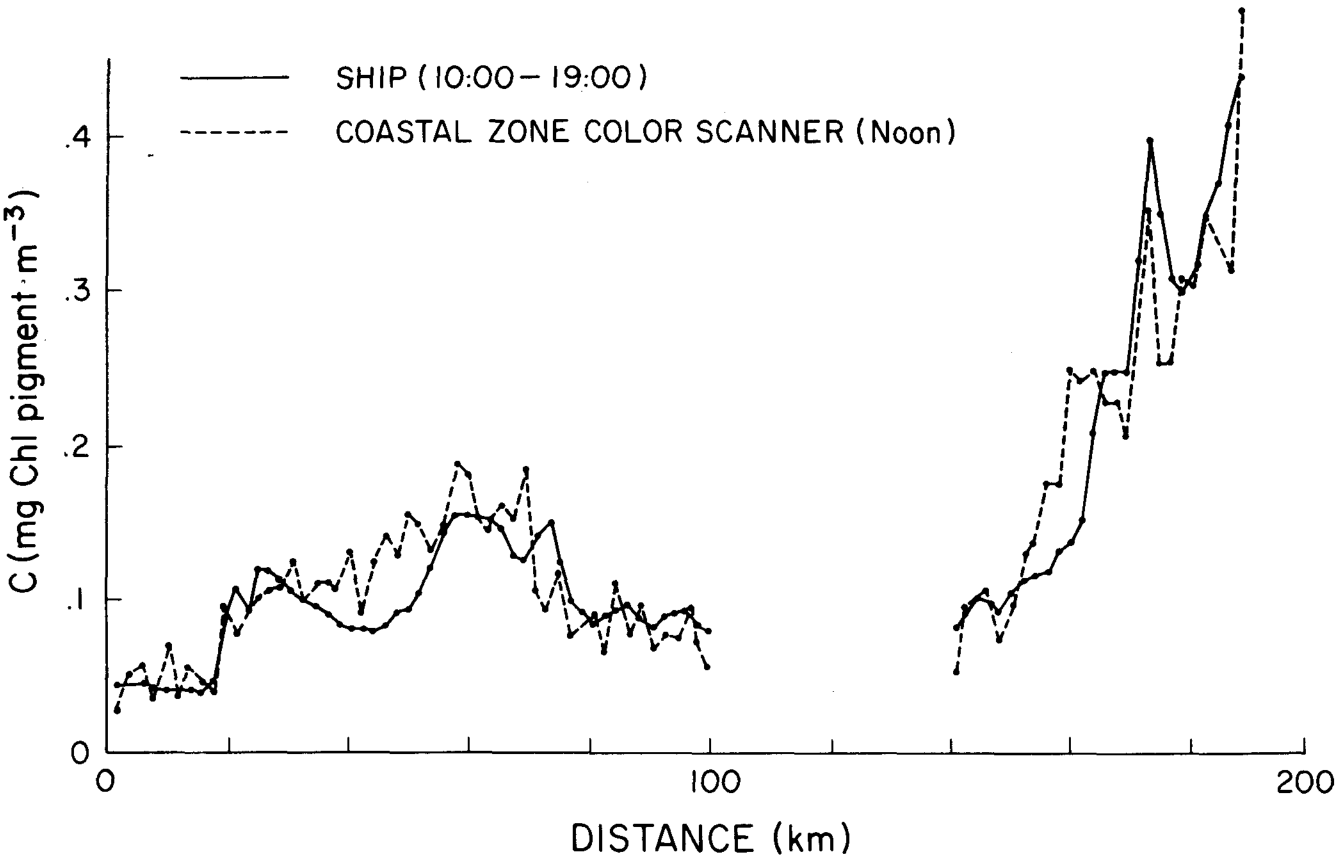

Figure 4. Comparison of independent shipboard and satellite chlorophyll-like pigment concentrations collected concurrently along the northern segment of track line shown in Figure 3, by R/V *David Starr Jordan* and by the Nimbus-7 CZCS (distance coordinate runs from tick mark to San Diego). Satellite data were sampled at full resolution (1 km) on every other image element. There is good agreement between the satellite and the shipboard measurements.

show that shape of satellite and shipboard horizontal chlorophyll profiles is quite similar, although some disparity exists at about 50 km from the origin of the transect. Chlorophyll features seem to be detected similarly by satellite and shipboard sensors, but satellite measurements appear to have larger high-frequency variability, especially in the areas of lower chlorophyll values. Relative displacement between the two profiles (right portion of Figure 4) added low-frequency variability to the comparison near the coast as the satellite overpass and the shipboard sampling became separated in time. The satellite sensor seems to be detecting low chlorophyll concentrations quite well, and there appears to be good agreement between the satellite and the shipboard measurements (notice that coordinates in both Figures 4 and 5 are linear).

The quantitative comparison of satellite and shipboard chlorophyll concentrations collected concurrently yielded a correlation coefficient of 0.92 (Figure 5). This accounts for about 85% of the variance (coefficient of determination $r^2 = 0.85$), and it seems unlikely that satellite and shipboard sensors would be measuring different things. We emphasize the point that satellite and shipboard information are two independent data sets. That is, no shipboard information is needed to process the CZCS imagery in order to obtain the quantitative chlorophyll field.

To get an idea of the temporal rate of change of chlorophyll in the ocean, the same shipboard transect was compared with a satellite transect obtained two days later and in the same location. The correlation coefficient dropped by 0.23, from 0.92 in the quasi-simultaneous case to 0.69 ($r^2 = 0.47$) in the two-day-lag case. Inspection of the later chlorophyll image showed that higher-chlorophyll water from the northwest was drifting across the ship track. This shows that advective transport may significantly change the chlorophyll concentrations in a short period of time. Another example is illustrated by the horizontal bar in Figure 5. This shows the temporal variability of surface chlorophyll as measured from the ship while it remained at a fixed location for two days. The range of values here is about the same as the point scatter in the regression.

Nonsimultaneity of shipboard and satellite measurements apparently added an important low-frequency variability component to the ship-satellite comparison. Noise in the satellite signal, and limitations imposed by the digitization scheme on board the spacecraft further introduced high-frquency variability. Variability was also introduced by possible navigation errors, and by the chlorophyll measurement process in the shipboard technique. All these added variabilities do not result from actual disaccord between the shipboard and satellite approaches, but do contribute to point scatter in the ship-satellite chlorophyll diagram. High-frequency variability in the satellite data could have been reduced by applying data-smoothing techniques, or by averaging contiguous image elements instead of sampling each element individually at full resolution. We did not do this because of concern with the results of the procedure in an image-element-by-image-element basis. Further simultaneous comparison of shipboard and satellite transects at higher chlorophyll concentrations than those shown in Figure 4 was obstructed by cloud cover. However, examination of the extensive 26-day shipboard continuous underway chlorophyll data set showed that the nonsimultaneous shipboard and satellite estimates of chlorophyll were also in good agreement in the areas of highest chlorophyll concentration (2-3 mg m^{-3}) encountered by R/V *David Starr Jordan*.

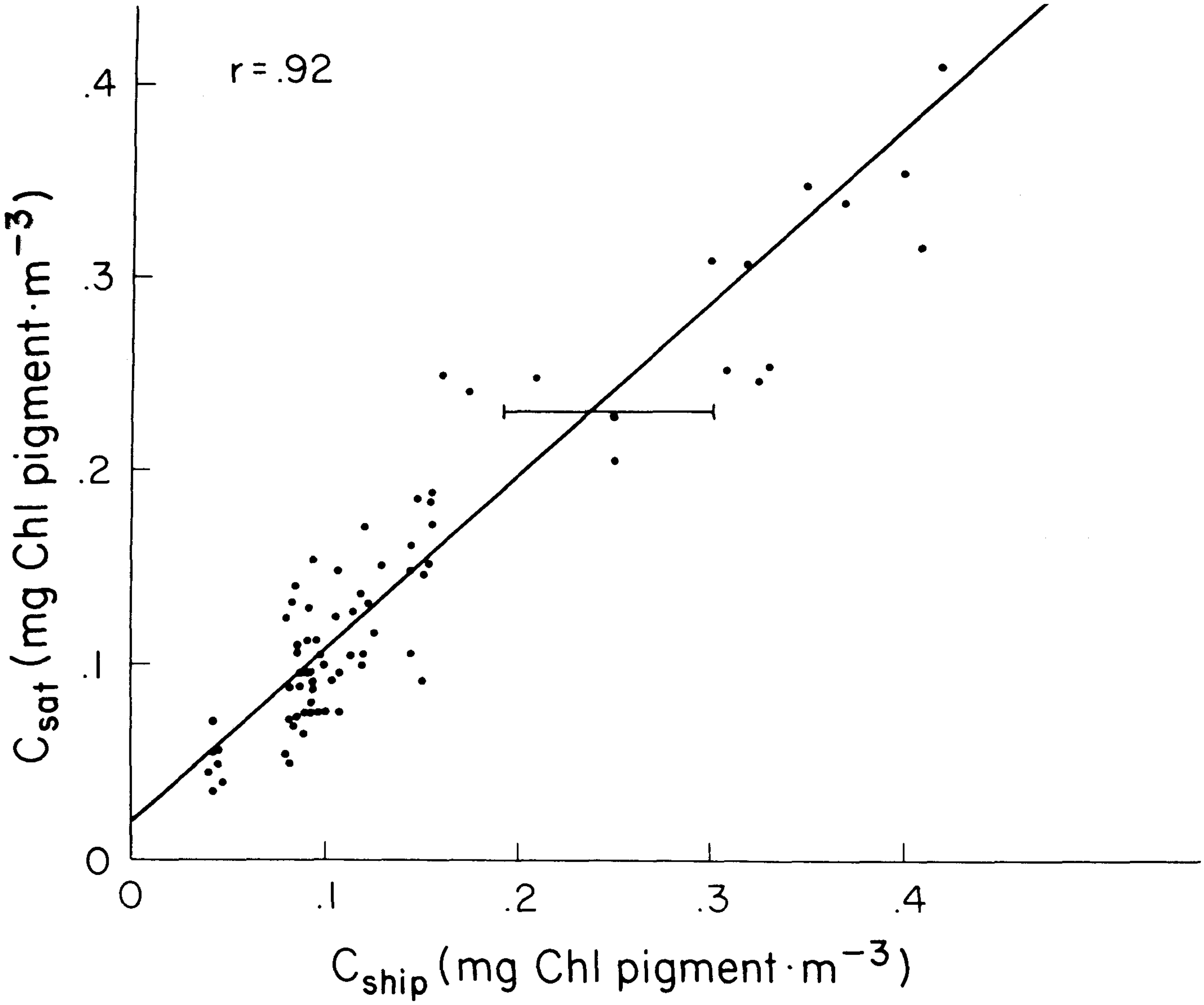

Figure 5. Quantitative comparison of independent shipboard and satellite chlorophyll-like pigment measurements (from Figure 4), collected almost concurrently, yielded a significant correlation coefficient (r = 0.92). Horizontal bar is a typical example of shipboard chlorophyll variability at a fixed location over a two-day period. Notice that the range of values here is about the same as the point scatter in the regression.

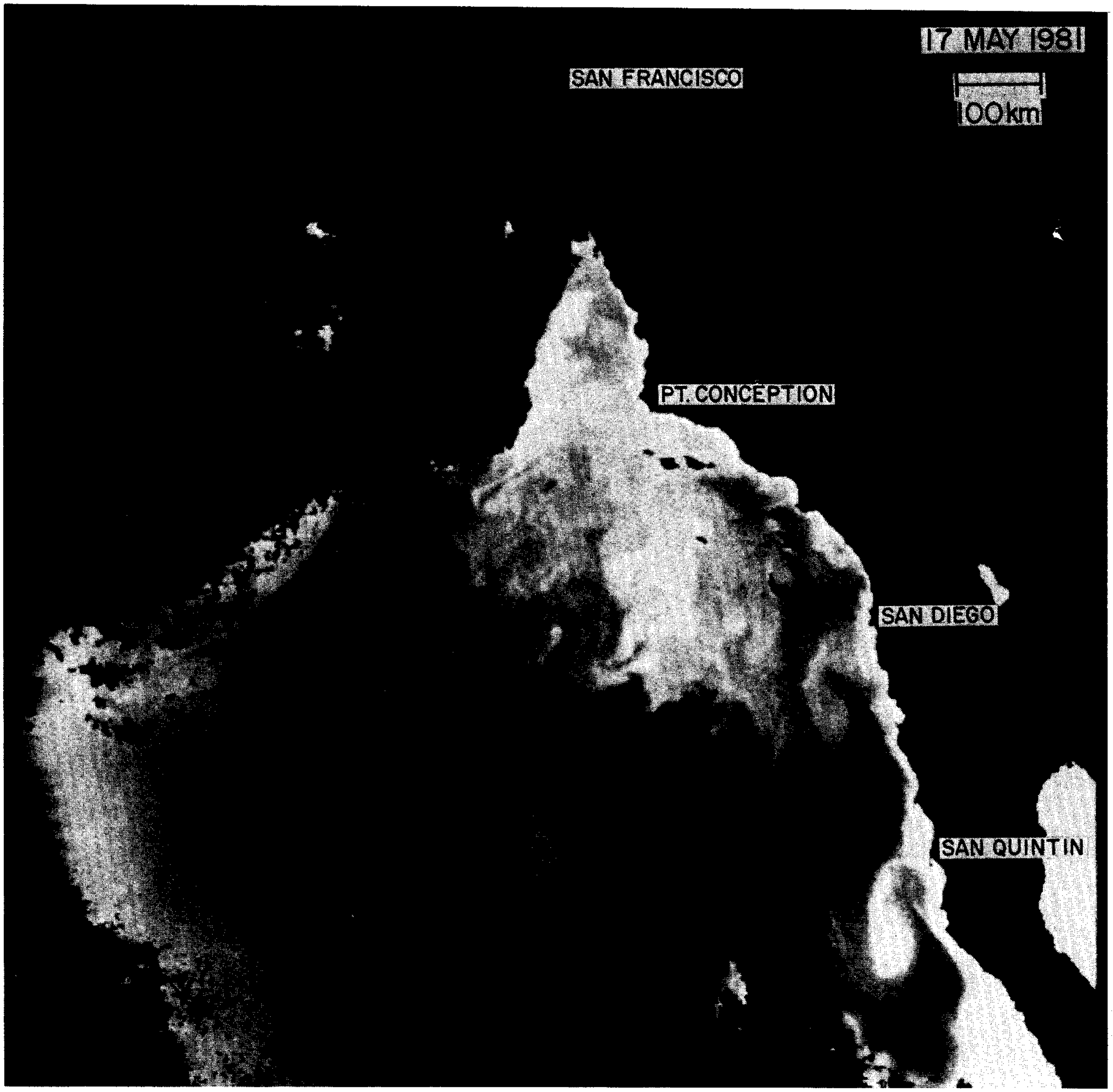

Figure 6. Processed chlorophyll-like pigment image off the Californias, near noon May 17, 1981, derived from the Nimbus-7 CZCS imagery. Lighter gray tones correspond to higher chlorophyll concentrations except in the vicinity of clouds, where they may be due to subimage-element-size cloud structures (these structures can escape cloud masking, and are not corrected by the atmospheric correction procedure). Notice "shelf-attached" eddies at San Quintín and south of San Diego, the higher-chlorophyll region farther offshore, and the large degree of heterogeneity in the chlorophyll distribution patterns at all scales (image is about 1260 km on a side).

Satellite Chlorophyll Distribution Patterns and Their Temporal Changes

The complete procedure to obtain chlorophyll concentrations was applied to the May 17, 1981, CZCS data off the Californias, from San Francisco to Vizcaíno Bay (about 38°N to about 28°N). A high degree of chlorophyll heterogeneity is evident in this 1260-km-on-a-side image (Figure 6). Intense high-chlorophyll areas (lighter gray tones) occur off Pt. Buchon, Pt. Conception, and in the Santa Barbara Channel. The largest high-chlorophyll (1-2 $\mathrm{mg\,m^{-3}}$) region occurs in the middle of the image, overlying the system of shallow submarine ridges and banks (shallower than 500 m, often less than 200 m) that extends from Santa Rosa Island to 200-300 km to the southeast. Complementary chlorophyll and thermal infrared satellite imagery analyses have shown that cooler water and higher-chlorophyll waters persist year round in this area, even if the areal extension and intensity of the signals do change with season (Peláez, in preparation). Geographic location of this "hot spot" corresponds to location of the Southern California Eddy (Sverdrup and Fleming 1941; Reid et al. 1958; Schwartzlose 1963; Owen 1980). According to chlorophyll and thermal infrared satellite observations, the Southern California Eddy appears to be associated with the shallow bottom topography of this region, and seems to be partly the result of water impinging against the system of shallow ridges and banks in this area.

The transition zone from the high-chlorophyll area in the middle of the image to the lower-chlorophyll regions surrounding it is characterized by tongues and eddies, usually bent clockwise. A narrow (a few km wide), high-chlorophyll (usually higher than 1 mg m^{-3}) band is present all along the coastline. Immediately offshore, a lower-chlorophyll (.2-.5 mg m^{-3}) region, about 100 km wide, overlies the deep troughs and basins that characterize most of inshore southern California. Two fairly large (about 100 by 50 km), high-chlorophyll (1-1.5 mg m^{-3}), counterclockwise eddies protrude into the lower-chlorophyll, nearshore region. These eddies have long stems or filaments "attaching" them to the Coronados (south of San Diego) and San Quintín (in Baja California) shelves. Both have been detected with satellite imagery on other occasions; they are recurrent features of the California coastal region. Both appear to be related to coastal upwelling centers detected with satellite thermal infrared imagery over the Coronados and the Colnett-San Quintín shelves (Peláez, in preparation). Also, a smaller, counterclockwise "attached" eddy is present in the Newport-Dana Pt. area. Two smaller free eddies occur off Pt. Conception and off Pt. Buchon.

By June 15, an overall decrease in the chlorophyll concentrations was apparent (Figure 7). Also, important changes in the chlorophyll distribution patterns had occurred, both inshore and offshore. An unexpected, latitudinally oriented sharp boundary, starting about 100 km off Ensenada and extending 400-500 km offshore, was detected. Also, enhanced eddy activity associated with a conspicuous meridional, frontal strengthening far offshore (200-500 km off the coast and about 400-500 km long) was concurrent with generalized offshore displacement (or extension) of the major high-chlorophyll structures. By mid-June, the "attached" eddies had disappeared. The low-chlorophyll inshore southern California waters became more continuous with lower-chlorophyll waters to the south. Some new features became apparent. Four large (about 200 km in diameter) clockwise vortices, or gyres, were lined up meridionally far away from the coastline. They appeared to be the low-chlorophyll (about .1 mg m^{-3}), offshore component of the meridional frontal zone mentioned above. New high-chlorophyll structures could also be seen by mid-June: a small counterclockwise eddy developing off Pt. Reyes, two adjacent eddies off Monterey, two joint eddies in the Santa Barbara Channel, a high-chlorophyll V-shaped structure associated with Cortes Bank, and a small chlorophyll patch (north of Guadalupe Island) in the middle of a large low-chlorophyll region. Thus in approximately one month there were significant large-scale and mesoscale changes in the chlorophyll patterns.

Meaning of Satellite Chlorophyll Measurements

The question often arises: How representative are the satellite chlorophyll measurements in terms of the chlorophyll content of the entire water column? The maximum depth penetration of the remotely sensed signal (Gordon and McCluney 1975; Gordon and Clark 1980b; Smith 1981) varies depending on the amount and vertical distribution of suspended matter in the water column. In areas not strongly influenced by terrigenous material, this depth is primarily determined by the light absorption of biological material, and is far less affected by scattering. Therefore, when chlorophyll concentrations are low in the surface layers, the remotely sensed signal will reach larger depths than when a surface layer of high chlorophyll is present (complications arise because this effect is dependent on the wavelength of light).

Hayward and Venrick (submitted), using data of the May-June 1981 CalCOFI cruises, found that surface chlorophyll had a highly significant correlation with integrated chlorophyll ($r = 0.86$, $p < 0.01$), and with integrated primary production ($r = 0.87$, $p < 0.01$) in the euphotic zone (from the surface to the one-percent light level) of the California Current. Smith and Baker (1978) used the average chlorophyll concentration from the surface to one attenuation depth (defined as the inverse of the total diffuse attenuation coefficient for irradiance) as an approximation of the remotely sensed chlorophyll. They found that it was significantly correlated with average chlorophyll ($r = 0.95$, $p < 0.01$) and with average primary production ($r = 0.85$, $p < 0.01$) in the water column, from the surface to the one-percent light level. They used a large shipboard data set, collected over a wide range of geographical regions. Hayward and Venrick's May-June 1981 CalCOFI data set allowed us to consider the weighted integral of the shipboard verti-

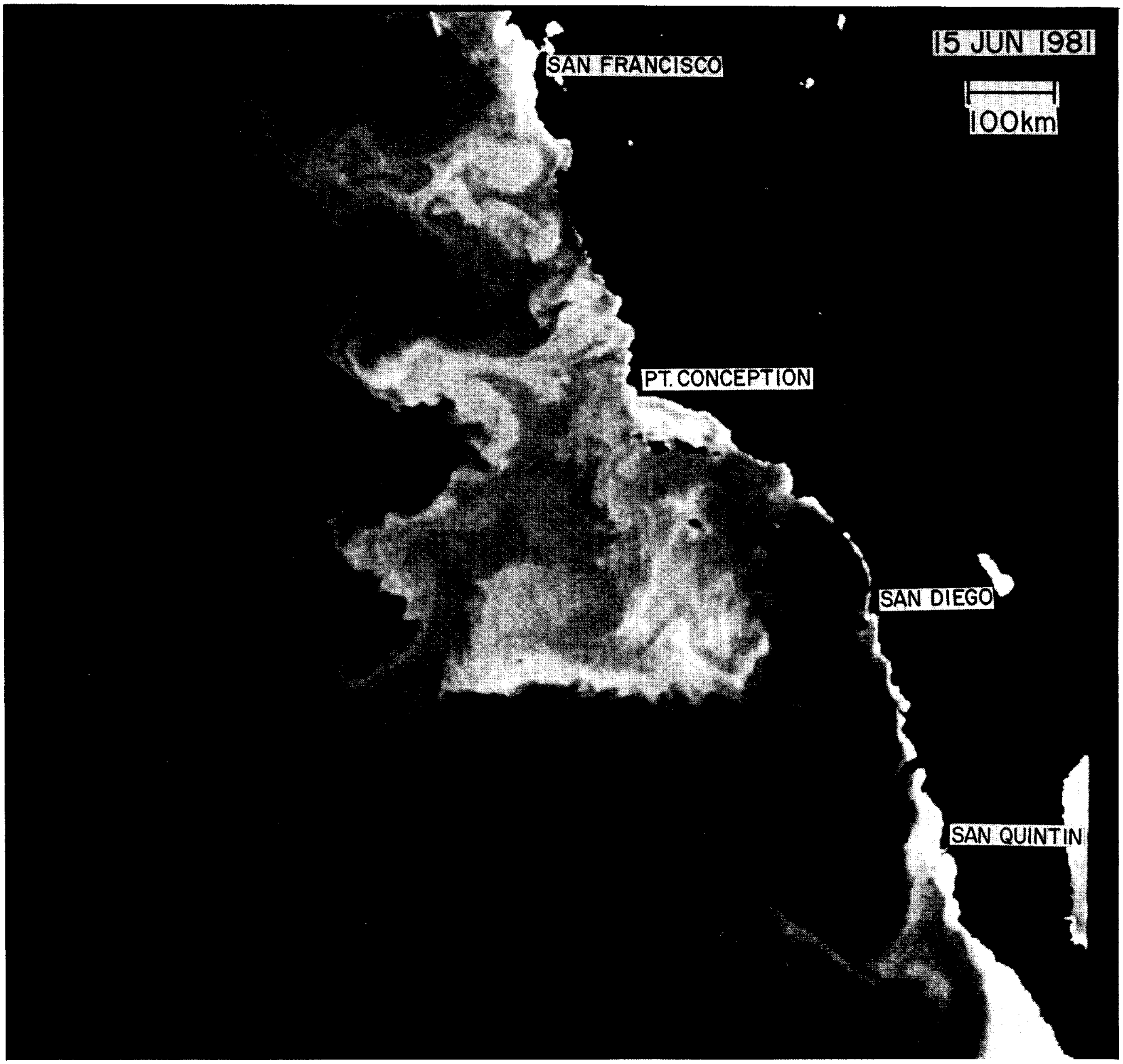

Figure 7. Similar to Figure 6 on June 15, 1981. Besides an overall decrease in the chlorophyll-like pigment concentrations, important changes have occurred in the chlorophyll distribution patterns, both inshore and offshore, during the intervening month. Note the unexpected, latitudinally oriented, sharp boundary offshore, south of San Diego.

cal profiles as an approximation of satellite chlorophyll. The weighting function represents the depth penetration of the remotely sensed signal under variable vertical distributions of chlorophyll. The weighted integral only slightly improved Hayward and Venrick's results ($r = 0.87$ for integrated chlorophyll, and $r = 0.90$ for integrated primary production). One should be careful in interpreting these high correlation coefficients (Smith 1981; Smith et al., submitted; Hayward and Venrick, submitted), especially for areas with significant changes in the vertical distribution of chlorophyll at larger depths than the maximum penetration depth of the remotely sensed signal. On the other hand, the high correlation coefficients suggest that, within regions like the California Current, the remotely sensed, upper-layer chlorophyll may indicate more general ecological conditions prevailing in the area.

Uses of Satellite Observations

Results presented here show that satellite measurements can help solve oceanographic problems. The wide range of spatial and temporal scales available in satellite observations can help resolve some questions difficult to answer with ships only. Ground resolution (800 m) and temporal coverage (daily, clouds permitting) of satellite determinations of chlorophyll with the CZCS appear adequate in terms of the spatial and temporal scales of phytoplankton populations (km's to 100's of km's; days to weeks). Upper-layer chlorophyll heterogeneity over large areas of the ocean, as well as rate of change of chlorophyll distribution patterns, may be assessed. However, one must be aware that satellite observations yield upper-layer chlorophyll concentrations; i.e., an index of only one component of the system, with some limitations. Therefore, satellite measurements should be coupled with detailed shipboard measurements if one expects to understand oceanographic phenomena and processes.

Extensive, long-term programs like CalCOFI may largely benefit from the synopticity and repetitive coverage of satellite observations. A balanced ship-satellite complementary approach to oceanographic questions can allow more efficient use of ships. Satellites rapidly survey large areas of ocean and can help in designing sound and flexible sampling schemes, allowing for real time ship-satellite collaboration, if necessary. Satellite observations are able to detect "hot spots," stable or variable regions, and northern, southern, or offshore influences. Also, they can rapidly spot frontal areas or other zones of specific interest. This information is important for appropriately defining "indicator stations," geographically and through time, in a heterogeneous and dynamic region like the California Current. Satellite imagery can also help assess the degree to which indicator stations are representative of larger areas of ocean. Furthermore, one can keep the spatial and temporal high-frequency part of the variability, which may be relevant to some oceanographic questions. The enhanced spatial and temporal resolution of observations may also provide insight into processes and dynamic characteristics of the California Current.

SUMMARY

1. A new procedure for quantitative measurement of chlorophyll concentrations from data collected by the Coastal Zone Color Scanner on board the Nimbus-7 spacecraft has been implemented.
2. Removal of atmospheric effects from the satellite data revealed ocean features not apparent in the original imagery.
3. Comparison of independent shipboard and satellite chlorophyll concentrations collected concurrently yielded a correlation coefficient of $r = 0.92$. Similar comparison with satellite data collected two days later (while higher-chlorophyll water was being advected across the ship track) showed a 0.23 decrease ($r = 0.69$) in the correlation coefficient.
4. Chlorophyll satellite images (1260 km on a side) showed a high degree of heterogeneity in the chlorophyll distribution patterns, at all scales. Comparison of two images collected one month apart showed important changes, both inshore and offshore.
5. A weighted integral of the shipboard chlorophyll vertical profiles (weighted by the depth penetration of the remotely sensed signal) was highly correlated with integrated chlorophyll ($r = 0.87$, $p < 0.01$) and with integrated primary production ($r = 0.90$, $p < 0.01$) in the euphotic zone (one-percent light level) of the California Current. This suggests that within this region the remotely sensed, upper-layer chlorophyll may indicate more general ecological conditions prevailing in the area.
6. Quantitative satellite determinations of chlorophyll should allow biological oceanographers to obtain the quasi-instantaneous chlorophyll field shortly after the fact. This should permit more efficient interdisciplinary research (by contributing to bridge the data-processing-time gap) with other more automated branches of oceanography.
7. The satellite imagery allowed us to detect new, recurrent, high-chlorophyll features in the California Current: eddy pairs off Monterey and in the Santa Barbara channel; counterclockwise eddies "attached" to the San Quintín, Coronados, and Pt. Reyes shelves; and a large, persistent, high-chlorophyll region overlying the shallow ridges and banks off southern California. A narrow (a few km) high-chlorophyll band was present all along the coastline. A lower-chlorophyll region (about 100 km wide) overlaid the deep troughs and basins of inshore southern California. Two intense frontal regions were also detected: an unexpected, latitudinally oriented, sharp boundary, starting about 100 km off Ensenada and extending 400-500 km offshore; and another, meridionally oriented, meandering far offshore (200-500 km), and about 400-500 km long. Four large, low-chlorophyll gryes, or vortices, were lined up longitudinally in the offshore side of the meridional front.
8. Extensive, long-term programs like CalCOFI may largely benefit from the synopticity and repetitive coverage of meaningful satellite observations. Complementary ship-satellite measurements can

allow more efficient use of ships, may help to appropriately define "indicator stations" (and assess their representativity later on), and can rapidly spot frontal areas or other zones of specific interest.

9. Satellite measurements yield upper-layer chlorophyll concentrations; i.e., an index of only one component of the system, and with some limitations. Therefore, satellite measurements should be coupled with detailed shipboard measurements.
10. The procedure used here to derive quantitative estimates of chlorophyll from satellite observations is being further tested, as concurrent shipboard and satellite data becomes available, to determine whether changes are needed to apply it to other seasons and to other areas.

ACKNOWLEDGMENTS

We are grateful to T. L. Hayward and E. L. Venrick, who kindly shared their extensive shipboard data of the May-June 1981 CalCOFI cruises. We are indebted to Ted L. Young and the rest of the staff at the Scripps Remote Sensing Facility for help and information from the housekeeping files of the CZCS telemetry stream. We are also grateful to Sharon McBride for typing the manuscript. We particularly wish to thank J. A. McGowan for his assistance and comments. This research was done under support of the Marine Life Research Group of the Scripps Institution of Oceanography.

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DISTRIBUTION AND MORTALITY OF NORTHERN ANCHOVY LARVAE IN 1978 AND 1979

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ABSTRACT

Eleven ichthyoplankton surveys, conducted during the winter and spring quarters of 1978 and 1979, indicate that spawning of the northern anchovy, *Engraulis mordax,* was contracted both spatially and temporally in 1978 relative to 1979. Larvae were farther offshore in 1979. Instantaneous daily larval mortality rate estimated from slope of the age-frequency distribution (yolk sac through 15 mm, ca. 25-30 days) varied insignificantly between 1978 and 1979 and averaged 0.168. Comparison to a simple model of spawning suggests that seasonal changes in the slopes are due solely to a systematic bias and not to real changes in the mortality rate.

Seasonal larval production was compared with birthdate distributions of fish surviving to the juvenile stage. In both years March had the greatest larval production and was the commonest month of birth among the survivors of the larval stage. Larval survivorship tended to increase within the 1978 spawning season and decrease within the 1979 season. Low survivorship in winter 1978 is consistent with the hypothesis that winter storms disrupted aggregations of prey necessary for larval feeding, but does not explain why apparent recruitment was greater in 1978 than 1979. Variation in larval survivorship could not be attributed to larval mortality. The offshore distribution of larvae in 1979 may have contributed to the relatively low survival.

RESUMEN

Once estudios de ictioplancton realizados durante los trimestres de invierno y primavera en 1978 y 1979 indican que el desove de la anchoveta *Engraulis mordax* en 1978 se produjo relativo al de 1979, tanto espacialmente como temporalmente. Las larvas estaban más lejos de la costa en 1979. El indice de mortalidad instantánea diaria de larvas que se estimó de la inclinación de la distribución de frecuencias de edades (vitelo hasta 15 mm, alrededor de 25-30 días) varió insignificativamente entre 1978 y 1979, con un promedio de 0.168. Una comparación con un modelo simple de desove sugiere que cambios temporales en las inclinaciones se deben únicamente a un sesgo sistemático y no a cambios verdaderos en el indice de mortalidad.

La producción larval temporal fue comparada con distribuciones de fechas de nacimiento de peces que sobrevivieron hasta la etapa juvenil. En ambos años, la mayor producción de larvas occurrió en marzo, y el haber nacido en este mes era más común entre los sobrevivientes de la etapa larval. La supervivencia larval tendía a aumentar en la época de desove de 1978 y a descender en la época de 1979. La supervivencia baja del invierno de 1978 es consistente con la hipótesis de que tormentas de invierno interrumpieron conjuntos de presas necesarias para alimentar las larvas, pero no explica porqué el reclutamiento era mayor en 1978 que en 1979. La variación en la supervivencia larval no se pudo atribuir a la mortalidad larval. La distribución de larvas fuera de la costa en 1979 pudo haber contribuído a la supervivencia relativamente baja.

INTRODUCTION

The planktonic phase of a schooling fish's life history is considered the most amenable to quantitative sampling (Smith and Richardson 1977). Egg and larvae surveys have been used to estimate the number of adults responsible for their production (e.g., Sette and Ahlstrom 1948; Saville 1964; Smith 1972). Fish larvae are also of interest because they are the link between the present adult stock and some future recruitment to the adult stock. The lack of a clear relationship between stock and recruitment has focused attention on events during the larval stage and their ultimate effect on survival to the juvenile and adult stages.

The literature on the pelagic fishes of the California Current is particularly rich. Smith (1981) summarized the influences on northern anchovy larval survival: (1) the availability of suitable prey for larvae exhausting their yolk sacs (Lasker 1978); (2) interspecific and intraspecific predation (Hunter 1976; Hunter and Kimbrell 1981); (3) starvation (Hunter 1976; O'Connell 1980); (4) effect of adult nutritional state on quality of eggs and fitness of larvae (Smith and Lasker 1978; Hunter and Leong 1981); (5) preschooling dispersal (Smith 1973; Hewitt 1981); and (6) larval transport to or from favorable areas (Sette 1950; Parrish et al. 1981).

In this report we describe the results of ichthyoplankton surveys conducted in 1978 and 1979, and discuss what may be inferred about factors affecting larval anchovy survival during those 2 years. Distri-

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[Manuscript received March 1, 1982.]

bution maps, abundance estimates, and mortality are reported for each of 11 surveys.

METHODS AND MATERIALS

The data presented here were obtained during 11 cruises (Table 1) conducted off the coast of the Californias (Figure 1) in 1978 and 1979, as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Plankton samples were taken obliquely from a depth of 210 m with 0.505-mm mesh nylon nets mounted on a bongo frame (see Kramer et al. 1972, for detailed methodology). Samples were preserved in a buffered Formalin solution and an ethyl alcohol solution. A subsample of the alcohol-preserved specimens of anchovy larvae was aged using daily increments in the otoliths (Methot 1981). Anchovy larvae in Formalin-preserved samples were enumerated in 1-mm classes of standard length. Preserved larval lengths were adjusted to live lengths using the shrinkage factors reported by Theilacker (1980).

We use two different summarization procedures. The first will be presented on a fine spatial scale but will not take into account extrusion, avoidance, and growth that affect the relation between larval production and the catch in each 1-mm size class. The results of this first summarization are used to describe the distribution and relative abundance of larvae. The second procedure incorporates factors affecting the relation between larval production and catch but requires a large sample size, so no within-cruise stratification was possible. The age-specific larval productions resulting from the second summarization are used to calculate mortality rates of larvae.

Only samples from the central population of anchovy are considered in the quantitative analyses. Electrophoretic and morphometric data indicate that anchovy along southern Baja California constitute a separate population (Vrooman and Smith 1971). We exclude samples collected south of CalCOFI line 110 (Figure 1). A third population occurs primarily along the coasts of Oregon and Washington.

TABLE 1
CalCOFI Surveys 1977 through 1979

Cruise	Dates	Number of stations occupied	% positive for anchovy larvae
7712	Dec 8-Dec 19	80	54
7801	Jan 5-Jan 31	211	46
7803	Feb 18-Mar 15	208	59
7804	Mar 29-Apr 25	147	48
7805	May 14-Jun 10	132	39
7807	Jun 20-Jul 17	219	23
7808	Jul 31-Aug 26	118	17
7901	Jan 12-Jan 22	46	67
7903	Feb 25-Mar 13	95	66
7904	Apr 1-Apr 17	61	54
7905	Apr 30-May 21	102	51

In the first summarization, larval catches were stratified into four classes of live length (2.6-4.9 mm, 5.0-8.3 mm, 8.4-11.3 mm, and 11.4-14.3 mm) and expressed as numbers of larvae under 10 m^2 of sea surface. Distribution maps of these summarized data were prepared. Each station's contribution to the larval census was weighted by the distance to adjacent stations along the CalCOFI line. Offshore stations were 40 miles apart; inshore stations were as close as 4 miles. The weighted sum of larvae was calculated for each line. Sums of unsampled lines were extrapolated from sums in adjacent lines and cruises. The total of the sums for CalCOFI lines 60-110 was the cruise's larval census.

Each station's contribution to the mean distance offshore of larvae was weighted by the distance to adjacent stations and by the catch of larvae at the station.

The second summarization procedure fits a negative binomial weighted model (Bissell 1972) to the frequency distributions of each 1-mm length class. The procedure was adapted for use on fish larvae by Zweifel and Smith (1981). The negative binomial distribution is described by two parameters: the mean, m; and the contagion parameter, k. The variance is related to these parameters by:

$$\mathrm{Var} = m + \frac{m^2}{k}$$

According to the weighted model, the frequency distribution of actual catches depends not only on the underlying m and k but also on the individual effective sampler volume w_i. We consider two factors affecting each sample: volume of water filtered per unit depth and avoidance of the net by larger larvae during the day (Smith 1972). We include a third factor, extrusion of small larvae through the mesh, to permit quantitative comparison between size classes. This extrusion factor does not vary between samples. A fourth factor, temperature-and-month-dependent growth rate, corrects for variation in the period larvae remain in each size class. This duration factor transforms the results from a standing crop in each size class to production or flux through the size class. Each of the above factors is defined to be typically about 1.0. The product of the 4 factors is the effective sample volume w_i, for the i^{th} sample.

The correction for volume of water filtered was calculated as:

$$f_1 = \left(\frac{V}{D}\right) \frac{1}{3.5}$$

where V is volume filtered, D is maximum depth sampled, and 3.5 is the standard sample of 3.5 m^3 per m of depth.

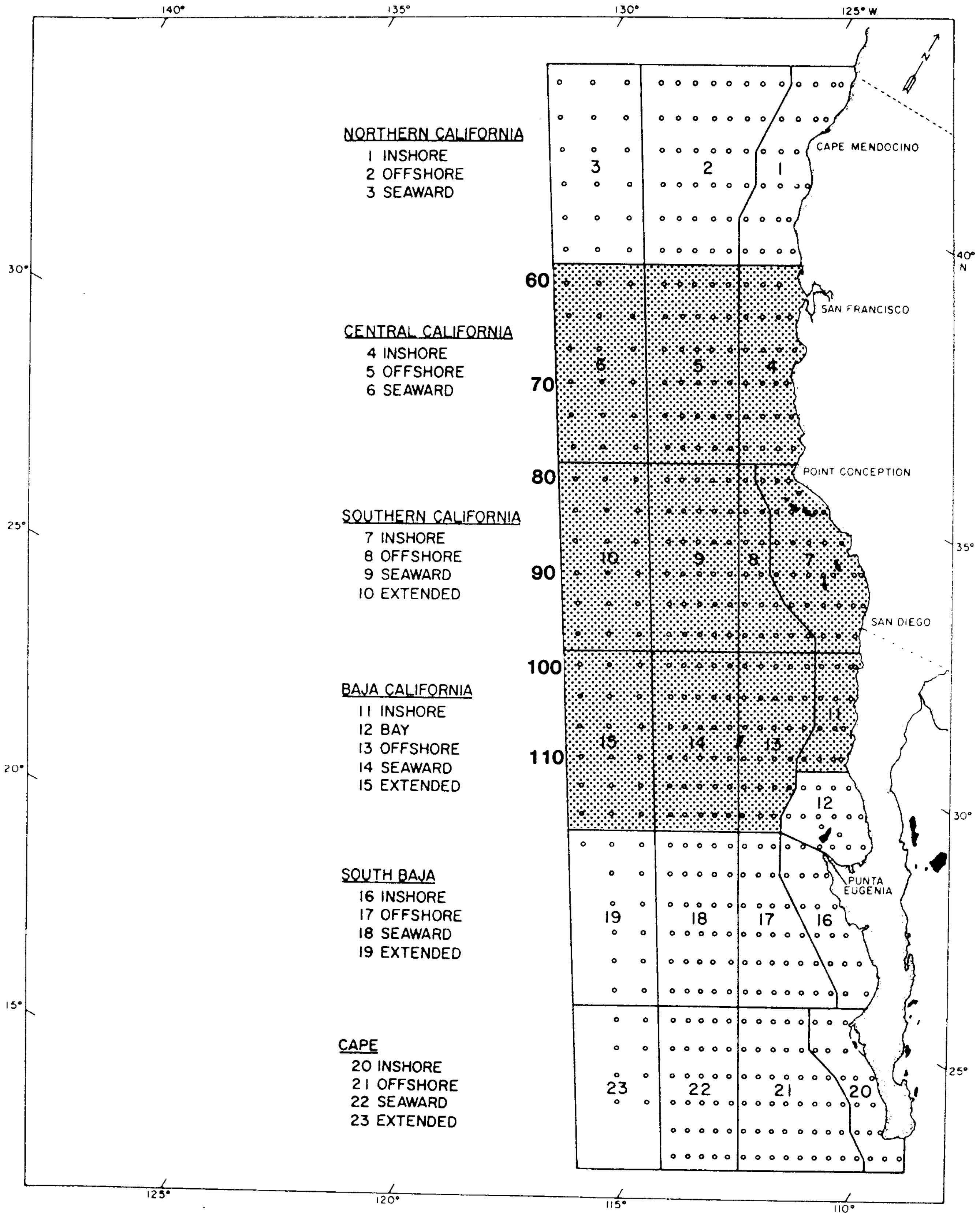


Figure 1. CalCOFI survey grid is divided into 23 regions. The central subpopulation of the northern anchovy is contained within the shaded regions (Vrooman and Smith 1971).

The correction for avoidance of the net during daylight was calculated by a sinusoidal function:

$$f_2 = \frac{(1 + DN_L)}{2} + \frac{(1 - DN_L)}{2} \cos\left(\frac{2\pi t}{24}\right)$$

where DN_L is the midday-to-midnight catch ratio of L-length larvae, and t is the hour of the tow. The factor is 1.0 at midnight and declines to a size-specific minimum DN_L, at noon. The ratios of mean catch during night (2030-0230 h) to mean catch during day (0830-1630 h) are presented in Figure 2 along with similar curves derived from catches by the 1-m bridled net (Ahlstrom 1954; Smith 1981).

The correction for extrusion of small larvae through 0.505-mm mesh was calculated as:

$$f_3 = 0.3311 \exp\left\{ 1.10526[1\text{-}\exp(-0.0165L^3)] \right\}$$

where L is the preserved length of the larvae. This correction was derived by Zweifel and Smith (1981) from the catch rates of nets with 0.333-mm mesh compared to paired catches by 0.505-mm mesh. The factor increases asymptotically to 1.0.

The correction for duration of each size class was calculated from temperature-specific growth of yolk-sac larvae (2.6-4.1 mm) in the laboratory (Zweifel and Lasker 1976; Zweifel and Hunter, unpubl. data) and growth of feeding larvae measured in the sea by daily increments in otoliths (Methot and Kramer 1979). Methot (1981) found that growth was similar to temperature-specific growth in the laboratory, but a month-specific model, which we use here (Methot and Hewitt 1980), was a more precise description. We divide the durations by a standard duration of 2 d/mm.

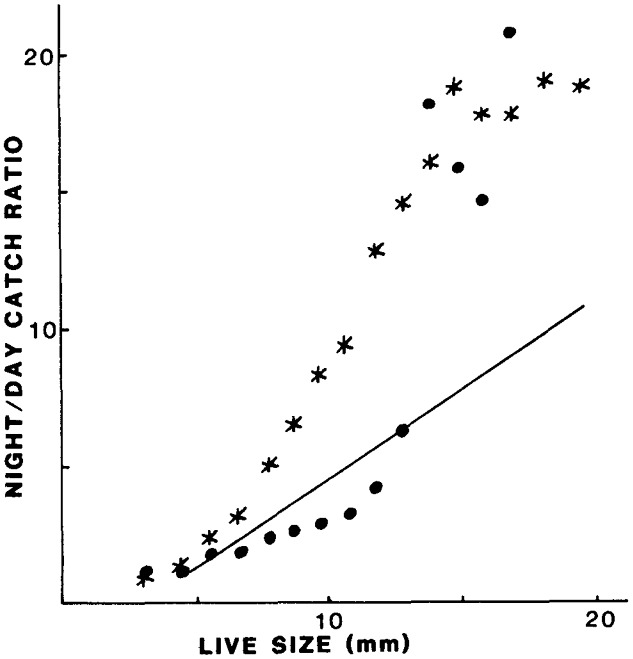


Figure 2. The night/day larval catch ratio increases with larval length. The dots were calculated from the 1978 and 1979 surveys using the bridle-free bongo net. The stars are similar ratios for anchovy larvae using the bridled 1-m net (Smith 1981). The solid line is a regression fit to the night/day catch ratios for sardine larvae using a bridled 1-m net (Ahlstrom 1954).

The slope of the relation between larval production (duration-corrected mean larval abundance) and age is an estimate of larval mortality rate. We calculate the linear regression of $\log_e$ (production) on age:

$$\log_e (m_t) = \log_e (m_o) - z(t)$$

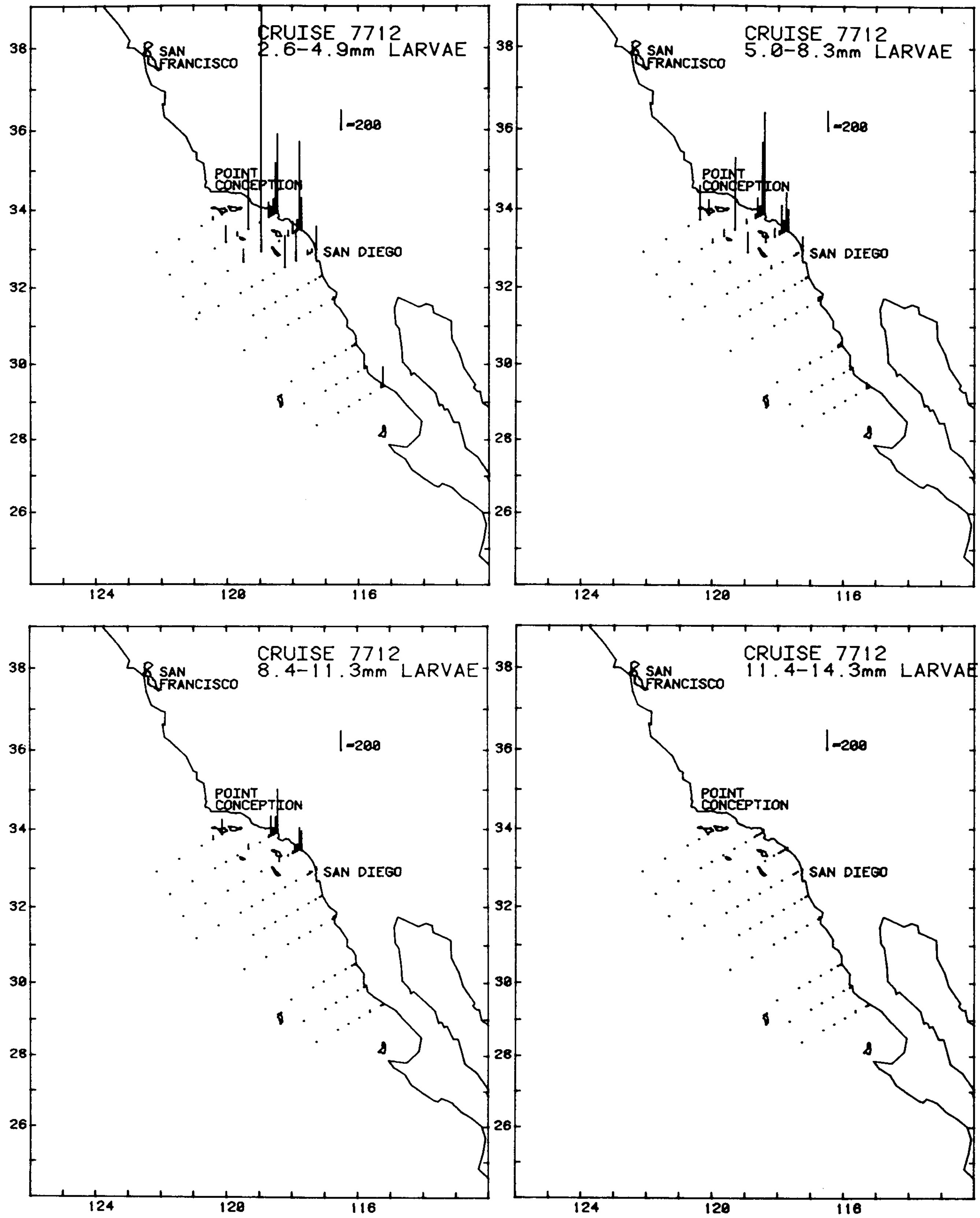
Where m_t is the mean production of the size class with mean age t, z is the instantaneous mortality rate, and m_o is the estimated production rate of hatching larvae (per 2 days). Interpretation of the slope as the mortality rate requires the assumption that the spawning rate is constant. Later we evaluate consequences of violating this assumption.

Hewitt (1982) makes use of patchiness indices derived from the contagion parameter, k.

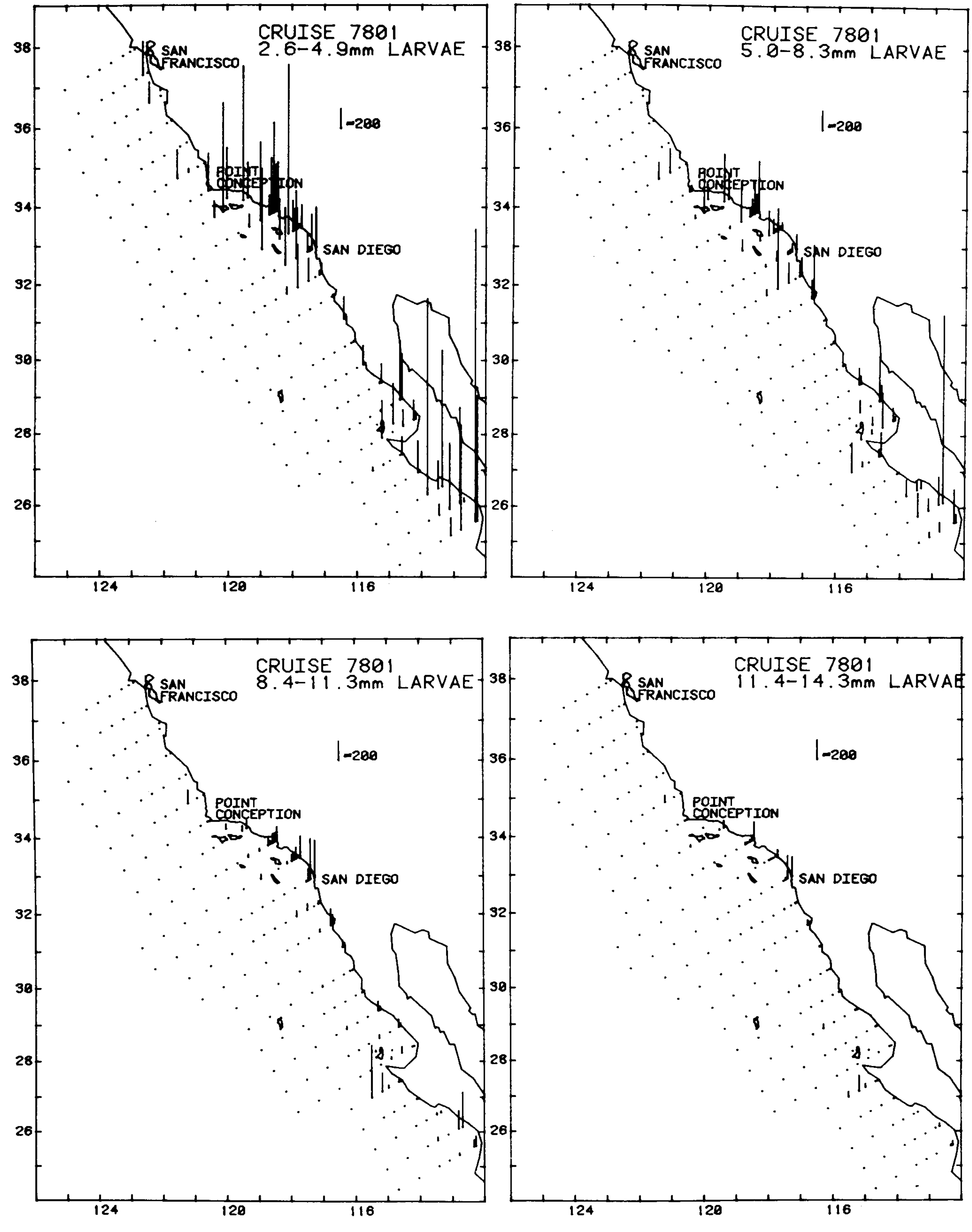
Some selection of stations was necessary for the second summarization procedure. Samples with no larvae presented a problem because they cannot be clearly interpreted: some result from sampling outside the habitat entirely, and others result from low densities within the habitat. The zero samples do not influence the census estimates, but they do influence the fit of the negative binomial model to the frequency distribution of larval catch for each size class. We defined the habitat as those areas where a larva of any size was found, and excluded samples containing no larvae. In the Los Angeles Bight (Pt. Conception to San Diego), and within 20 miles of the coast, sampling effort was often increased. To correct for the effect of oversampling, data from up to 6 stations on the inshore end of a station line were averaged to a composite station.

RESULTS

The geographic distribution of spawning differed between the 2 years. In 1978 larvae were found throughout the surveyed region, but most occurred between Pt. Conception and San Diego (Figures 3-9). During May to August all larvae of the central population were in this subregion. In 1979 the distribution of spawning was displaced southward (Figures 10-13). In the region north of Pt. Conception (CalCOFI lines 60-77) the census of 2.6-4.9-mm larvae for the 4 cruises between January and May was 587 in 1978 and 109 in 1979 (Tables 2 and 3). In the region including lines 80-97 the censuses were 19,853 in 1978 and 13,240 in 1979. In the south, lines 100-110, only 2 cruises, March and May, can be compared. In 1978 the census for 2.6-4.9-mm larvae in March and May was 418; in 1979 it increased to 6258.



Figures 3 through 13. "Orchard" charts depict spatial disposition of four groups of larvae for each cruise. Height of "tree" is proportional to the number of larvae per 10 m² of sea surface.


CRUISE 7801
2.6-4.9mm LARVAE
CRUISE 7801
5.0-8.3mm LARVAE
CRUISE 7801
8.4-11.3mm LARVAE
CRUISE 7801
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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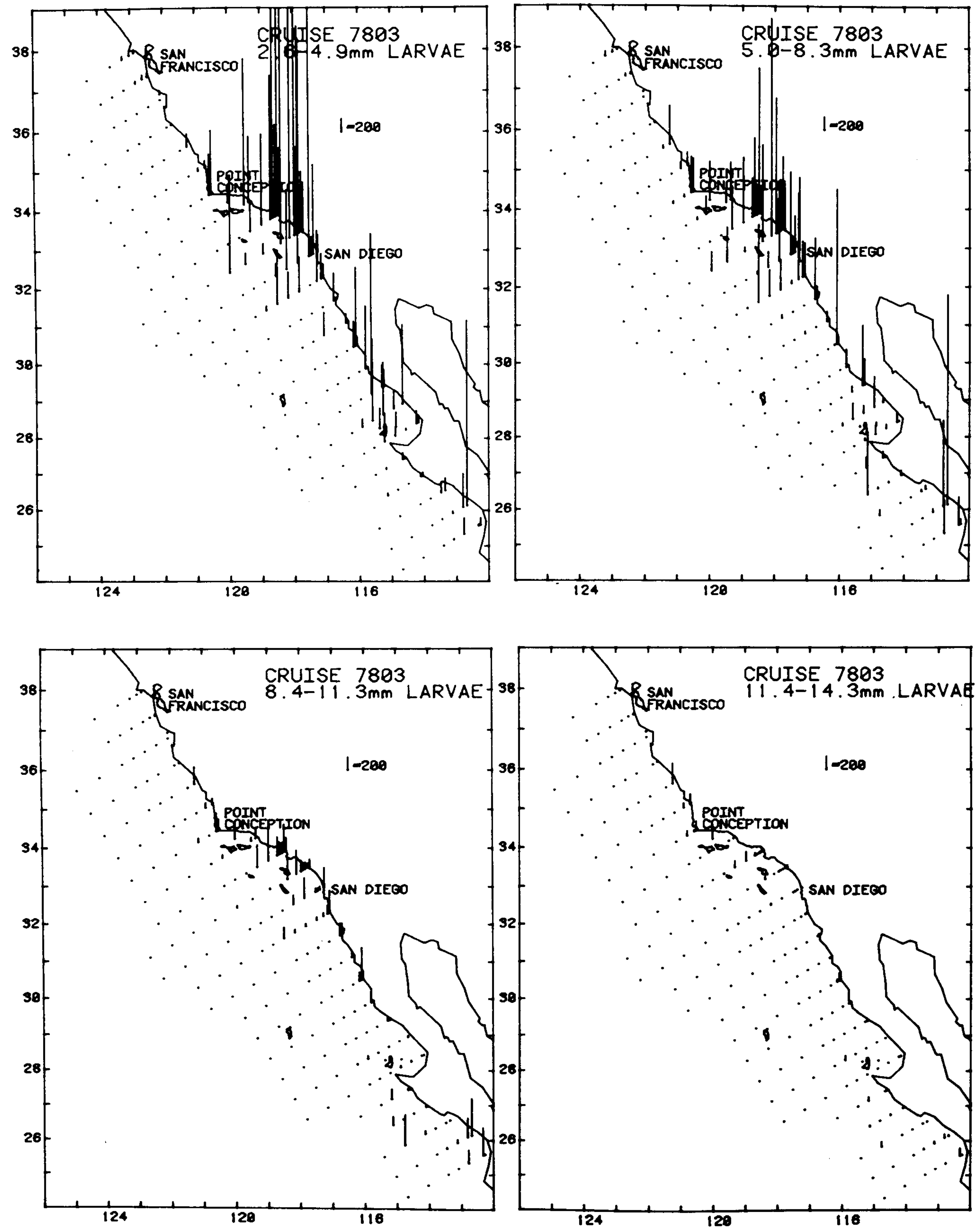
124
120
116

Figure 4.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CRUISE 7803
5.0-8.3mm LARVAE
CRUISE 7803
8.4-11.3mm LARVAE
CRUISE 7803
11.4-14.3mm LARVAE
I=200
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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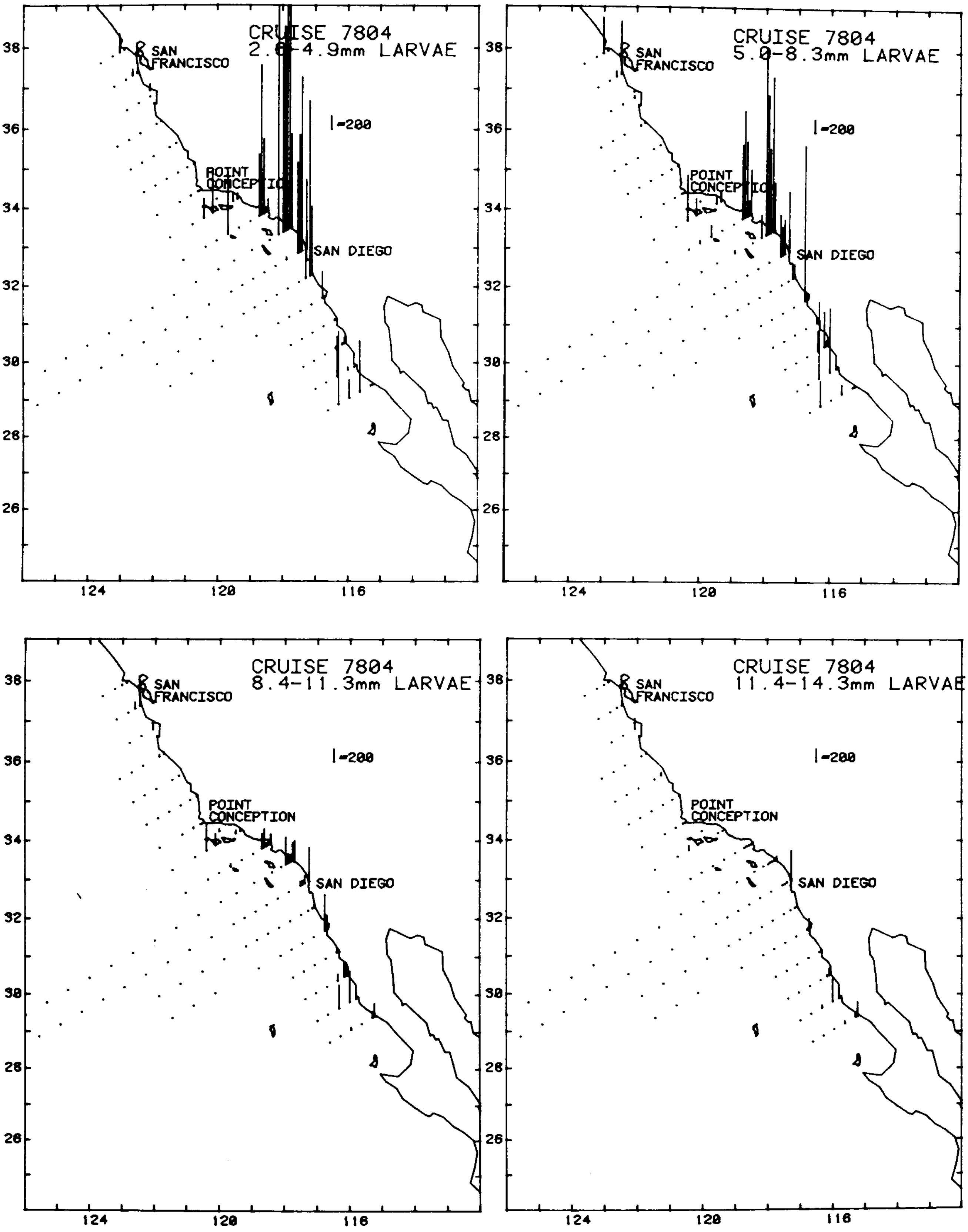
Figure 5.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CRUISE 7804
5.0-8.3mm LARVAE
CRUISE 7804
8.4-11.3mm LARVAE
CRUISE 7804
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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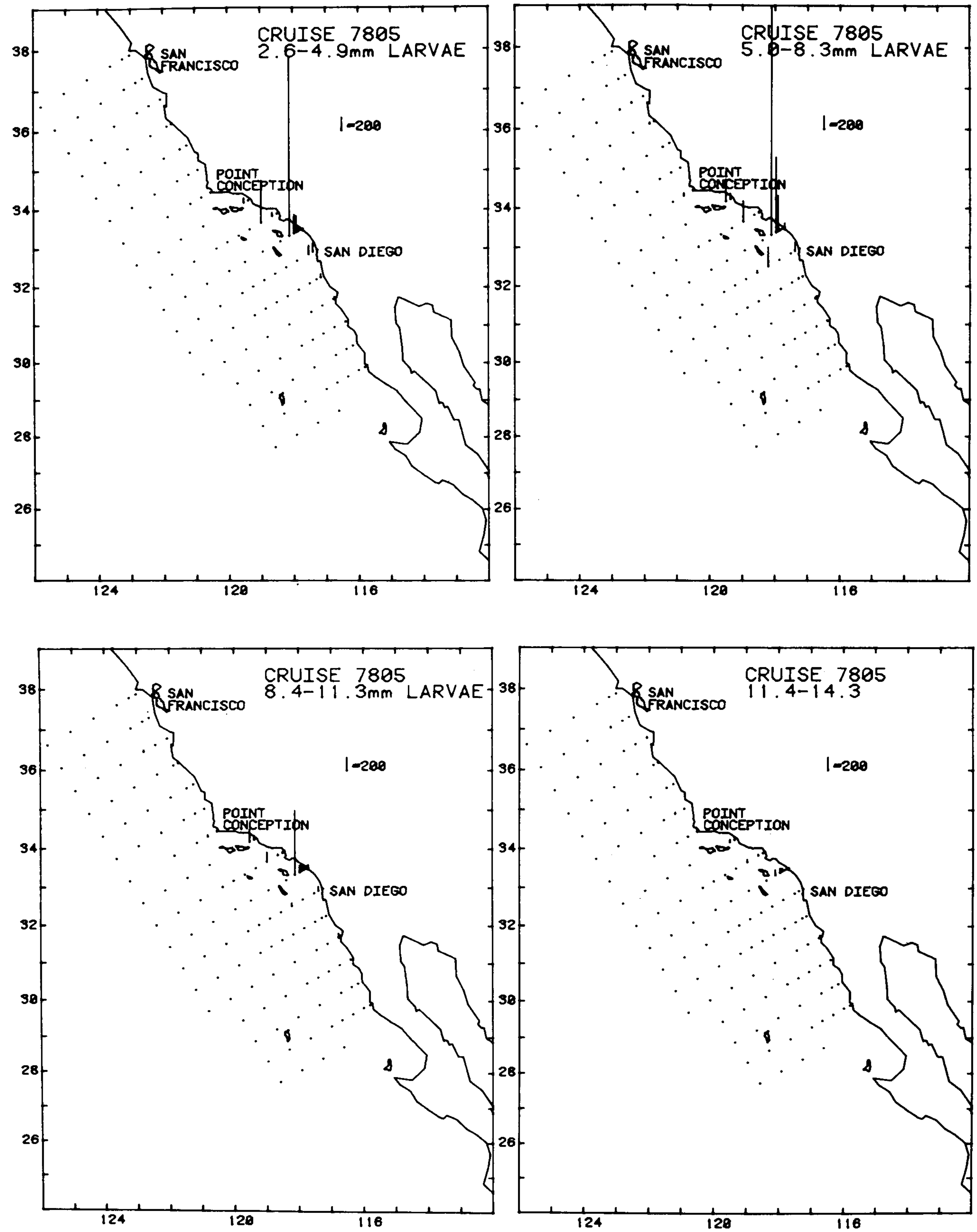
Figure 6.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CRUISE 7805
5.0-8.3mm LARVAE
CRUISE 7805
8.4-11.3mm LARVAE
CRUISE 7805
11.4-14.3
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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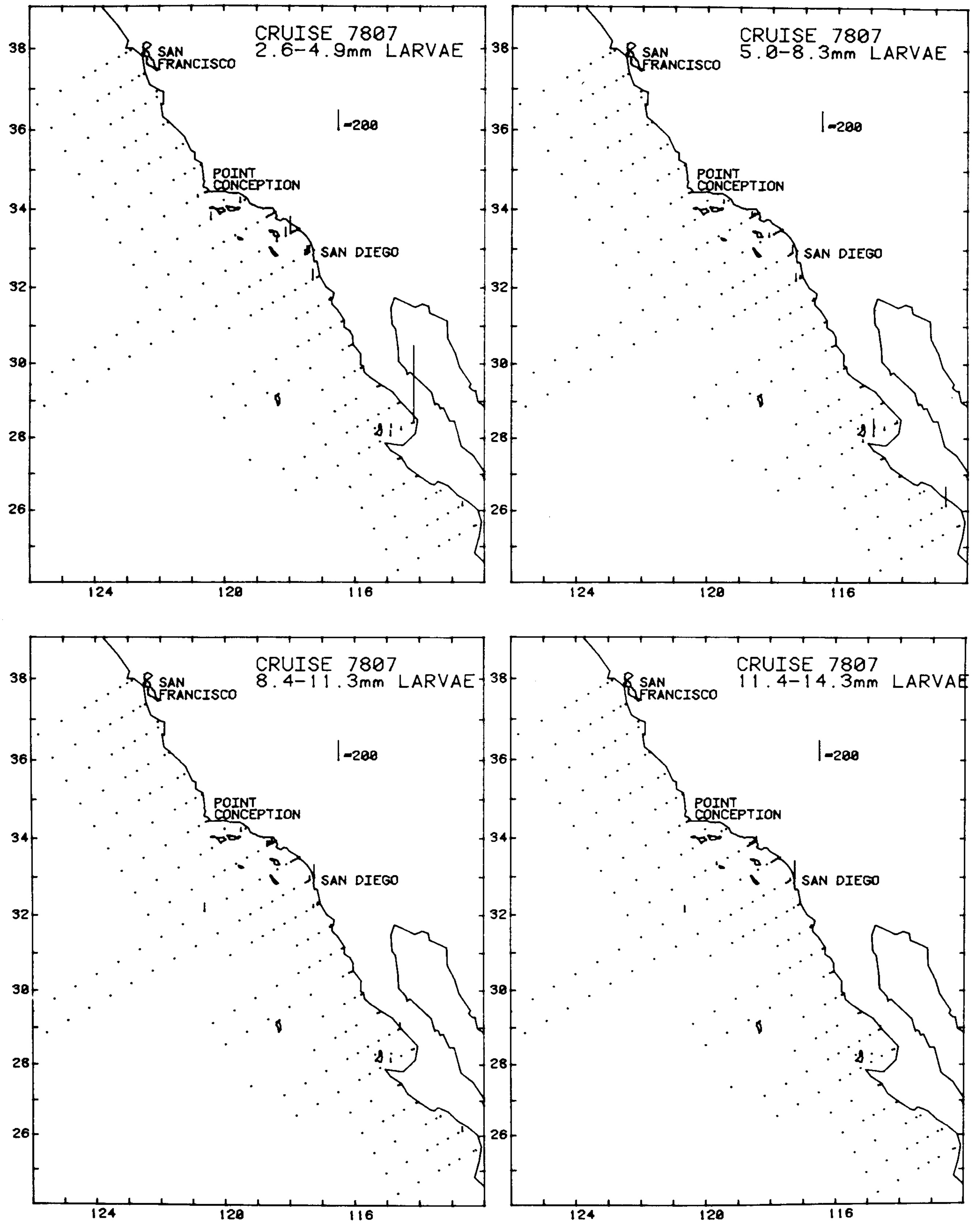
Figure 7.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CRUISE 7807
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CRUISE 7807
8.4-11.3mm LARVAE
CRUISE 7807
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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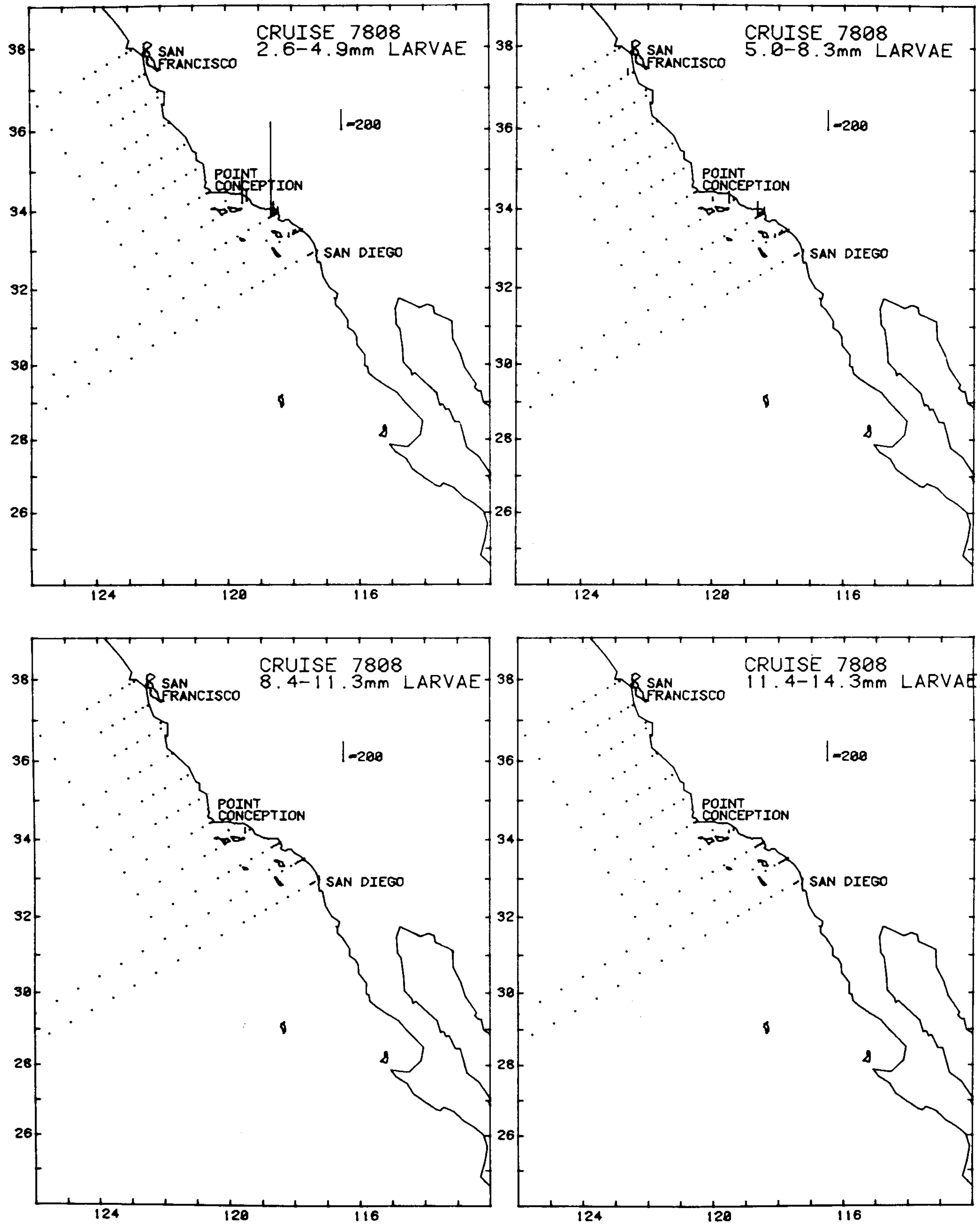
Figure 8.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CRUISE 7808
5.0-8.3mm LARVAE
CRUISE 7808
8.4-11.3mm LARVAE
CRUISE 7808
11.4-14.3mm LARVA
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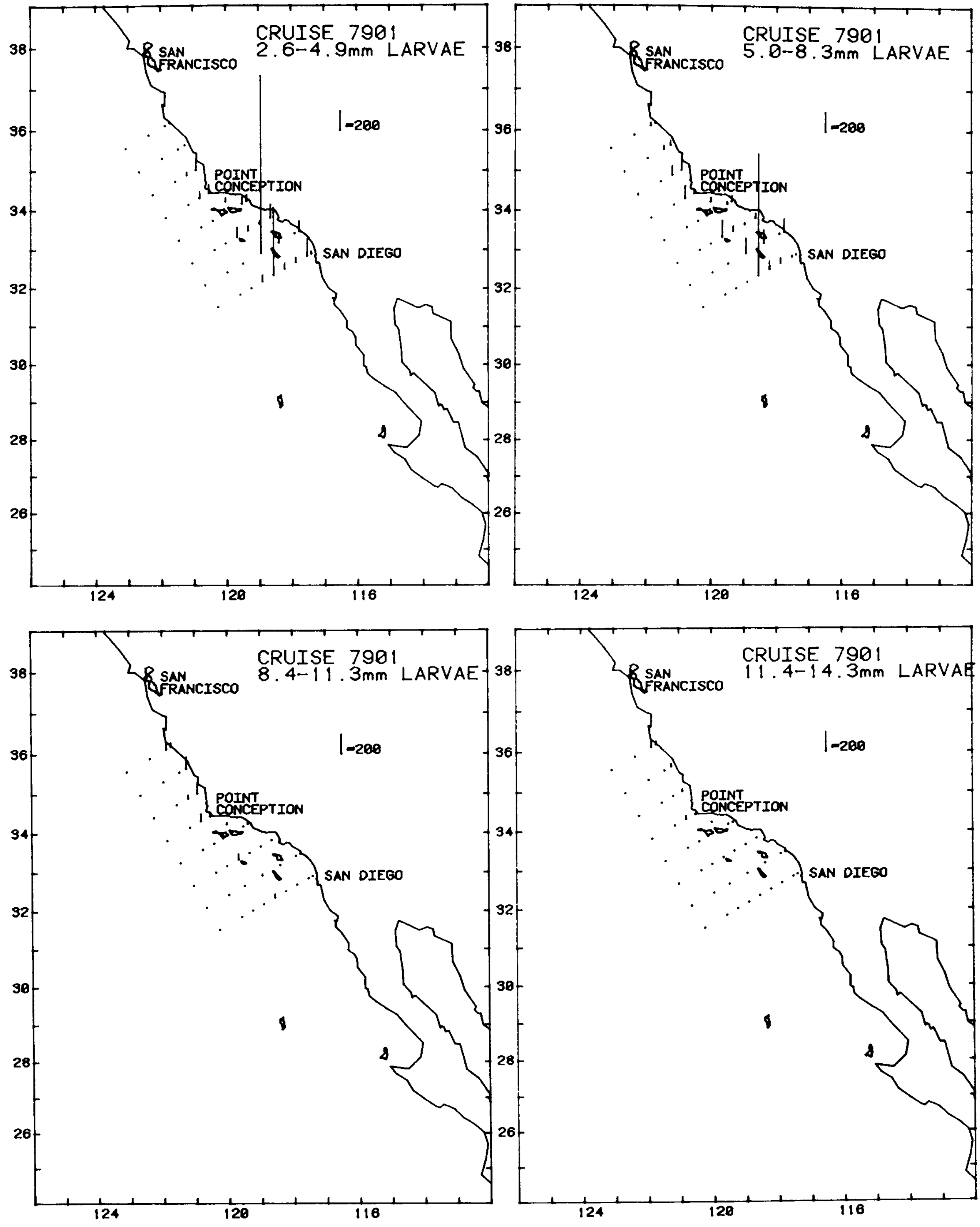
Figure 9.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2.6–4.9mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
-200
CRUISE 7901
5.0–8.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
-200
CRUISE 7901
8.4–11.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
-200
CRUISE 7901
11.4–14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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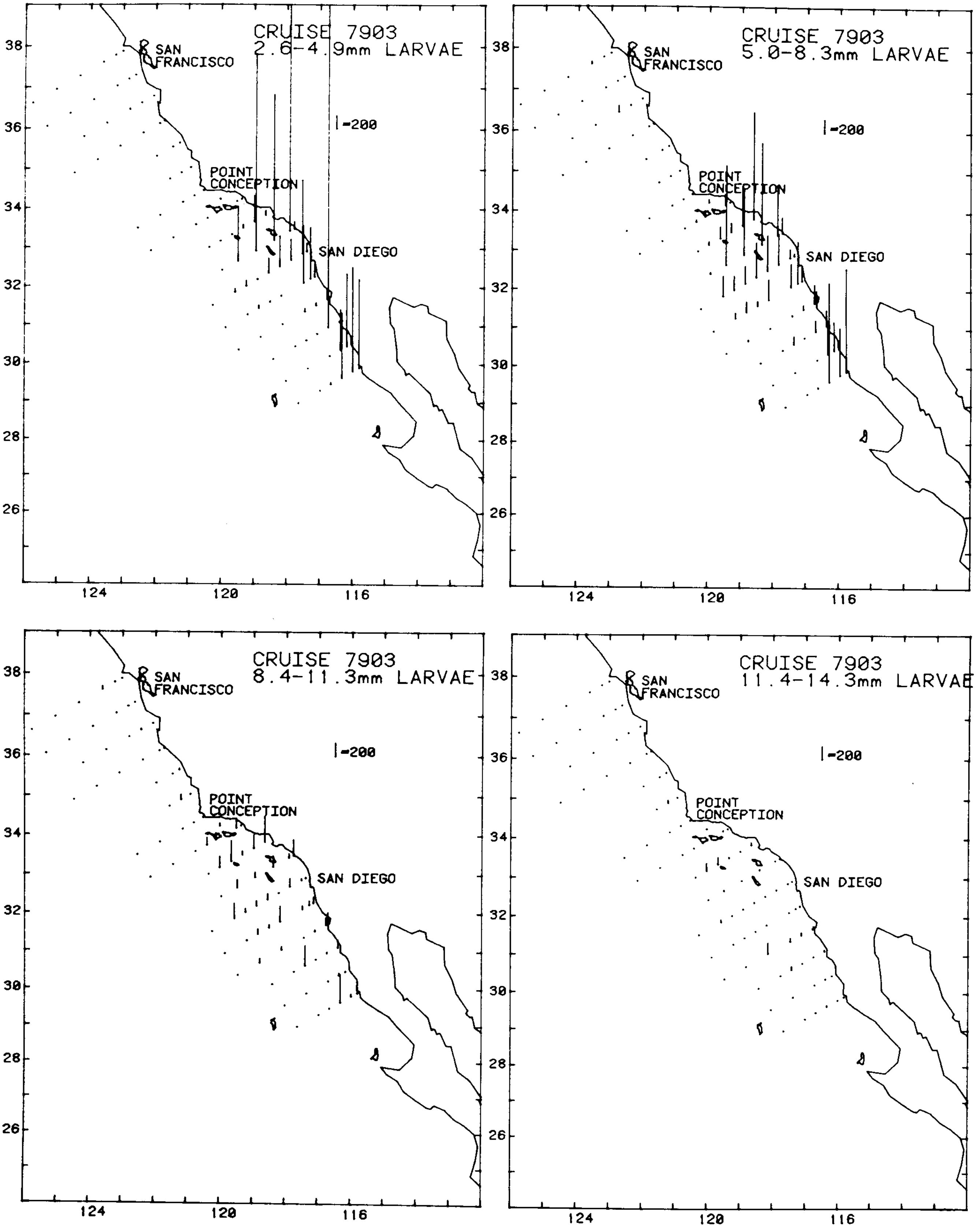
Figure 10.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CRUISE 7903
5.0-8.3mm LARVAE
CRUISE 7903
8.4-11.3mm LARVAE
CRUISE 7903
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
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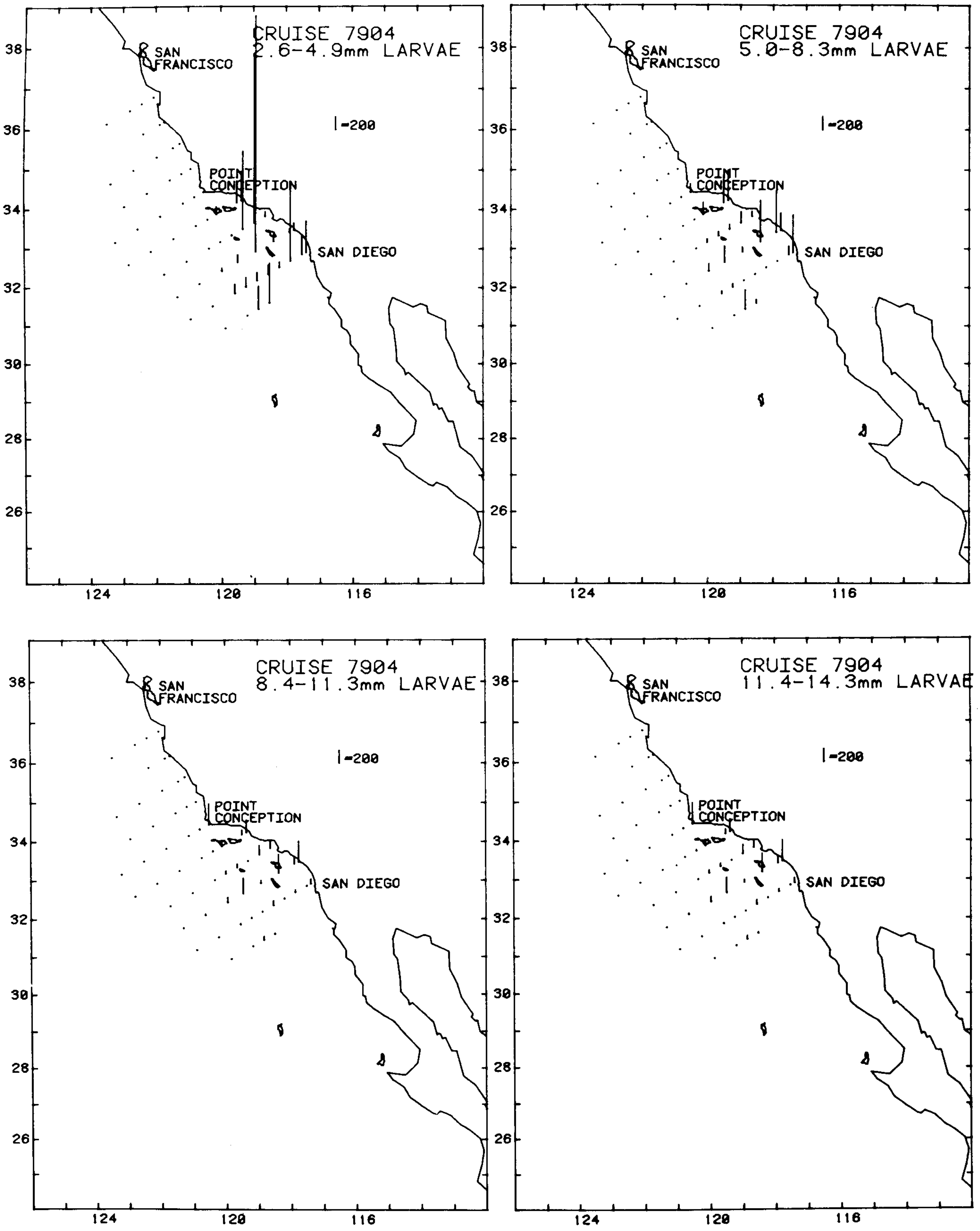
Figure 11.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CRUISE 7904
5.0-8.3mm LARVAE
CRUISE 7904
8.4-11.3mm LARVAE
CRUISE 7904
11.4-14.3mm LARVAE
I-200
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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Figure 12.

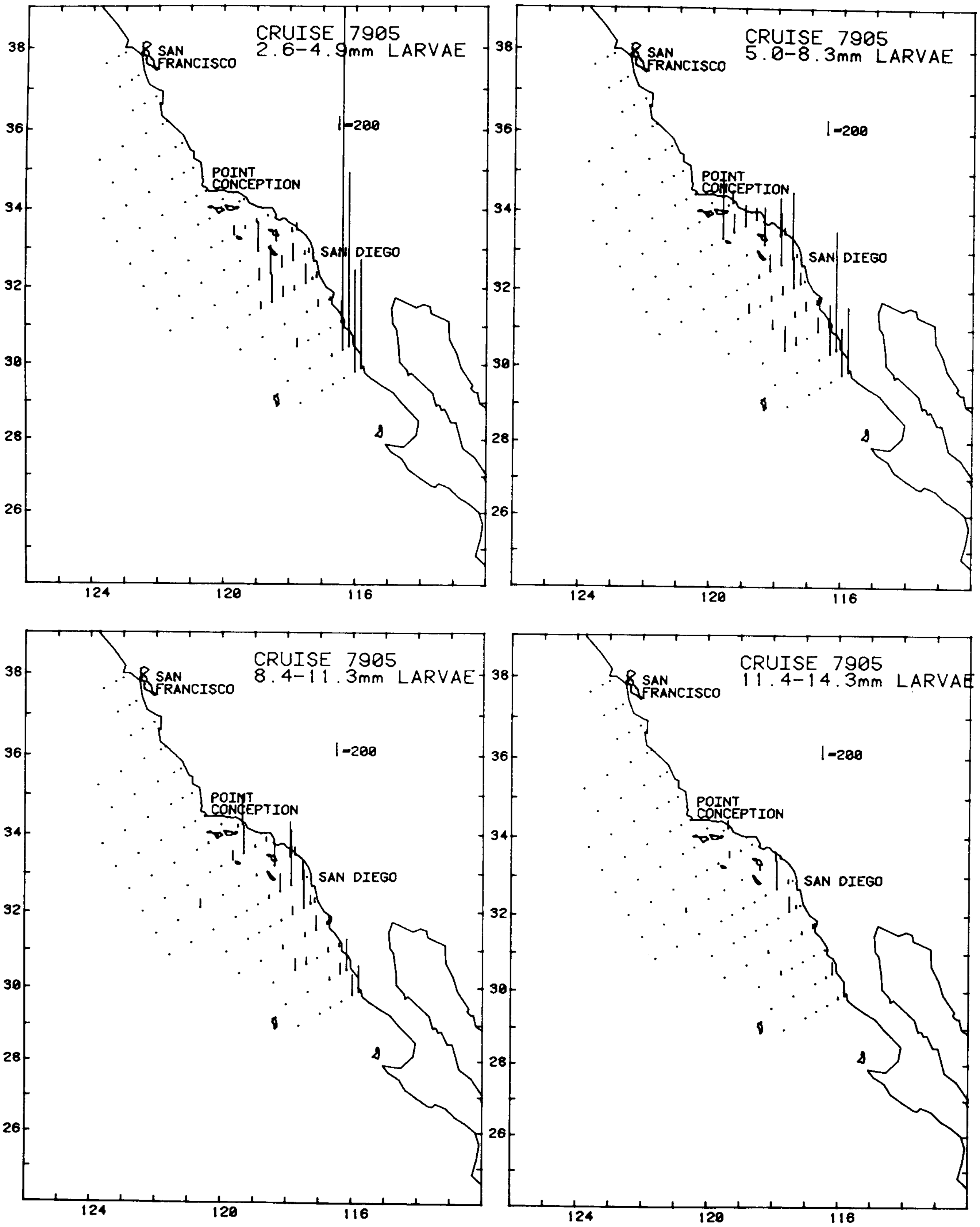
CRUISE 7905
2.6-4.9mm LARVAE
CRUISE 7905
5.0-8.3mm LARVAE
CRUISE 7905
8.4-11.3mm LARVAE
CRUISE 7905
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
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Figure 13.

TABLE 2

Temporal and Spatial Distribution of Anchovy Larvae during 1978

Between lines	Size group	7712	7801	7803	7804	7805	7807	7808
60-70	2.6-4.9	(93	110	44	77	0	0	0
	5.0-8.3	44	0	44	214	16	0	11
	8.4-11.3	19	5	16	110	16	0	0
	11.4-14.3	0	0	0	16	11	0	0
	Total	159)	115	104	429	44	0	11
70-80	2.6-4.9	(93	137	203	11	5	5	0
	5.0-8-3	44	121	264	11	27	0	0
	8.4-11.3	19	49	154	16	49	5	0
	11.4-14.3	0	22	115	11	33	5	0
	Total	159)	324	814	49	181	22	0
80-90	2.6-4.9	2002	2156	9355	2574	737	110	170
	5.0-8.3	726	654	2755	1391	1023	33	66
	8.4-11.3	231	132	643	352	368	93	38
	11.4-14.3	5	38	104	22	60	66	11
	Total	3025	3129	13249	4609	2299	379	302
90-100	2.6-4.9	209	660	3283	1039	49	33	(0
	5.0-8.3	27	429	1765	671	115	16	0
	8.4-11.3	5	137	346	148	44	16	0
	11.4-14.3	0	44	33	22	0	16	0
	Total	264	1369	5676	1969	236	104	0)
100-110	2.6-4.9	16	165	418	203	0	0	(0
	5.0-8.3	38	5	302	715	5	0	0
	8.4-11.3	5	49	93	308	5	0	0
	11.4-14.3	0	11	33	132	0	0	0
	Total	60	269	913	1485	11	0	0)
60-110	2.6-4.9	2413	3129	13303	3904	791	148	170
	5.0-8.3	879	1209	5130	3002	1186	49	77
	8.4-11.3	279	372	1252	934	482	114	38
	11.4-14.3	5	115	285	203	104	87	11
	Total	3667	5206	20951	8541	2771	505	313

Values are x 10^9 larvae; parentheses denote extrapolated values.

TABLE 3

Temporal and Spatial Distribution of Anchovy Larvae During 1979

Between lines	Size group	7901	7903	7904	7905
60-70	2.6-4.9	(0	16	0	0
	5.0-8.3	22	60	0	0
	8.4-11.3	88	33	0	0
	11.4-14.3	66	5	0	0
	Total	198)	132	0	0
70-80	2.6-4.9	71	0	22	0
	5.0-8.3	132	0	55	0
	8.4-11.3	82	33	11	0
	11.4-14.3	27	16	0	0
	Total	319	49	93	5
80-90	2.6-4.9	968	3894	3003	374
	5.0-8.3	253	2805	1017	924
	8.4-11.3	49	544	544	671
	11.4-14.3	11	155	137	176
	Total	1369	7771	4884	2266
90-100	2.6-4.9	(858	1116	2373	654
	5.0-8.3	1171	1325	639	924
	8.4-11.3	33	495	236	737
	11.4-14.3	16	181	92	269
	Total	2145)	3377	3718	2794
100-110	2.6-4.9	(858	3536	(2384	2722
	5.0-8.3	1171	1149	961	1138
	8.4-11.3	33	297	363	434
	11.4-14.3	16	33	111	88
	Total	2145)	5115	3993)	4636
60-110	2.6-4.9	2755	8562	7782	3750
	5.0-8.3	2749	5339	2672	2986
	8.4-11.3	285	1402	1154	1842
	11.4-14.3	136	350	340	533
	Total	6176	16444	12688	9701

Values are x 10^9 larvae; parentheses denote extrapolated values.

In addition to being displaced southward, larvae were farther offshore in 1979 (Table 4). Few larvae were collected offshore of the islands in 1978 (Figures 3-9), and offshore larvae commonly occurred in 1979 (Figures 10-13). The mean distances offshore of larvae for the 4 cruises between January and May (with larval census as weighting factor) were as follows:

	2.6-4.9mm	*5.0-8.3*	*8.4-11.3*	*11.4-14.3*
1978	60 km	56	53	46
1979	85	86	89	117

The trend with size differs between the years; however, the magnitudes of the trends are small unless one includes values for large larvae, which are based on few positive samples.

The temporal distribution of spawning also differed between the years. In 1978, anchovy spawning was moderately low during December and January, increased to a pronounced peak in early March, and decreased to a low level in May; larval abundance was very low by July and August (Table 2). In 1979, spawning was moderately low in January, and increased to a peak in early March. The peak was not as sharp as in 1978, and spawning was sustained at a

TABLE 4

Average Distance Offshore (km) of Anchovy Larvae

	Cruise						
	7712	7801	7803	7804	7805	7807	7808
2.6-4.9 mm	119	65	65	41	44	72	22
5.0 to 8.3	83	61	67	39	48	52	26
8.4 to 11.3	70	39	60	46	57	174	56
11.4 to 14.3	126	41	46	33	74	172	41
		7901	7903	7904	7905		
2.6 to 4.9 mm		111	65	113	54		
5.0 to 8.3		104	89	89	63		
8.4 to 11.3		59	104	104	74		
11.4 to 14.3		41	130	174	91		

moderate level through May (Table 3)[1]. Integrated over January, March, April, and May, anchovy larvae were 1.2 times more abundant in 1979 than in 1978.

To summarize: spawning during 1978 was compressed spatially and temporally relative to 1979. Spawning during 1979 was displaced southward and offshore, and took place later in the year.

An example of the second summarization procedure is presented in Figure 14. The frequency distributions are highly skewed but adequately described by the mean, m, and contagion parameter, k, of the negative binomial distribution. The slopes of the regressions of $\log_e (m)$ on t ranged from 0.23 to 0.15 during December 1977 and the first 4 months of 1978 (Table 5). We will not interpret slopes based on the low and probably sporadic level of spawning during the summer. During the first 5 months of 1979 the slopes ranged from 0.19 to 0.13.

Interpretation of the slopes of the above regressions as mortality rates requires the assumption of a stable age distribution (i.e., continuous and constant production of newly hatched larvae). The March larval abundance peak clearly violates this assumption, so we set up a hypothetical population to examine the extent of bias that may arise. The simulated population had a seasonal spawning cycle approximated by the normal curve, with peak spawning occurring at the end of March. A number of larvae were hatched each day, according to the distribution, and allowed to die at an instantaneous mortality rate of 0.15. Numbers of surviving larvae by age were summarized by month, and the instantaneous mortality was recalculated. Mortality is overestimated when spawning is increasing and underestimated when spawning is declining; the bias increases with seasonal contraction in spawning (Table 6). The bias is asymmetrical, greater when spawning is increasing; however, when larval numbers are accumulated over the entire season, the biases tend to cancel out. The observed seasonal decline in the slope of the larval catch curve (Table 5) is exactly as expected from constant mortality and the observed seasonal changes in larval production.

TABLE 5
Regressions of Larval Production Rates on Age

	Cruise 7712	7801	7803	7804	7805	7807	7808
A	4.87+.36	4.39+.18	5.53+.11	4.82+.17	2.87+.30	1.13+.35	3.62+.24
B	0.23+.03	0.16+.01	0.18+.01	0.15+.01	0.11+.02	0.03+.03	0.22+.02
C	.91	.96	.98	.95	.72	.01	.92

	7901	7903	7904	7905
A	4.23+.26	5.32+.16	5.10+.36	4.82+.16
B	0.19+.02	0.17+.01	0.19+.02	0.13+.01
C	.93	.97	.88	.93

A = ln (m_O)+s.e.
B = z +s.e.
C = r^2

TABLE 6
Estimated Mortality Rates from Age Distributions Pooled over 30 Days When Actual Mortality is Constant at 0.15, and Spawning Follows a Normal Distribution in Time

Std. deviation of spawning curve	Jan.	Feb.	Mar.	Apr.	May	June	Summed over season
30 days	0.24	0.20	0.17	0.14	0.11	0.08	0.15
45	0.22	0.18	0.16	0.15	0.13	0.12	0.15
60	0.21	0.16	0.15	0.15	0.14	0.13	0.15

We calculated an annual estimate of mortality using the larval catch accumulated over each spawning season. The instantaneous mortality of young larvae in 1978—0.175—was not significantly different from that for 1979—0.161.

DISCUSSION

The ultimate importance of events in the larval stage is their effect on survival into the juvenile stage. We have information regarding the between-year and also within-year variation in survival. Differences in larval anchovy survival between 1978 and 1979 may be inferred from the age distribution of the commercial landings of anchovy; despite greater production of larvae in 1979, the 1978 year class was about twice the size of the 1979 year class (J. Sunada, California Department of Fish and Game, pers. comm.). Methot (1981) described the temporal distributions of birthdates of juvenile fish sampled from these 2 year classes. In both years larval abundance peaked in March, and March was the commonest birthmonth (Figure 15). Neither year class was dominated by individuals born during some short period. Thus survivorship within 1978 and 1979 was proportional, for the most part, to larval production. Deviations from constant survivorship may be characterized as greater survivorship of spring 1978 spawn relative to winter 1978 spawn and the reversed seasonal pattern in 1979. This pattern of deviations was not evident in our estimates of early larval mortality. The twofold difference in survival between the years appears to be at least as large as the survival variability within the years.

In discussing the above survival patterns, we must consider the environmental conditions during these 2 years. Winter mixed-layer temperatures were cooler in 1979 than 1978; the Los Angeles Bight temperature ranged from 14° to 15°C in March 1978 and 12° to 13°C in March 1979. The incursion of a cold-water tongue into the Los Angeles Bight was evident in April 1978 and not in April 1979; the southern shift of spawning in 1979 may have been a reaction to thermal conditions or avoidance of an upwelled water mass

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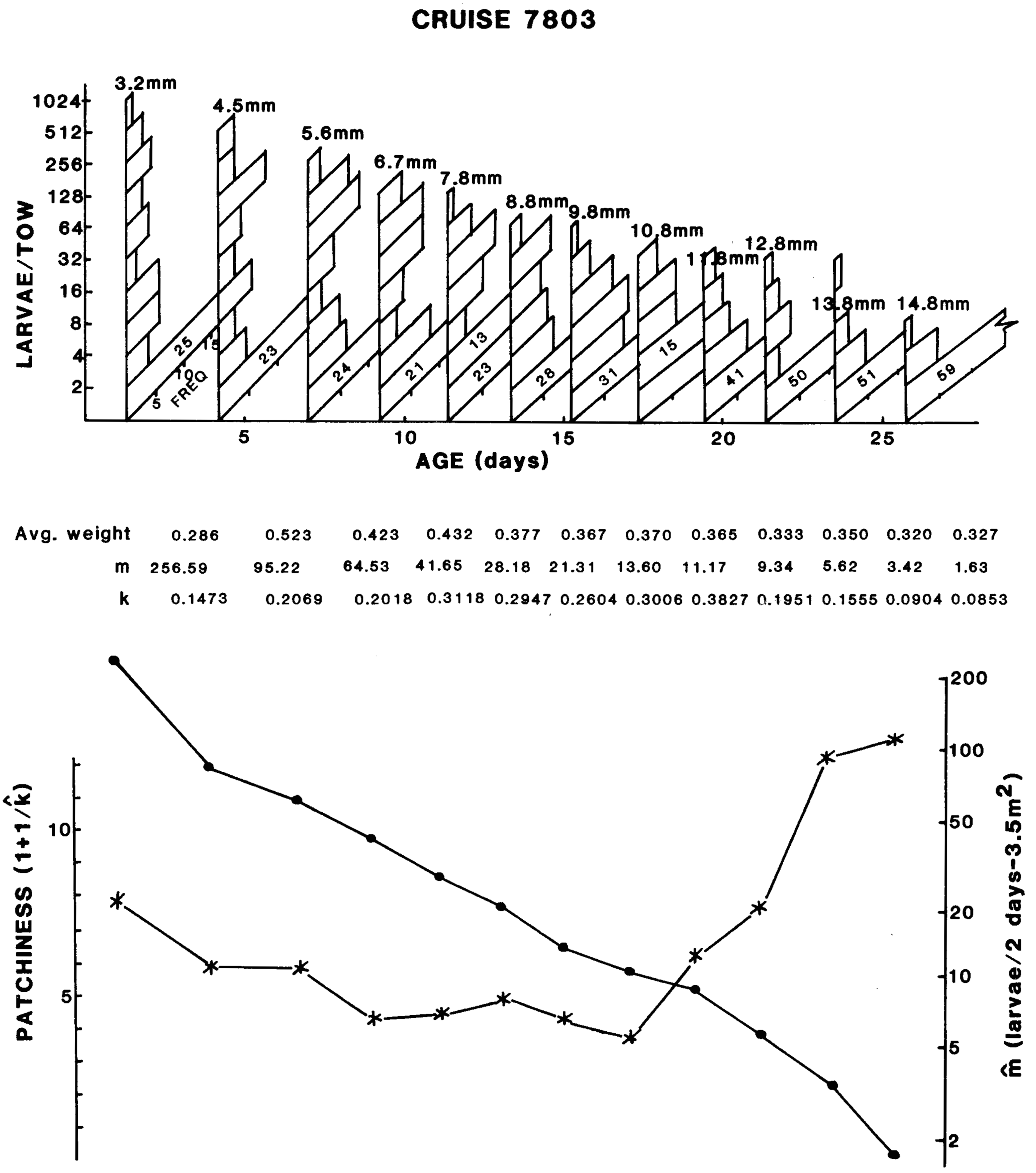
[1] No eggs and a few small larvae were detected during a nonstandard cruise in June 1979 (Methot, unpubl. data).



Avg. weight	0.286	0.523	0.423	0.432	0.377	0.367	0.370	0.365	0.333	0.350	0.320	0.327
m	256.59	95.22	64.53	41.65	28.18	21.31	13.60	11.17	9.34	5.62	3.42	1.63
k	0.1473	0.2069	0.2018	0.3118	0.2947	0.2604	0.3006	0.3827	0.1951	0.1555	0.0904	0.0853

Figure 14. The sample distributions of sized larvae, from cruise 7803, can be approximated by negative binomial distributions defined by the parameters *m* and *k*.

(Lasker et al. 1981). By May of both years, a tongue of cool water extended southeastward off Pt. Conception; pockets of cold water were adjacent to the central California and northern Baja California coasts; and a warm-water plume trailed to the southeast off Santa Catalina Island. There were no obvious differences in

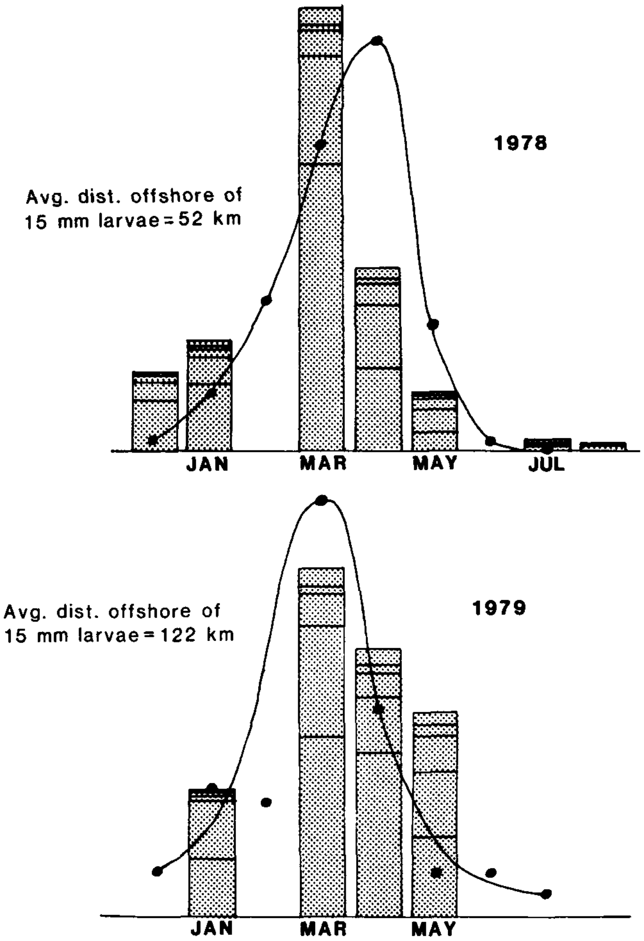


Figure 15. The seasonal distribution of larvae (bars) agreed generally with the birthdate distribution of survivors (line). The height of the bars is proportional to the abundance of larvae; bar subdivisions are proportional to the abundance of four size groups of larvae. The dots represent the fraction of juvenile fish that were spawned in each month.

the May temperature distributions that correlated with the dramatic difference in spawning activity.

Strong storms occurred during the winter of 1978, and substantial stratification of the upper water column was delayed until March 1978. Lasker (1981) suggests that this turbulence prevented formation of prey aggregations considered necessary to anchovy larvae. We did not find increased larval mortality during winter 1978, but Methot (1981) did find that survivorship increased during the 1978 spawning season. However, if larval survival was low during winter 1978 then postlarval survival must have been high throughout 1978 because the 1978 year class was abundant. Also, the winter of 1979 was less stormy, and the 1979 year class was only half as abundant as that from 1978.

Transport of larvae may be responsible for the difference in survivorship between 1978 and 1979. Upwelling and offshore transport of surface water caused by the stress of NW winds were extremely low during winter 1978, and remained below normal through May 1978. Upwelling was again low during winter 1979 but returned to normal by spring. Parrish, Nelson, and Bakun (1981) suggest low upwelling will entrain larvae closer to shore and lead to higher survivorship. Changes in the onshore-offshore distribution of larvae need not affect our estimates of early larval mortality rates. The important affected factor is the fraction of larvae capable of being recruited to the nearshore juvenile habitat. The seasonal pattern of survivorship in 1978 is not consistent with the drift hypothesis, but the seasonal pattern in 1979, the offshore distribution of larvae in 1979, and the relative year-class strengths do support this hypothesis.

We conclude that, in 1978 and 1979, significant variations in survival occurred during the late larval through juvenile stages. We also conclude that there is reason to doubt that larval surveys alone are sufficient to consistently predict recruitment.

In addition to the factors affecting survival of spawn, attention should be addressed to the factors affecting the production of spawn and its distribution in time and space. Since 1966, the central population of the northern anchovy has contracted spatially, expanded the spawning season, exhibited north/south shifts in the spawning center, and varied the month of peak spawning activity from January to May (Hewitt 1980).

ACKNOWLEDGMENTS

The material presented here has been extracted from our Ph.D. dissertations. The work was accomplished with the support and encouragement of our doctoral committees and the Southwest Fisheries Center. We especially wish to thank Drs. Reuben Lasker, John Hunter, and Paul Smith for their advice and critical review.

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THE ONSET OF SCHOOLING IN NORTHERN ANCHOVY LARVAE, *ENGRAULIS MORDAX*

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ABSTRACT

Laboratory measurements indicate that schooling begins in larval northern anchovy when they are between 11 and 12 mm standard length and is well established when they reach 13-15 mm. The onset of schooling closely parallels an increase in patchiness of larvae in the sea, and it begins during the period that larvae form a duplex retina and undergo major changes in their respiratory and locomotor systems.

RESUMEN

Observaciones sobre larvas de *Engraulis mordax* en el laboratorio indican que la formación de cardúmenes se inicia cuando las larvas alcanzan de 11 a 12 mm de longitud normalizada, y el cardumen ya está bien definido en larvas de 13 a 15 mm de longitud. La formación del cardumen se produce coincidiendo bastante con el período en que la distribución de las larvas en el mar muestra un incremento en la formación de agrupaciones, y además se inicia cuando la larva adquiere una doble retina y experimenta cambios notables en sus sistemas respiratorio y natatorio.

INTRODUCTION

Except for a portion of the larval stage, all life activities of northern anchovy—feeding, avoiding predators, migrating, and reproducing—are conducted within schools. Thus the time at which schooling begins is an important event in the life history of anchovy, for it identifies the first time that they may be able to profit from schooling. In the larval stage the most important benefit of schooling may be a reduction in predation and cannibalism, although facilitation of the search for food and timing of vertical migration might be additional benefits. For example, fry of the freshwater fish *Gobiomorus dormitor* have a 30 percent chance of being eaten when alone, whereas one individual in a school has a chance of less than 1.5 percent (McKaye et al. 1979). Thus, identifying the larval size at which schooling begins is necessary to properly understand the effects of predation, cannibalism, and food abundance on size-specific mortality rates.

Our objective was to identify the period when schooling begins, by observing the behavior of northern anchovy larvae reared in the laboratory. The ontogeny of schooling behavior has been studied in detail in *Menidia menidia* by Shaw (1960 and 1961) and Williams and Shaw (1971), in *Atherina mochon* by Jorné-Safriel and Shaw (1966) and Williams (1976), and in various cichlids by Dambach (1963). The focus of these past studies was on describing the development of this behavior, the effects of isolation, and the behavioral mechanisms underlying school development. Our focus was more limited, as we wished simply to determine the minimum larval size or age at which schooling might be expected to begin in the sea. Thus larvae were maintained in large communal rearing containers rather than in isolation, and behavioral measurements were designed to identify the onset of schooling but not to understand the underlying behavioral mechanisms.

METHODS

Culture

Three groups of anchovy larvae were reared on a diet of *Gymnodinium splendens*, *Brachionus plicatilis*, and the harpacticoid copepod *Tigriopus californicus*, using methods outlined by Hunter (1976). Eggs were obtained from the induced spawning of fish maintained in the laboratory (Leong 1971). Three thousand eggs were stocked in each of three black fiberglass cylindrical tanks (122 cm diameter, 36 cm deep); the initial water depth was 18 cm (200 l) and increased from daily additions of seawater containing algae and food to about 400 l in about 20 days. Larval density in the three tanks during the time schooling occurred were 3.5 larvae/l (group 1), 1.7 larvae/l (group 2), and 4.3 larvae/l (group 3). In group 3 the water volume of the tank was reduced just before the behavior observations were begun, increasing the density from 2.1 to 4.3 larvae/l. Larvae were not transferred but were observed directly in the rearing tank. Each tank received about 2000 mc at the surface for 12 hours and dark for 12 hours; water temperature was maintained between 15.6 and 16.4°C. Ten or more larvae were sampled every other day to measure growth, and the daily change in schooling behavior was expressed as a function of mean larval length.

[Manuscript received December 4, 1981.]

Indices of Schooling Behavior

In active fishes such as the northern anchovy, schooling produces cohesive groups in which the individuals maintain more or less parallel orientation. In some species of schooling fishes, parallel orientation may not be a good index of schooling, but in anchovy it is a natural consequence of their continuous movement and mutual attraction. Thus as schooling develops in larval anchovy, the social attraction among individuals will become stronger, groups or pairs will be more cohesive (remain together for longer periods), individuals will approach one another more often by parallel alignment, and parallel orientation will persist for longer periods. To measure the onset of schooling in larval anchovy we used three indices of these schooling characteristics: frequency of parallel orientation, the cohesion of pairs, and pair cohesion with parallel orientation.

Each morning seven individual larvae were observed for 5 minutes each; another seven were observed in the same manner for 5 minutes each afternoon. Observations were taken at least 2 hours after food was added to the tank. Daily observations began when larvae reached 10-13 mm and ended when the schools became highly reactive to the observer's presence. Interactions of the selected larva with other larvae in the rearing container were recorded with a keyboard and a multiple-pen event recorder. An interaction was defined as an encounter between a selected larva and another larva at a distance of 1 body length or less (a 1-cm grid etched on the bottom of the tank was used to judge distances). The duration of each interaction (seconds the pair remained at 1 body length) was recorded, as was the orientation of the interacting pair. Orientation was classified (Figure 1A) as (a) parallel (aligned side by side or head to tail); (b) head-to-head; and (c) perpendicular (aligned body to head). If the initial encounter were head-to-head or perpendicular, but subsequently one larva followed the other, resulting in parallel alignment, the event was classed as parallel orientation. The frequency of parallel orientation was estimated for each larva by calculating the percentage of all parallel interactions. The cohesion of pairs was estimated by calculating the total time the selected larva was within one body length of any other larva (regardless of orientation) and expressed as a percentage of the total observation time (5 minutes). Pair cohesion with parallel orientation was estimated by calculating the total time the selected larva was parallel to and swam within one body length of any other larva; this was expressed as a percentage of the total observation time. Means for each of these three indices were calculated for each daily set of 14 larval observations.

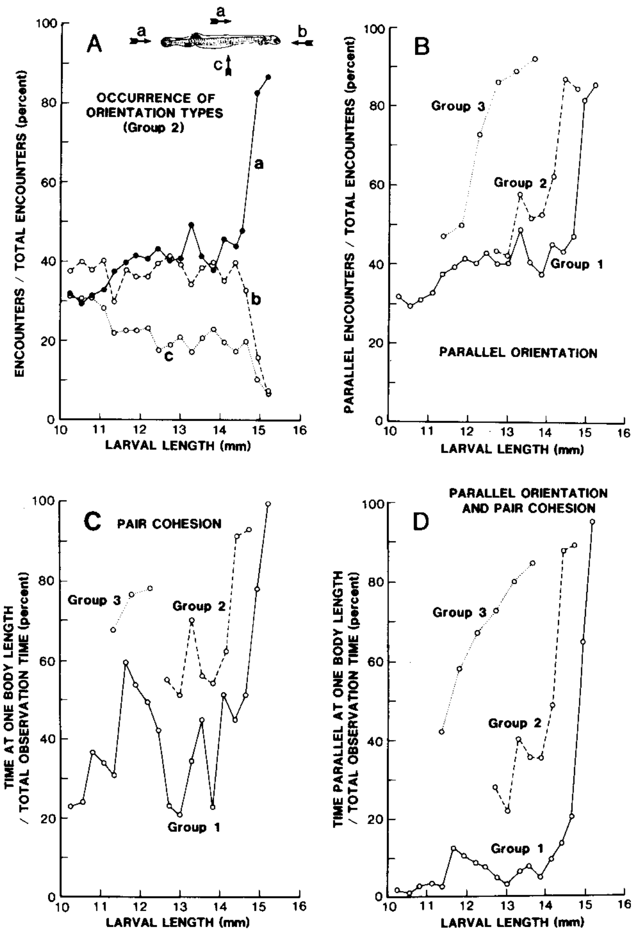

Figure 1. Indices of schooling as a function of the mean length of larval northern anchovy in three rearing containers (groups 1, 2, and 3). Each point is the mean of 14 five-minute behavior observations on different larvae.

A. Percentage occurrence of the three orientation classes during encounters between an observed larva and other larvae in group 2; orientation classes illustrated at top of panel: a, parallel; b, head to head; and c, perpendicular.

B. Percentage of encounters in which parallel orientation occurred in groups 1-3.

C. Percentage of the observation time a larva was within 1 body length of another larva (regardless of orientation).

D. Percentage of the observation time that a larva was aligned parallel to and swimming within one body length of another larva.

RESULTS

Larvae began showing signs of parallel orientation when they reached between 11 and 12 mm standard length. Before this time, when a larva approached another larva head on or perpendicular to the body, one of the pair would dart away in the opposite direction or occasionally would continue in a straight path showing no change in behavior. When larvae reached 11-12 mm a perpendicular approach often resulted in a turn by one of the larvae and a brief period of parallel swimming. Such events were scored as parallel encounters, although the initial approach was not parallel. The frequency of these encounters increased rapidly as the larvae grew (Figure 1 A, B). A sharp increase in the frequency of parallel encounters oc-

TABLE 1
Percentage of Observation Time Larval Northern Anchovy in Groups 1, 2, and 3[1] Were Schooling at Various Ages and Mean Lengths

	Group 1			Group 2			Group 3		
Larval length[3] (mm)	Larval age (days)	Schooling[2] (percent) mean	Schooling[2] (percent) 2XSE[4]	Larval age (days)	Schooling[2] (percent) mean	Schooling[2] (percent) 2XSE[4]	Larval age (days)	Schooling[2] (percent) mean	Schooling[2] (percent) 2XSE[4]
10.3				16	2	1			
.4									
.5				17	1	1			
.6									
.7									
.8				18	3	1			
.9									
11.0									
.1				19	3	1			
.2									
.3							23	42	19
.4				20	3	1			
.5									
.6				21	13	4			
.7									
.8							24	58	29
.9				22	11	3			
12.0									
.1									
.2				23	9	4			
.3							25	67	28
.4									
.5				24	8	3			
.6									
.7	31	28	11	25	5	2	26	72	12
.8									
.9									
13.0	32	22	7	26	3	1			
.1									
.2							27	80	13
.3	33	40	11	27	7	2			
.4									
.5									
.6	34	35	15	28	8	3	28	85	14
.7									
.8				29	5	3			
.9	35	35	14						
14.0									
.1				30	10	2			
.2	36	48	14						
.3				31	14	6			
.4	37	88	14						
.5									
.6									
.7	38	88	15	32	20	7			
.8									
.9				33	65	13			
15.0									
.1									
.2				34	95	4			

[1] Larvae were first observed at age 31d (group 1), 16d (group 2), and 23d (group 3).
[2] Percentage of observation period pairs are at 1 body length and swimming parallel.
[3] From regression of larval standard length on age in each group rounded to the nearest 0.1 mm.
[4] 2 X standard error of the mean where N = 14.

curred between 12 and 14 mm, depending on the laboratory group. By 15 mm all laboratory groups showed a strong schooling response. At this time they also became much more reactive to movements of the observer, although we moved as little as possible.

Within a particular group the three indices of schooling behavior (Figure 1 B, C, and D) showed the same trend with larval length (r^2 values for comparisons between pairs of indices within each of the three experimental groups ranged from 0.72 to 0.99). Thus to document the rest of this presentation we shall use only one index, the percentage of time spent swimming at one body length in parallel orientation (Figure 1 D). This index incorporates both the cohesive and the orientation properties of school structure. We also give the error terms for this index in Table 1, but for clarity they are deleted in Figure 1.

The timing of the onset of schooling varied among the three groups. It was the earliest in group 3 where the index for cohesion with parallel orientation attained values of 80-90 percent at 13.3 mm (age 27 days). Comparable values for group 1 occurred at 14.4 mm (age 37 days) and in group 2 at 15.2 mm (age 34 days).

Thus schooling had become clearly established in anchovy larvae by the time they attained a length of 13 to 15 mm. In other words, 13-15-mm larvae swam parallel to their neighbors at about a body length apart for 80-90 percent of the observation time. In group 3 the water in the tank was reduced by one-half when the larvae averaged 11.4 mm. After this disturbance the larvae immediately began to show signs of schooling, and they formed a relatively uniform school by 12.5 mm. It is not known if the increase in larval density (by a factor of 2) caused the early onset of schooling in group 3. The timing of the onset of schooling in the other two larval groups displayed a reverse pattern with larval density. We are more inclined to believe that the disturbance of changing the water and the resulting fright response induced an early onset of schooling. Examination of Figure 1 D or Table 1 indicates that the rate of change was more rapid in groups 1 and 2, where the onset of schooling began at somewhat longer length. This may indicate that the capability for schooling develops between 11 and 12 mm, but that external stimuli, perhaps a fright response, trigger the behavior. Schooling was not obvious in any group until 1 to 1½ hours after feeding, and if food

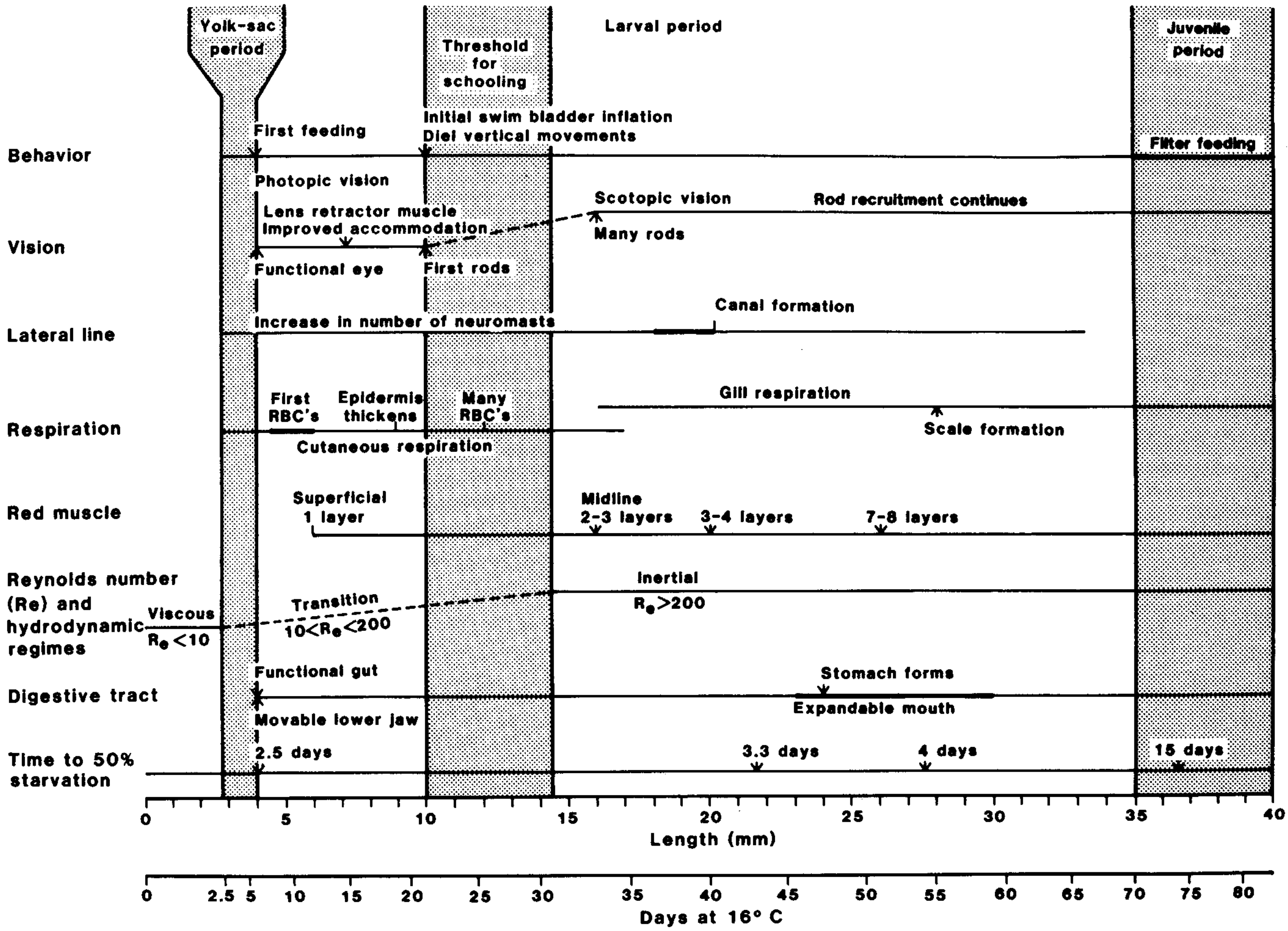

Figure 2. The timing of the onset of schooling in relation to events in the maturation of northern anchovy larvae. Structural events are from O'Connell (1981); hydrodynamic events from Weihs (1980); and all others from Hunter (1976), and Hunter unpublished data.
RBC = red blood cells. Time to 50 percent starvation is number of days of starvation at which 50 percent of the fish died.

was insufficient the larvae appeared not to school. All data presented here were taken at least 2 hours after feeding on an abundant supply of food.

DISCUSSION

The size of anchovy larvae at the onset of schooling is about the same as that determined for the marine silversides *Menidia*. Schooling (swimming continuously as a group) in *Menidia* is clearly established when they reach 10-12 mm (about 20 days old) (Shaw 1960; Williams and Shaw 1971). The period in larval development at which schooling begins is probably partially a function of the maturation rates of organ systems. Anchovy of this size (12-15 mm) are characterized by rapid structural and behavioral changes (Figure 2). At 7 mm, shortly before the onset of schooling, the lens retractor muscle becomes functional, increasing visual accommodation (O'Connell 1981). At 10 mm the swim bladder is inflated for the first time at the water surface; larvae begin nightly migrations to the water surface (Hunter and Sanchez 1976); and the first rods appear in the retina. Over the interval in which schooling begins (12-15 mm) the number of rods increases, perhaps improving peripheral vision; the red muscle deepens from a superficial layer to 2-3 layers deep; and the larva changes from a cutaneous respirator to a gill respirator (O'Connell 1981). In addition, by the time they reach 15 mm larvae have passed a transitory hydrodynamic regime where water viscosity has an important effect on swimming performance, and entered one in which performance is independent of viscosity effects, thus permitting maximum efficiency in the beat-and-glide swimming characteristic of anchovy (Weihs 1980). All organ systems continue maturing throughout the larval phase, but the above circumstantial evidence indicates that onset may be tied to changes related to locomotor efficiency (metabolism and swimming kinetics) and improvements in the visual system.

Although structural developments may set the stage for the onset of schooling, the actual initiation may be triggered by environmental events. In the laboratory, schooling seemed to be triggered by various disturbances such as changing the tank water, cleaning the tank, or other fright-inducing stimuli. In the sea the appearance of predators or perhaps initiation of diel vertical movements to the sea surface could be triggering mechanisms. Such disturbances could act as a trigger only after the larvae reach the appropriate age for onset of schooling.

Hewitt (1981a and b) measured the mean patchiness of the eggs and larvae of northern anchovy taken in ichthyoplankton surveys over the years 1951-79 (6,000+ samples) using Lloyd's (1967) index of patchiness. He showed that initially anchovy eggs are quite patchy in the sea, as could be expected from the schooling habits of the parents. After spawning, however, a gradual process of dispersion begins; eggs and, subsequently, larvae become more and more dispersed until the larvae reach about 10 mm (20 days old), whereupon this trend is reversed, and larvae become increasingly more patchy with larval size or age. We have reproduced Hewitt's (1981b) data and plotted on Figure 3 the average schooling index for the data given in Table 1. The increase in patchiness with larval length in the sea closely matches the onset of schooling averaged for the three groups. Thus as Hewitt (1981a) suggested, the change in patchiness—a statistical property of the spatial distribution of larvae—is an effective measure of the onset of schooling in the sea.

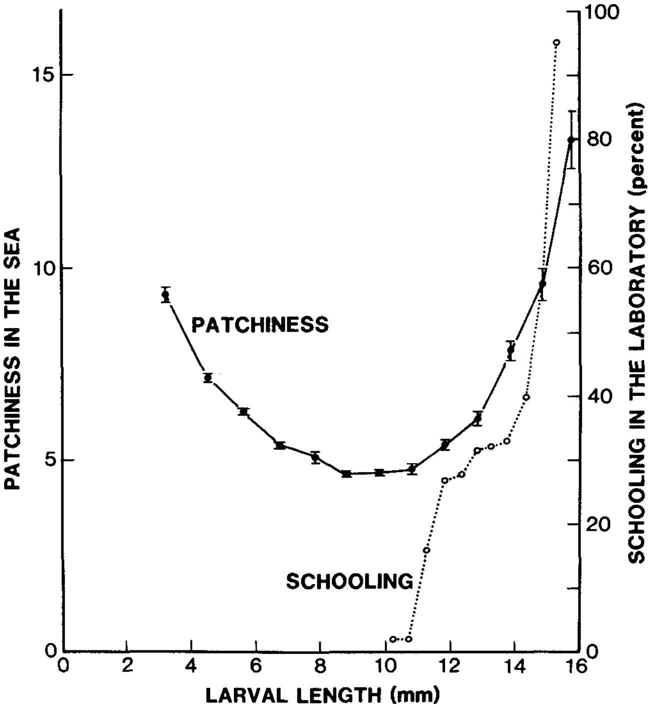

Figure 3. Patchiness of larval anchovy in the sea as a function of larval length (from Hewitt 1981b) and the onset of schooling in the laboratory. Patchiness (solid line), measured by Lloyd's (1967) index, is a measure of the degree of departure of larval spatial distributions in the sea from random dispersion; bars are two standard errors for the index of patchiness. The onset of schooling in the laboratory (dotted line) is measured by the mean percentage of the observation time that larvae were parallel and swimming one body length apart; points are the mean for three laboratory groups combined by length classes.

A salient feature of larval anchovy schools in the laboratory was that they were dispersed before the daily additions of food, and schooling was not obvious until the larvae had fed. Schools of juvenile jack mackerel also are less cohesive before feeding (Hunter 1966). The restriction of our measurements to post-feeding groups was appropriate for a threshold estimation, but it did mask the fact that the time spent in organized cohesive schools increases throughout the anchovy's larval and juvenile periods (van Olst and Hunter 1970). This gradual increase in the time spent in schools may be related to the maturation of the digestive and feeding systems, which occurs in the juvenile period. Maturation of the digestive system, onset of satiation mechanisms, increases in body reserves, and increases in feeding efficiency probably reduce the time required for feeding and food search and consequently permit schooling to continue for longer periods each day. For example, northern anchovy larvae < 10 mm feed throughout the day and do not appear to satiate. On the other hand, adults satiate rapidly when they feed by biting large prey, and consume a full ration in less than an hour. Satiation is not evident when they feed by filtering smaller prey, but this behavior causes little disruption of school organization, whereas biting behavior affects school structure (Leong and O'Connell 1969).

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DEVELOPMENTAL STAGES OF THREE CALIFORNIA SEA BASSES (*PARALABRAX*, PISCES, SERRANIDAE)

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ABSTRACT

Eggs, larvae, and juveniles of kelp bass, *Paralabrax clathratus,* barred sand bass, *P. nebulifer,* and spotted sand bass, *P. maculatofasciatus,* are described from specimens reared in the laboratory and from specimens collected in the field. Eggs of spotted sand bass are 0.80-0.89 mm in diameter; eggs of kelp bass and barred sand bass are 0.94-0.97 mm in diameter. Larvae and juveniles of the three species may be distinguished by differences in pigmentation during most stages of development. Larvae of the two species of sand bass are indistinguishable during notochord flexion. Yolk-sac larvae of all three species are indistinguishable.

RESUMEN

Se describen los huevecillos, las larvas, y los juveniles de *Paralabrax clathratus, P. nebulifer,* y *P. maculatofasciatus,* tomadas de especímenes cultivados en el laboratorio y de especímenes recolectados en el mar. Los huevecillos de *P. maculatofasciatus* son de 0.80-0.89 mm de diámetro; los de *P. clathratus* y de *P. nebulifer* son de 0.94-0.97 mm de diámetro. Larvas y juveniles de las tres especies pueden ser distinguidos por las diferencias in pigmentación durante casi todos los estadios del desarrollo. Las larvas de *P. nebulifer* y *P. maculatofasciatus* no se pueden identificar durante la flexión del notocordio. Las larvas con saco vitelino no pueden separarse en las tres especies.

INTRODUCTION

Three species of the genus *Paralabrax* commonly occur off California. The kelp bass, *Paralabrax clathratus,* is found from Magdalena Bay, Baja California, to the Columbia River. The barred sand bass, *P. nebulifer,* is found from Magdalena Bay to Santa Cruz. The spotted sand bass, *P. maculatofasciatus,* is found from Mazatlan to Monterey (Miller and Lea 1972). A fourth species, the gold spotted bass, *P. auroguttatus,* has been reported on one occasion (Fitch and Schultz 1978). Prior to this record, the species was known from Cedros Island south to Cabo San Lucas and the Gulf of California (Fitch and Shultz 1978). Larvae of *Paralabrax* sp. have been illustrated by Kendall (1979) from CalCOFI specimens, which we have identified as *P. clathratus.* All three species are found in nearshore areas from the surface to about 600 feet (Miller and Lea 1972).

The kelp and sand basses combined rank second in the California sport fish catch (Oliphant 1979). Identifying these three species in ichthyoplankton collections may be important in monitoring population changes and assessing the impact of human activities on the nearshore environment. This paper describes the early life history of kelp bass, barred sand bass, and spotted sand bass from laboratory-reared and field-collected material.

METHODS

Eggs and larvae of *P. clathratus* were initially reared from artificially spawned eggs. Two ripe kelp bass, a 42-cm female and a 40-cm male, were caught by hook and line near Bird Rock, Santa Catalina Island, California, on June 22, 1978. Gonads were removed from the fish and taken to the laboratory, where eggs were collected into finger bowls. The eggs were flooded with seawater immediately before the introduction of several drops of sperm. The eggs and sperm were agitated for several seconds, followed by several changes of seawater. When the eggs hatched, a mixture of plankton and ground Tetramin was added as food. Although the larvae fed, they did not survive beyond yolk absorption.

Eggs and larvae of *P. clathratus, P. maculatofasciatus,* and *P. nebulifer* were reared from eggs collected off San Diego with plankton nets during May through September 1978 and 1979. For each collection a 60-cm, 505-mm mesh plankton net was towed at the surface for 15-20 minutes. Plankton was placed in 14-liter buckets filled with seawater. The samples were brought to the laboratory, and the fish eggs were sorted from the plankton. *Paralabrax clathratus* and *P. nebulifer* larvae were reared from eggs measuring 0.94-0.97 mm in diameter in several mixed cultures from June 1978 through 1979. Since eggs of two

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[Manuscript received February 2, 1982.]

species were indistinguishable, developmental series were determined by working backwards from identified juveniles. On July 26, 1979, a large number of eggs measuring 0.82-0.86 mm were sorted from plankton collected off Mission Bay, California. This culture yielded only *P. maculatofasciatus* larvae and juveniles.

Larvae were reared to juveniles in a closed system on a diet of *Brachionus biplicata* and field-collected plankton. After about two weeks, the diet was gradually shifted to field-collected plankton supplemented with *Artemia* nauplii. Representative stages were photographed under anesthesia and preserved in 4 percent Formalin. A series of larvae was stained to study development of head spines. Additional material was obtained from the field collections of various institutions.

DEVELOPMENT

At 19°C, *P. clathratus* hatched at 36-40.5 hours after fertilization. Yolk-sac absorption was complete at 121.5 hours, or about 5 days. In larvae reared at 21°C from eggs collected in the plankton, notochord flexion began 11 days after hatching and was complete in some specimens on day 13. The earliest transformed juvenile was preserved 28 days after hatching.

Hatching time of *P. maculatofasciatus* is uncertain, since all eggs with the same diameter and size of oil globule regardless of stage of development made up the initial culture. All eggs hatched at 21.5°C within 24 hours after collection. Yolk-sac absorption was complete by day 4. Notochord flexion began on day 12 and was complete by day 19. The earliest transformed juvenile was preserved on day 28.

DESCRIPTION OF *PARALABRAX CLATHRATUS* AND *P. MACULATOFASCIATUS* EGGS

Eggs of both species are spherical in shape with clear, unsegmented yolk, a single large oil globule, and a clear, unsculptured chorion. Eggs of *P. clathratus* and *P. nebulifer* have a mean diameter of 0.95 mm, with a range from 0.94-0.97 mm (n=25). The mean diameter of the oil globule is 0.20 (n=25). Eggs of *P. maculatofasciatus* have a mean diameter of .84 with a range of 0.80-0.89 (n=11). The oil globule has a mean diameter of 0.17 with a range of 0.16-0.19 (n=11). Late-stage embryos of both species have similar pigmentation. At 24 hours, the embryo of *P. clathratus* is uniformly pigmented with small (0.1 mm) melanophores on the dorsal surface. Two to four melanophores are present on the oil globule, which lies midway between the head and tail of the embryo.

DESCRIPTION OF LARVAE AND JUVENILES

Paralabrax clathratus ***(Girard 1854) Kelp Bass*** (Figures 1-4)

Distinguishing characters. Preflexion larvae may be distinguished from *P. nebulifer* by the number of the postanal melanophores, and from *P. maculatofasciatus* preflexion larvae by the position of those melanophores. The large ventral melanophore is on the eighth or ninth postanal myomere in *P. clathratus*. In preflexion *P. maculatofasciatus* the large ventral melanophore is on the sixth or seventh postanal myomere. Preflexion *P. nebulifer* have more small postanal, midventral melanophores, 11-20 ($\bar{x}$ = 14.5), than *P. clathratus* 4-8 ($\bar{x}$ = 6.2), or *P. maculatofasciatus*, 6-11 ($\bar{x}$ = 8.0). The abdominal fin-fold pigment is heavier on *P. clathratus* than on the other two species. It forms a heavy broad triangle anterior to the anus. The postanal dorsal pigment patch is retained in *P. clathratus* until after 4.1 mm, but it is lost in *P. maculatofasciatus* by 3.4 mm. Larvae of *P. nebulifer* typically lack postanal dorsal pigment at all stages.

From early flexion (ca. 5.0 mm) through midflexion (ca. 5.9 mm), *P. clathratus* may be distinguished from the other two species by the large postanal pigment patch, the heavy preanal abdominal fin-fold pigment, and the lack of pigment on the lateral line. From late flexion through the end of the larval phase, *P. clathratus* may be distinguished by the presence of pigment on the upper jaw, the heavy pigment on the first dorsal fin, and the absence of pigment on the lateral line. Transformation to the juvenile stage takes place at about 11 mm. At this time vertical bars form on the body; they are quite different from the horizontal stripes of juvenile sand basses. Pigment anterior to each pectoral fin base forms a characteristic acute angle.

Description. Early yolk-sac larvae (Figure 1A) are fairly uniformly pigmented along the dorsal surface from the nape to the end of the tail. Pigment is also present over the oil globule. As the yolk is absorbed the dorsal pigment becomes concentrated into discrete patches. The first dorsal patches to become distinct are lateral to the midline and over the center of the yolk sac.

During the yolk-sac period, the dorsal pigment is concentrated into three areas: over the middle of the yolk sac, over the end of the gut, and midway between the anus and the end of the notochord (Figure 1B). Pigment is also present on the head anterior and dorsal to the unpigmented eyes. Pigment is present lateral to the gut in the region of the yolk sac and ventral to the gut posterior to the yolk sac, becoming heaviest near the anus. A ventral midline series of melanophores is

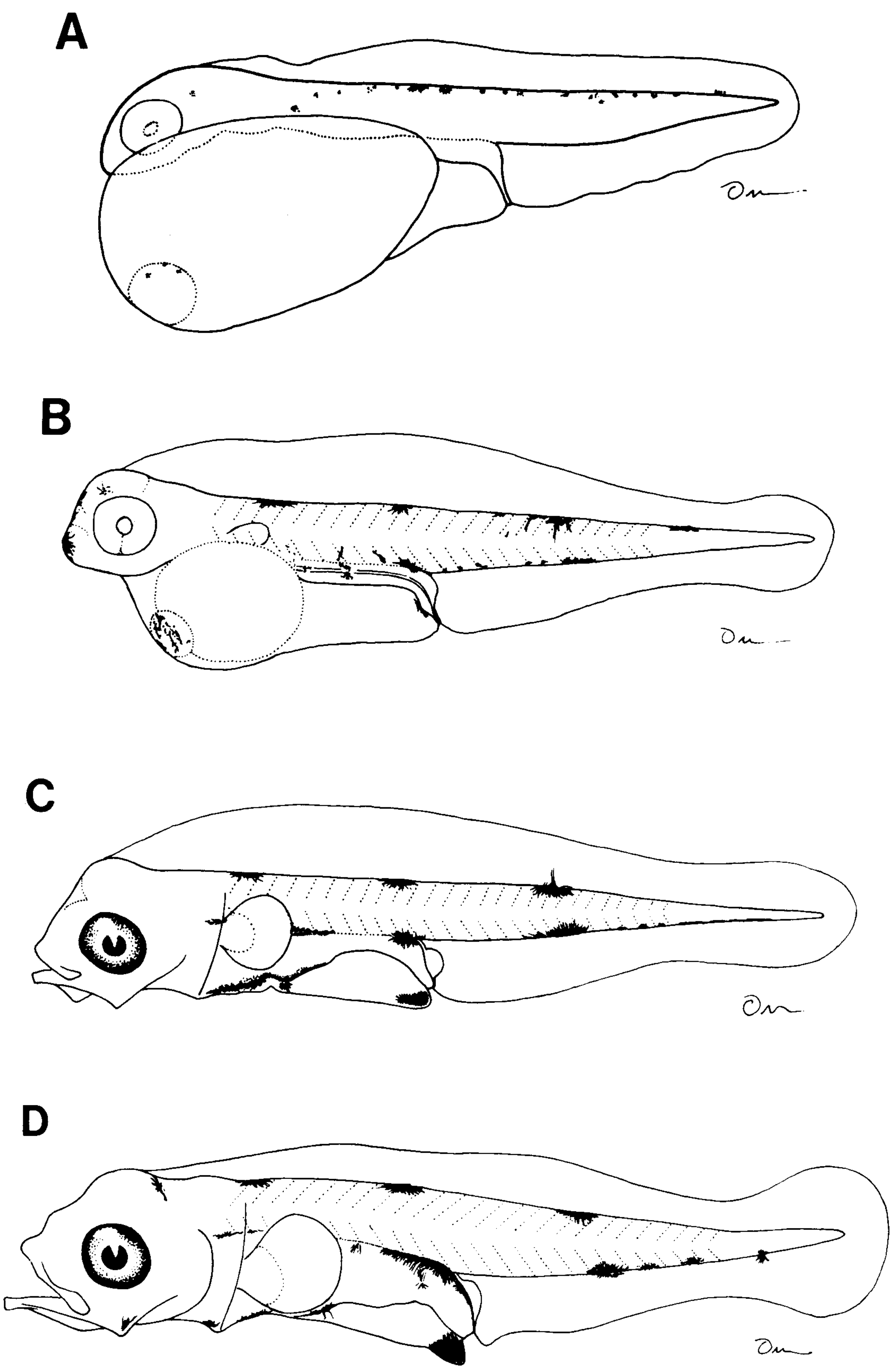

Figure 1. Larvae of *Paralabrax clathratus: A.* 2.2-mm yolk-sac larva, 1 day; *B.* 2.8-mm yolk-sac larva, 1 day; *C.* 3.0-mm preflexion larva, 4 days; *D.* 4.1-mm preflexion larva, 7 days.

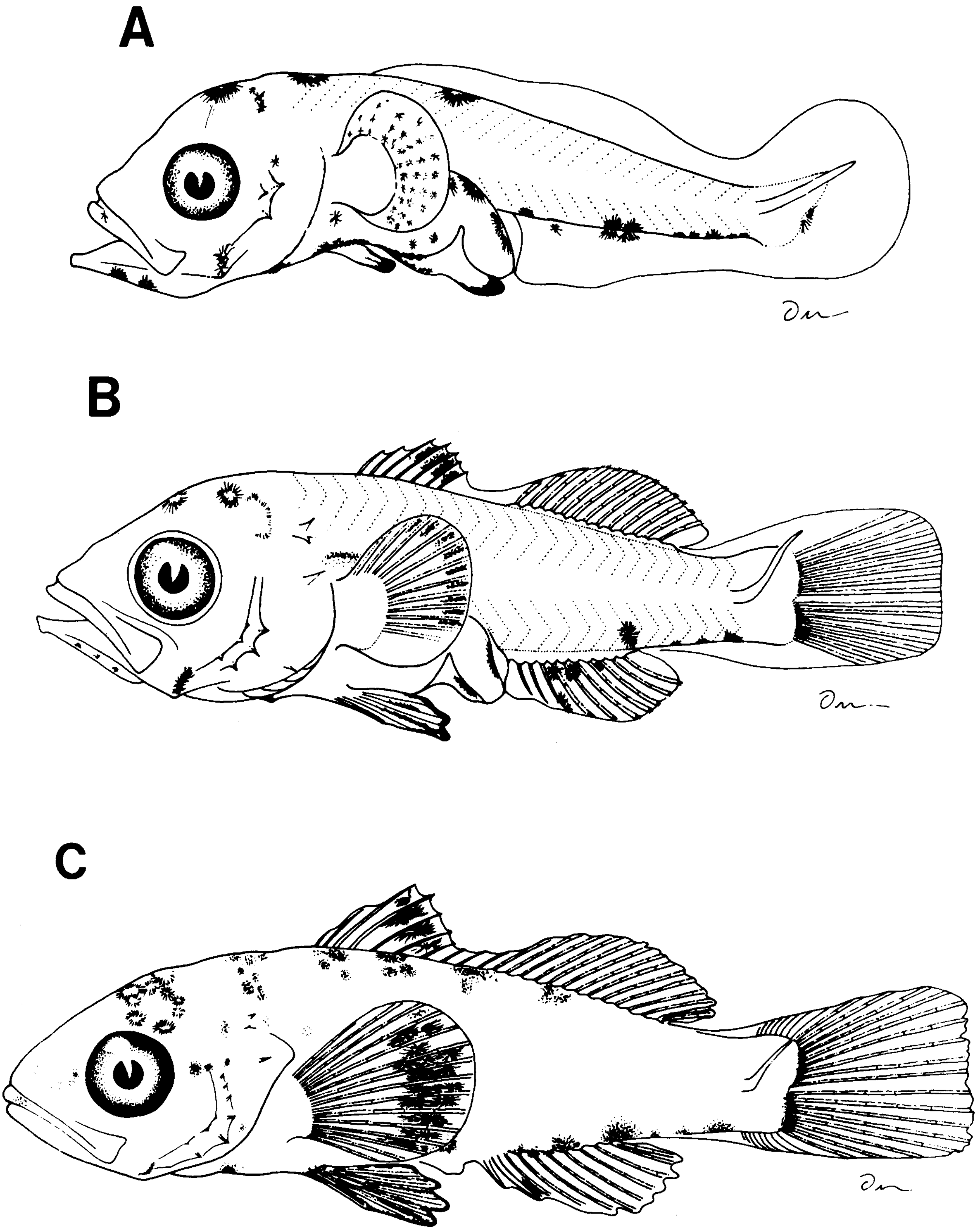

Figure 2. Larvae of *Paralabrax clathratus: A.* 5.1-mm flexion larva, 12 days; *B.* 7.4-mm postflexion larva, 25 days; *C.* 10.0-mm postflexion larva.

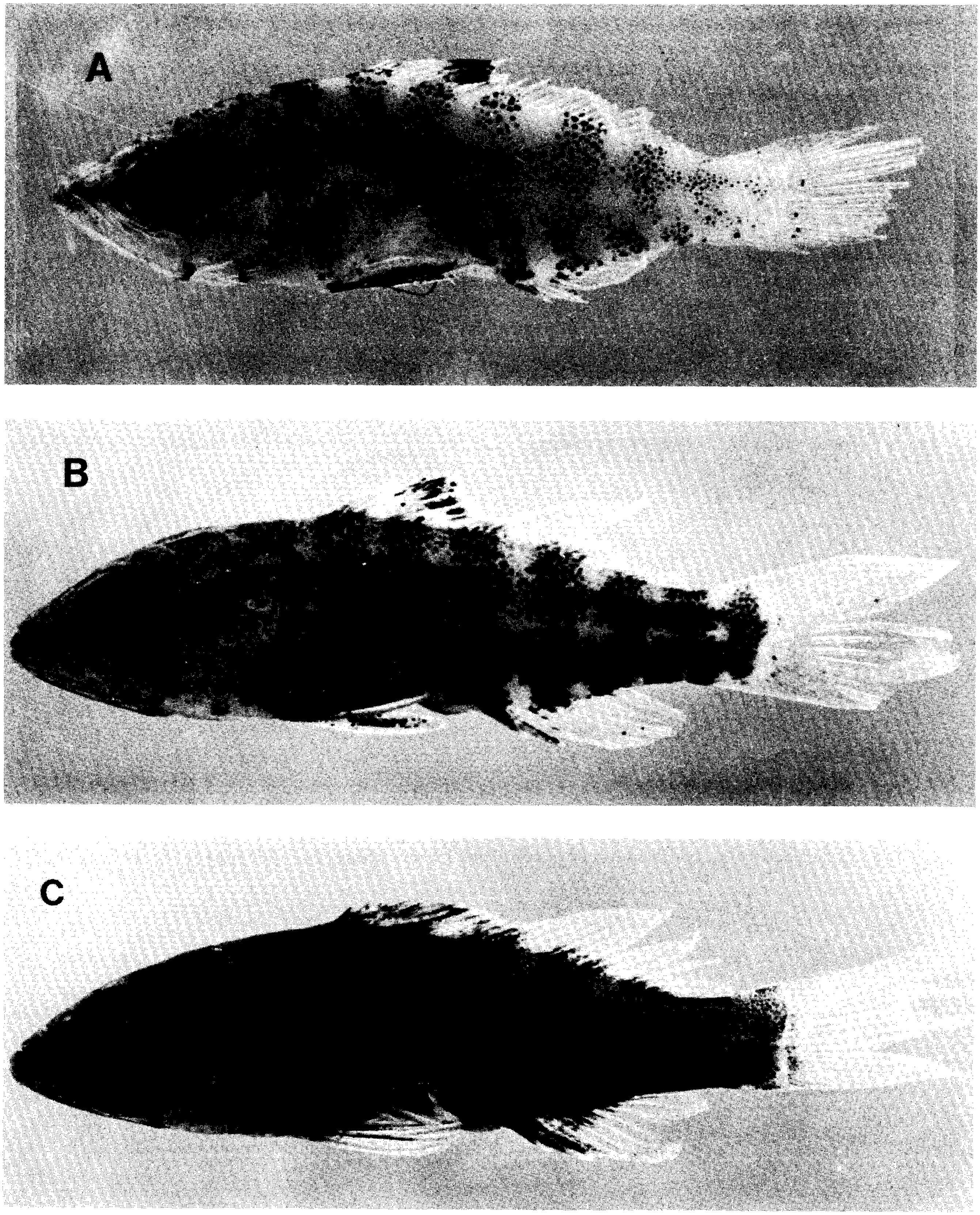

Figure 3. Developmental stages of *Paralabrax clathratus: A.* 11.1-mm transforming specimen, SIO 75-468; *B.* 11.2-mm transforming specimen, SIO 75-468; *C.* 16.6-mm newly transformed juvenile, SIO 75-468.

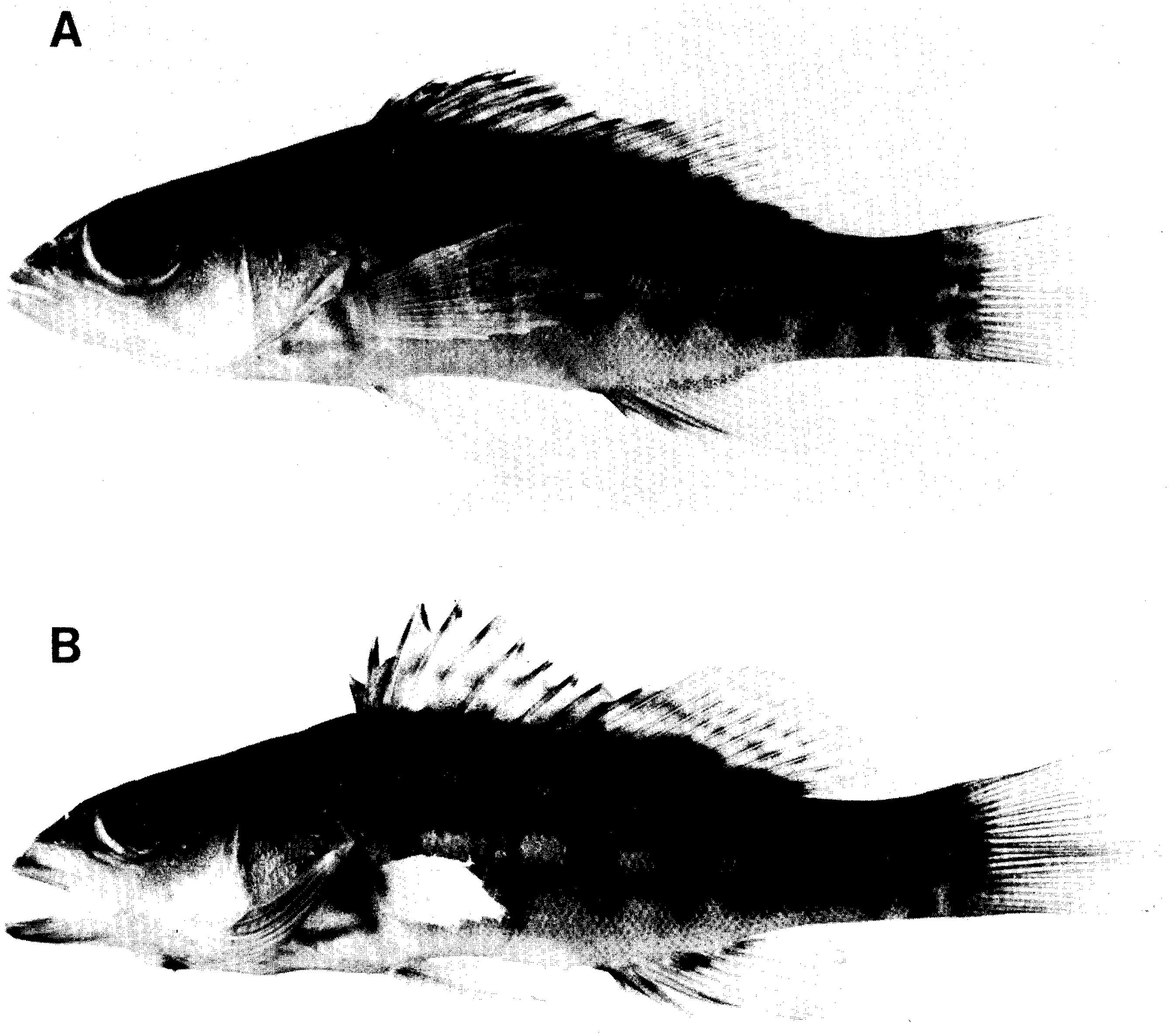

Figure 4. Juveniles of *Paralabrax clathratus: A.* 36.3-mm juvenile, SIO 73-345, Mission Bay, San Diego; *B.* 46-mm juvenile, SIO 73-345, Mission Bay, San Diego.

present from the end of the gut midway to the end of the tail, with heaviest concentration over the anus and midway to the end of the tail. The eyes become pigmented as the yolk is completely absorbed. Pigment on the snout and on the head is lost at this time. Dorsal pigment is concentrated into three large melanophores: midway between the snout and the anus, over the anus, and midway from the anus to the end of the notochord (Figure 1C). Pigment is present dorsal to the gut below the second dorsal midline melanophore at the point where the gut is deflected ventrally from the body. Pigment is present ventral to the gut from the junction of the cleithra posteriorly to the midpoint of the gut. A large, triangularly shaped pigment patch is present in the abdominal fin fold just anterior to the anus. A large ventral melanophore is present midway from the anus to the end of the tail, and a series of small melanophores continues posteriad almost to the end of the notochord.

This basic pigmentation pattern changes only slightly from yolk absorption at about 3.0 mm to just prior to caudal flexion (Figure 1D). Between 4.2 mm and 4.6 mm, the posteriormost dorsal pigment patch is lost. During this time pigment forms on the dorsal surface of the head and on the isthmus.

During notochord flexion (5.0-6.2 mm), the anal and pelvic fins form, and the abdominal fin fold is partially resorbed. Pigment forms on the pectoral fins and on the upper jaw (Figure 2A). The posteriormost ventral tail pigment becomes associated with the hypurals and, by the end of caudal flexion, forms a line at the posterior end of the hypural bones (Figure 2B). The large ventral tail spot lies at the posterior end of the forming anal fin (Figure 2B). Some of this pigment becomes internal when the fin is completely formed. The more anterior ventral pigment migrates onto the base of the anal fin. The dorsal midline melanophore located above the gut migrates onto the spinous dorsal fin, which forms at the end of flexion. The anterior dorsal midline melanophore either migrates to the head or is lost. It is absent in larvae larger than 6.9 mm. The characteristic triangular patch of pigment on the preanal abdominal fin fold becomes located on the ventral surface of the gut as the fin fold is resorbed (Figure 2B). The pelvic fins become heavily pigmented, particularly at their posterior margins. Pigment is absent over the lateral body surface.

Changes in postflexion larvae from about 7.4 mm to 10 or 11 mm are gradual. The most important pigment change is the addition of pigment on the snout and on the operculum behind the eye to form a prominent horizontal eye bar (Figure 2C). Reared larvae are heavily pigmented on the membranes of the spinous dorsal, pectoral, and pelvic fins, whereas pigmentation on field specimens is usually lighter in these areas. Postanal pigment coalesces along anterior rays, and dorsal pigment coalesces in discrete patches. In some field-collected larvae the vertical barring of the juveniles is faintly visible (Figure 2C).

The development of this striking pattern of vertical pigment bars is shown in the series of transforming individuals (Figure 3). A broad bar extends ventrad from the nape; three bars underlie the spinous dorsal fin; two extend between the soft dorsal fin and anal fin; one is at the caudal peduncle; and one overlies the hypural region. These are partially interrupted by two horizontal stripes: one is a continuation of the stripe through the eye and extends posteriad to the caudal fin base, and the other runs between the pectoral fin base and the caudal base. In larger juveniles the bars and stripes become obscured by the more prominent pattern of large, pale blotches (Figure 4). Juveniles of this stage have a characteristic angulate pigment blotch anterior to the pectoral fin.

The development of prominent vertical barring in early juveniles (Figure 4) may be rapid and associated with environmental stimuli. The juveniles are found under floating kelp where the disruptive coloration of the vertical bars would be cryptic. This type of coloration is also found in carangids and stromateoids that also associate with floating objects.

Kendall (1979) described the general morphology of *Paralabrax* larvae and made comparisons with other serranid genera. His material was not identified as to species, but his illustrations were of *P. clathratus*. We found the larvae of *P. clathratus* to be morphologically similar to the other two species studied (Tables 1 and 2). Ontogenetic trends of increasing snout-anus distance, head length, and body depth, relative to standard length, occur in all three species. Relative eye size decreases during the larval period in all three species and then increases in the juveniles. In *P. clathratus* and *P. nebulifer*, relative snout length reaches a maximum at notochord flexion and declines during later stages, whereas in *P. maculatofasciatus* the maximum is in postflexion larvae (Table 2). Relative snout length is greater in *P. clathratus* than in the other two species during all stages of development, and older larvae and early juveniles of *P. clathratus* have a more pointed snout than the other two species (Table 2).

Kendall (1979) described the complement of head spines for *Paralabrax* larvae (presumably *P. clathratus*), but did not give the sequence of development. The first spines to appear in *P. clathratus* are on the preopercle. At 4.7 mm a single preopercular spine is present in association with a single spine anterior to it on the preopercular ridge. Spines are added dorsally and ventrally to the initial spines to form anterior and posterior preopercular series. A maximum of three spines develops in the anterior series in postflexion larvae. These spines become obsolete at the end of the larval period and are absent in specimens larger than 11.0 mm. The posterior series contains a maximum of 6 spines at the end of the larval period and 7 in transition specimens. Spines continue to accrue on the upper region of the preopercular series in early juveniles, while the spines on the lower portion of the series are lost. Our largest stained specimen had 18 comb-like preopercular spines.

Upper and lower posttemporal spines appear first in a 5.9-mm specimen. The upper spine remains prominent throughout the larval period and is present in juveniles. The lower posttemporal spine disappears during the transitional stage after 10 mm SL.

The spine on the interopercle appears first in a 5.9-mm larva, remains throughout the larval and transitional stages, but is absent in most early juveniles. A subopercular spine was present on one 6.5-mm larva and two transitional specimens but was

TABLE 1
Measurements (mm) of *Paralabrax clathratus*

Age (days)	Body length	Snout to anus	Head length	Snout length	Eye	Body depth at P_2	Caudal peduncle depth	Caudal peduncle length
1	2.2	1.4						
1	2.7	1.4						
4	3.0	1.5	0.6	0.16	0.22	0.4		
2	3.1	1.6	—	—	—	—		
5	3.2	1.7	0.8	0.20	0.28	0.5		
5	3.4	1.8	0.7	0.16	0.30	0.5		
5	3.8	2.0	0.9	0.22	0.28	0.6		
5	3.8	2.1	1.0	0.24	0.28	0.6		
5	4.1	2.2	1.0	0.28	0.32	0.6		
7	4.1	2.2	1.0	0.28	0.32	0.6		
11	4.6	2.4	1.3	0.36	0.40	0.9		
12	5.0	2.8	1.6	0.5	0.5	1.2		
19	5.5	2.9	1.7	0.5	0.4	1.2		
25	5.9	3.3	2.1	0.6	0.6	1.6		
13	6.2	3.8	2.2	0.6	0.6	2.0		
25	6.8	3.9	2.5	0.7	0.7	1.8	0.6	1.2
25	7.3	4.4	2.7	0.7	0.7	2.2	0.8	1.2
—	8.3	5.0	3.0	1.0	0.9	2.4	1.1	1.4
—	8.9	5.2	3.1	0.7	0.8	2.7	1.2	1.4
—	9.2	5.2	3.2	0.8	0.8	2.7	1.2	1.5
—	9.8	5.7	3.6	1.1	1.0	2.8	1.3	1.5
28	10.0	5.8	3.6	0.9	1.0	3.1	1.4	1.7
—	10.3	6.3	4.1	1.1	1.0	3.1	1.3	1.7
—	10.5	6.4	4.1	1.1	1.2	3.0	1.3	1.8
—	10.7	6.4	4.2	1.1	1.2	3.0	1.4	1.8
—	11.3	6.7	4.6	1.2	1.2	3.2	1.5	1.8
—	12.0	7.2	4.7	1.2	1.2	3.6	1.5	1.9
—	12.3	7.5	4.8	1.3	1.2	3.8	1.5	1.9
—	13.0	7.8	5.2	1.7	1.3	3.7	1.7	2.2
—	13.5	8.3	5.2	1.3	1.3	3.7	1.6	2.1
—	14.0	8.8	5.7	1.7	1.3	4.5	1.8	2.2
—	14.2	8.7	5.8	1.5	1.5	4.0	1.8	2.2
—	15.6	9.3	6.2	1.7	1.3	4.6	2.1	2.5
—	15.8	9.3	5.8	1.3	1.7	4.7	2.0	2.6
—	18.2	11.0	6.4	1.5	1.7	5.5	2.6	2.9
—	21.0	12.8	8.0	1.7	2.0	6.4	3.0	3.1
—	23.0	14.0	8.5	2.3	2.2	6.8	3.2	3.5

Specimens between dashed lines are undergoing notochord flexion.

absent on all other specimens examined. The upper opercular spine appears at 6.5 mm and persists throughout development. The lower opercular spine is the last of the head spines to develop and is first evident on a 13.5-mm juvenile.

Development of head spines does not differ significantly among the three species studied. Each type of spine appears at about the same size in the three species, persists to a comparable stage of ontogenesis, and therefore is not helpful in species identification.

Paralabrax nebulifer *(Girard 1854) Barred Sand Bass* (Figures 5-7)

Distinguishing characters. Yolk-sac larvae of *P. nebulifer* were not distinguishable from *P. clathratus* or *P. maculatofasciatus*. Preflexion larvae may be distinguished from those of *P. clathratus* and *P. maculatofasciatus* by the large number, (11-20)$\bar{x}$ = 14.5, of small ventral melanophores on the tail. The second dorsal midline melanophore is more anterior than in the other two species. In addition, most preflexion *P. nebulifer* larvae lack the posteriormost dorsal midline melanophore and have pigment on the horizontal septum. Flexion larvae of *P. nebulifer* may be distinguished from *P. clathratus* by the pigment along the horizontal septum; however, *P. nebulifer* appears to be indistinguishable from *P. maculatofasciatus* at this stage. In postflexion larvae of *P. nebulifer* (ca. 8.8 mm), pigment forms in a broad saddle under the first dorsal fin, rather than in several discrete saddles as found in *P. clathratus*. Similar sized *P. maculatofasciatus* are more heavily pigmented. Early juveniles (ca. 12-16 mm) of *P. nebulifer* are more uniformly pigmented with less pronounced vertical barring than

TABLE 2
Body Proportions of Larvae and Early Juveniles of California *Paralabrax* species

Body proportion*	*Paralabrax clathratus*	*Paralabrax nebulifer*	*Paralabrax maculatofasciatus*
Snout to anus/body length			
Preflexion	529 ± 15 (500-553)	512 ± 12 (500-529)	520 ± 35 (484-556)
Flexion	564 ± 36 (527-613)	577 ± 21 (551-604)	553 ± 35 (521-621)
Postflexion	594 ± 16 (574-621)	582 ± 18 (565-608)	611 ± 18 (597-646)
Juvenile	606 ± 10 (589-628)	607 ± 10 (598-618)	626 ± 14 (607-650)
Head length/body length			
Preflexion	240 ± 27 (200-283)	255 ± 11 (235-270)	224 ± 8 (214-235)
Flexion	335 ± 24 (309-356)	336 ± 23 (306-368)	299 ± 28 (261-345)
Postflexion	375 ± 21 (360-408)	369 ± 18 (353-392)	354 ± 9 (342-364)
Juvenile	386 ± 18 (352-408)	376 ± 7 (369-385)	373 ± 17 (338-389)
Snout length/head length			
Preflexion	258 ± 20 (240-280)	248 ± 45 (150-308)	233 ± 26 (200-267)
Flexion	291 ± 16 (273-312)	264 ± 26 (222-286)	242 ± 24 (200-267)
Postflexion	265 ± 29 (222-306)	241 ± 22 (214-267)	250 ± 16 (226-273)
Juvenile	261 ± 32 (212-327)	221 ± 21 (200-244)	224 ± 32 (190-262)
Eye diameter/head length			
Preflexion	335 ± 46 (280-428)	295 ± 38 (250-356)	337 ± 16 (311-350)
Flexion	276 ± 32 (235-312)	295 ± 25 (267-333)	276 ± 20 (240-300)
Postflexion	273 ± 19 (250-306)	267 ± 18 (242-286)	282 ± 15 (273-303)
Juvenile	251 ± 20 (210-293)	280 ± 17 (255-293)	298 ± 21 (273-341)
Body depth at pectoral fin base/body length			
Preflexion	155 ± 18 (133-196)	184 ± 20 (159-223)	173 ± 25 (143-200)
Flexion	263 ± 45 (218-323)	260 ± 32 (204-265)	227 ± 36 (186-293)
Postflexion	289 ± 12 (265-310)	288 ± 15 (271-307)	288 ± 16 (273-314)
Juvenile	296 ± 13 (273-321)	297 ± 5 (294-304)	304 ± 12 (290-323)
Caudal peduncle depth/body depth			
Preflexion	—	—	—
Flexion	—	—	—
Postflexion	126 ± 13 (88-140)	129 ± 6 (122-136)	128 ± 15 (107-146)
Juvenile	130 ± 8 (122-143)	140 ± 5 (134-145)	153 ± 5 (148-162)
Caudal peduncle length/body length			
Preflexion	—	—	—
Flexion	—	—	—
Postflexion	166 ± 7 (159-176)	146 ± 14 (136-168)	160 ± 10 (146-177)
Juvenile	157 ± 6 (148-165)	149 ± 10 (134-156)	145 ± 7 (136-157)

*Values given for each body proportion expressed as thousandths of body length or head length: mean, standard deviation, and range.

P. clathratus. They have horizontal stripes that are less dense than those of *P. maculatofasciatus*. Large juveniles have a conspicuous diagonal pigment bar below the eye, and two short diagonal bars anterior to the pectoral fin base.

Description. Morphometrics of *P. nebulifer* are presented in Tables 2 and 3. Preflexion larvae are similar to the other two species, but differ in the sequence and detail of pigmentation. The posterior dorsal melanophore is lost at 3.4 mm, in contrast to its loss at 4.6 mm in *P. clathratus* (Figure 5A). The marginal pigment of the abdominal fin fold is comparatively heavier than in the other two species and usually appears as a continuous line. The postanal ventral midline pigment is a continuous series of uniform melanophores from the end of the gut to near the end of the notochord. Pigment appears in the horizontal septum above the anus (Figure 5B) by 3.6 mm.

During notochord flexion additional pigment appears along the horizontal septum above the gut, along the sides of the gut, and on the body below the dorsal fin (Figure 5C). Similar pigment appears in flexion larvae of *P. maculatofasciatus*. Although subtle differences in pigmentation exist between reared specimens of *P. nebulifer* and *P. maculatofasciatus*, identification of field-collected larvae undergoing notochord flexion may not be possible.

Postflexion larvae between 6 and 11 mm add pigment on the head, and on the snout and operculum to form a line of pigment across the eye (Figure 5E). Pigment also appears on the cranium and below the base of the spinous dorsal fin. Late-stage larvae lack the incipient body bars present as dorsal pigment saddles in *P. clathratus* and are generally lighter in pigmentation than late-stage *P. maculatofasciatus* larvae.

Metamorphosis occurs at about 11 mm. The juveniles become heavily and more uniformly pigmented than *P. clathratus* (Figure 6). A dark stripe extends from the snout through the eye and along the lateral line to the base of the caudal fin. A second stripe runs from the base of the pectoral fin to the caudal fin base. The stripes are interrupted by six faint

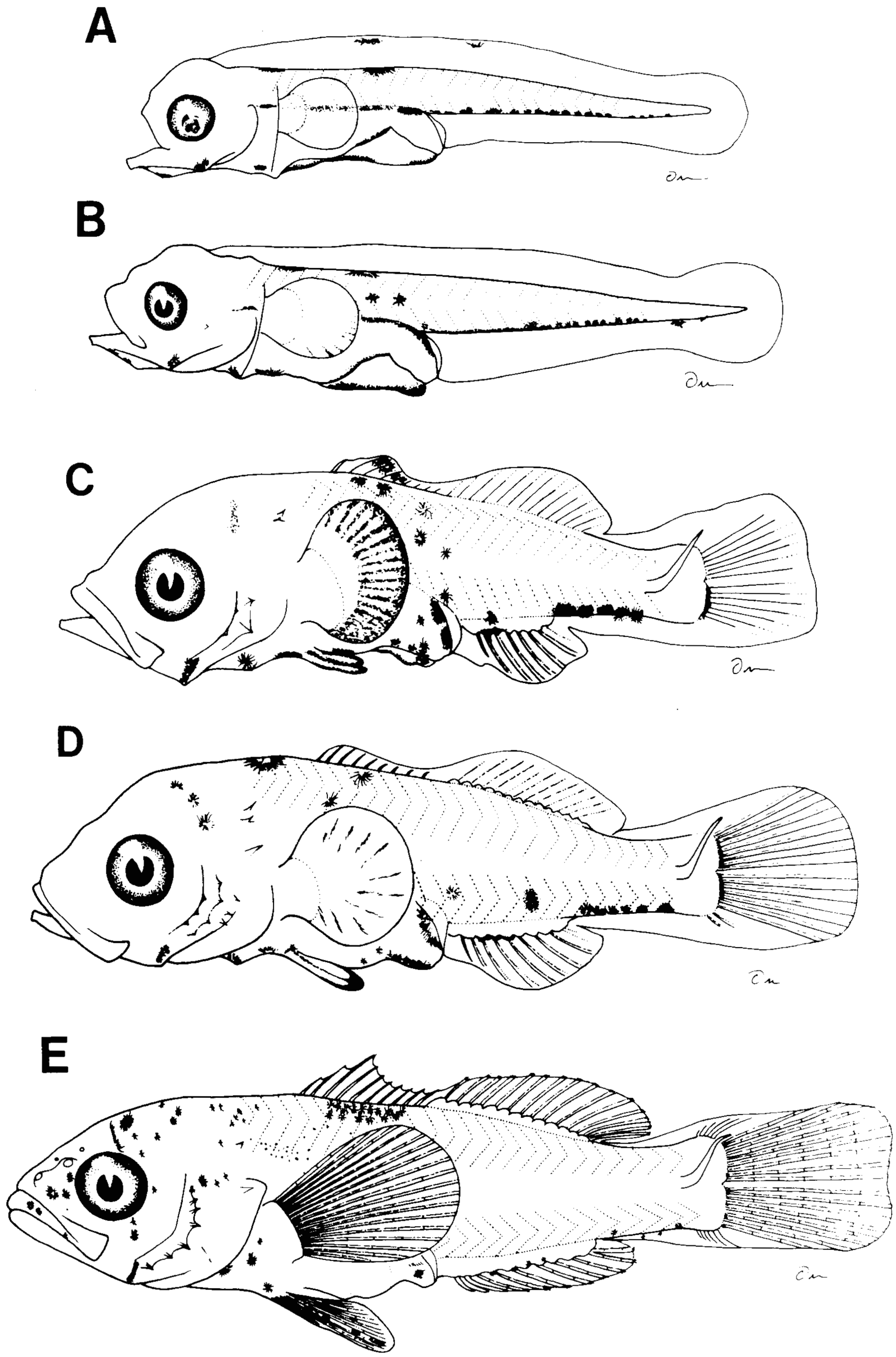

Figure 5. Larvae of *Paralabrax nebulifer: A.* 3.4-mm preflexion larva, 11 days; *B.* 4.4-mm preflexion larva, 10 days; *C.* 5.7-mm flexion larva, 29 days; *D.* 6.8-mm postflexion larva, 22 days; *E.* 9.4-mm postflexion larva.

TABLE 3
Measurements (mm) of Barred Sand Bass, *Paralabrax nebulifer*

Age (days)	Body length	Snout to anus	Head length	Snout length	Eye	Body depth at P_2	Caudal peduncle depth	Caudal peduncle length
11	3.4	1.8	0.8	0.12	0.28	0.76		
14	3.6	1.8	0.9	0.2	0.32	0.64		
11	3.6	1.8	0.9	0.2	0.28	0.64		
14	4.0	2.0	1.0	0.28	0.28	0.68		
14	4.2	2.1	1.1	0.28	0.28	0.72		
—	4.2	2.2	1.1	0.3	0.3	0.8		
10	4.4	2.3	1.1	0.3	0.3	0.72		
16	4.5	2.3	1.2	0.3	0.3	0.8		
17	4.8	2.5	1.3	0.4	0.4	1.0		
22	4.9	2.7	1.5	0.4	0.4	1.0		
25	5.5	3.1	1.8	0.4	0.6	1.5		
29	5.7	3.4	2.1	0.6	0.6	1.6		
22	6.8	4.1	2.3	0.6	0.7	1.8		
—	8.5	4.8	3.0	0.8	0.8	2.5	1.1	1.2
—	8.8	5.1	3.3	0.8	0.9	2.7	1.2	1.2
—	9.2	5.3	3.3	0.8	0.8	2.6	1.2	1.3
—	10.7	6.8	4.2	0.9	1.2	2.9	1.3	1.8
—	11.7	7.0	4.5	1.1	1.3	3.5	1.7	1.8
28	12.5	7.5	4.7	1.1	1.2	3.8	1.8	1.9
—	15.7	9.7	5.8	1.2	1.7	4.6	2.1	2.1
35	16.0	9.8	6.0	1.2	1.7	4.7	2.2	2.5

Specimens between dashed lines are undergoing notochord flexion.

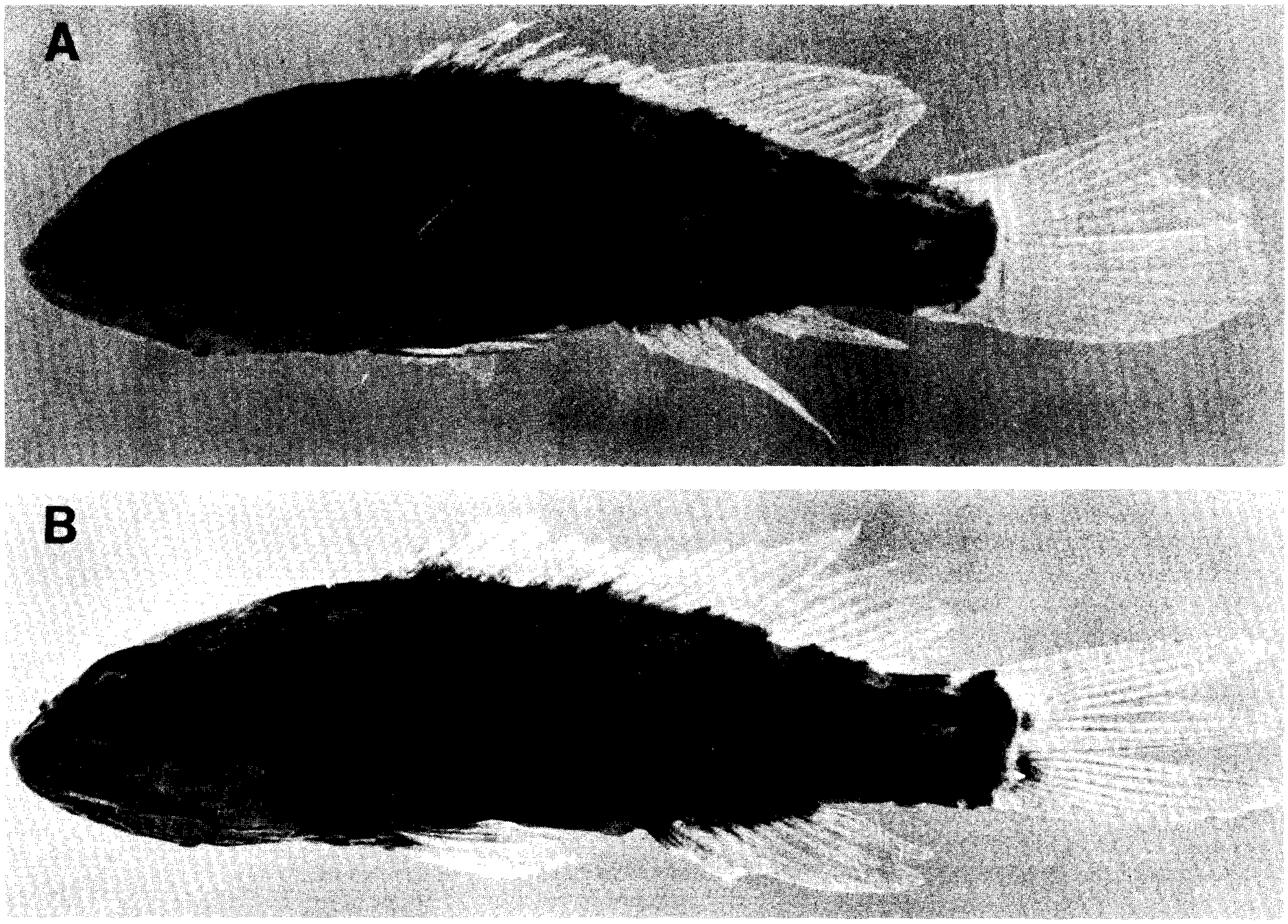

Figure 6. Juveniles of *Paralabrax nebulifer: A.* 10.8-mm newly transformed juvenile; *B.* 13.3-mm juvenile, 28 days.

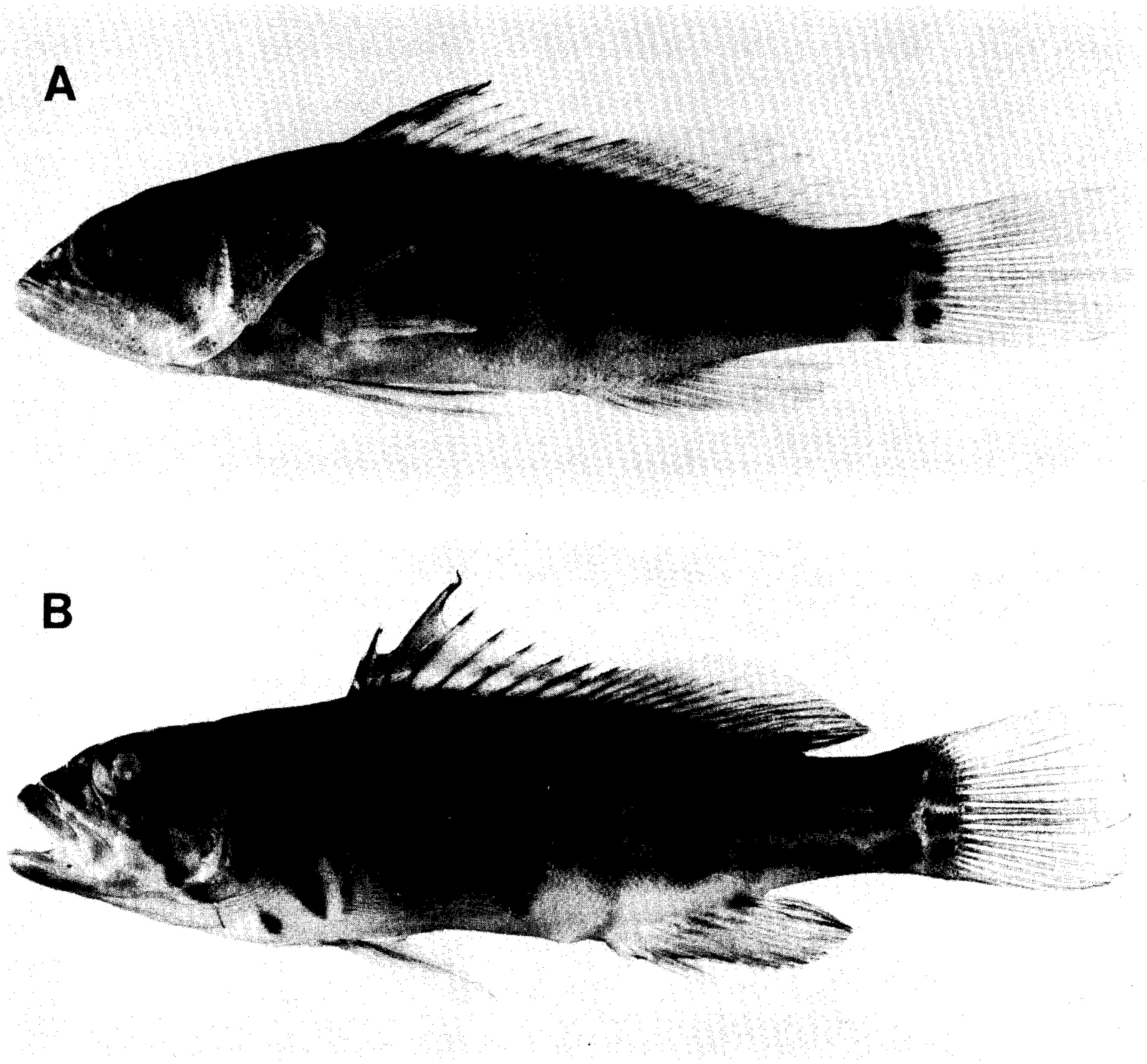

Figure 7. Juveniles of *Paralabrax nebulifer*: *A*. 33-mm juvenile, SIO 73-345, Mission Bay, San Diego; *B*. 45-mm juvenile, 99 days.

vertical bars: two beneath the spinous dorsal fin, two between the soft dorsal and anal fins, one on the caudal peduncle, and one over the hypural region. The bars extend onto the bases of the dorsal and anal fins (Figure 7). In larger juveniles the axial stripe and the upper portions of the bars blend with the uniformly heavy dorsal pigmentation; however, the bars are readily distinguishable ventrally (Figure 7). Juveniles at this stage have a prominent diagonal bar below the eye and two short diagonal bars anterior to the pectoral fin base (Figure 7).

Paralabrax maculatofasciatus *(Steindachner 1868)* *Spotted Sand Bass* (Figures 8-10)

Distinguishing characters. Preflexion larvae of *P. maculatofasciatus* may be distinguished from those of *P. clathratus* by the shape of the melanistic blotch on the preanal abdominal fin fold and by the absence of a third dorsal midline melanophore in larvae larger than 3.0 mm. Melanistic pigment is almost continuous along the ventral margin of the abdominal fin fold and does not form a triangular patch. Preflexion larvae of *P. maculatofasciatus* may be distinguished from those

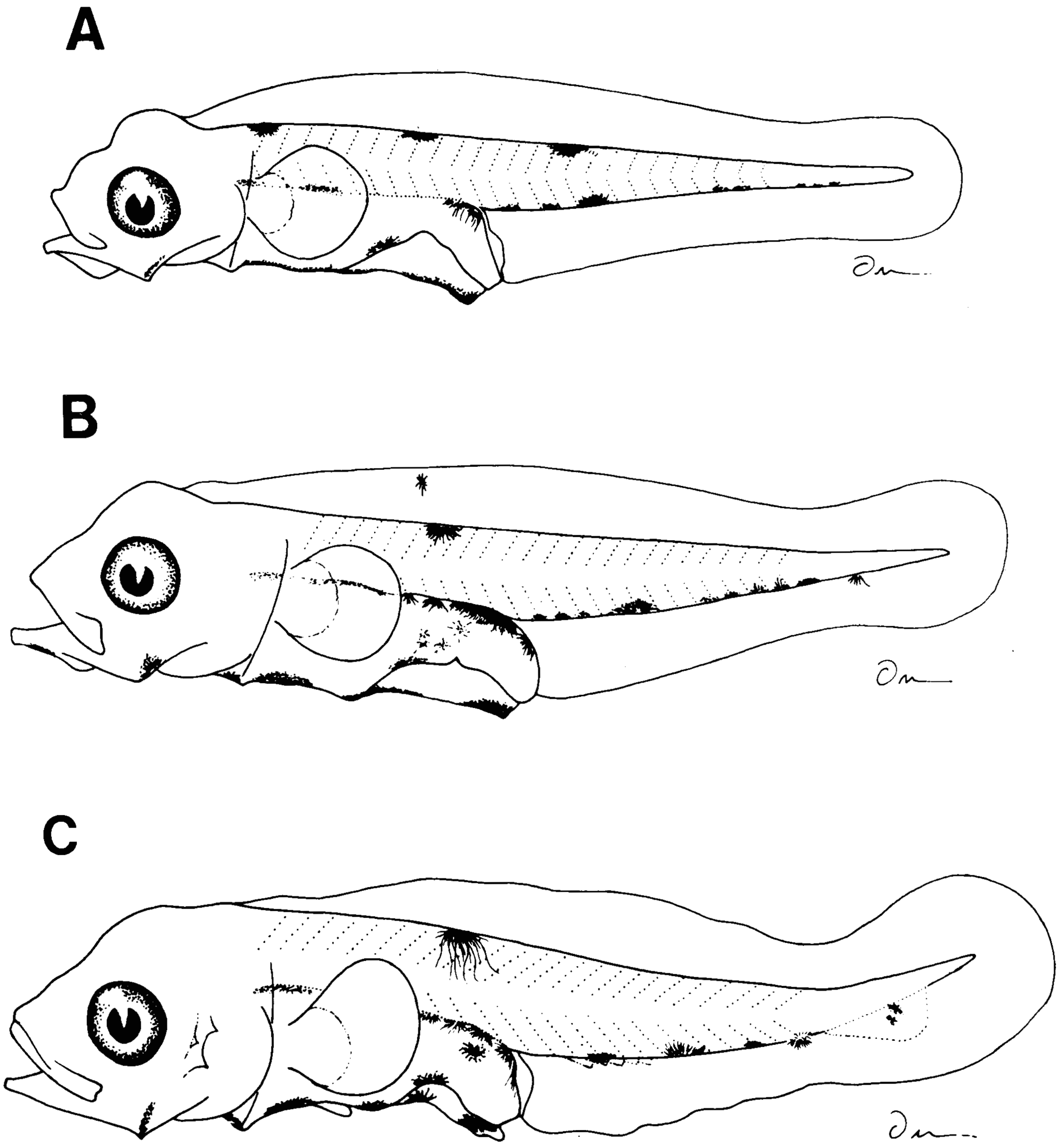

Figure 8. Larvae of *Paralabrax maculatofasciatus: A.* 3.1-mm preflexion larva, 5 days; *B.* 3.6-mm preflexion larva, 8 days; *C.* 4.5-mm preflexion larva, 12 days.

of *P. nebulifer* by the absence of horizontal septal melanophores and by their discontinuous and nonuniform ventral tail pigment.

Flexion larvae of *P. maculatofasciatus* can be distinguished from those of *P. clathratus* by the presence of melanophores along the horizontal septum and on the trunk. Flexion larvae of the two species of sand basses appear to be indistinguishable.

Late postflexion larvae of *P. maculatofasciatus* are distinguished from both *P. clathratus* and *P. nebulifer*

TABLE 4
Measurements (mm) of Spotted Sand Bass, *Paralabrax maculatofasciatus*

Age (days)	Body length	Snout to anus	Head length	Snout length	Eye	Body depth at P_2	Caudal peduncle depth	Caudal peduncle length
2	2.2							
4	2.8	1.4	0.6	0.16	0.20	0.40		
5	3.1	1.5	0.7	0.16	0.24	0.48		
8	3.4	1.9	0.8	0.16	0.28	0.68		
8	3.6	2.0	0.8	0.20	0.28	0.7		
9	4.0	2.0	0.9	0.20	0.28	0.7		
13	4.3	2.3	1.2	0.24	0.32	0.8		
12	4.5	2.4	1.3	0.32	0.36	0.9		
13	4.6	2.5	1.2	0.32	0.36	1.0		
14	4.8	2.5	1.4	0.32	0.4	1.0		
13	5.0	2.7	1.5	0.4	0.4	1.2		
23	5.2	3.0	1.7	0.4	0.5	1.3		
23	5.8	3.6	2.0	0.5	0.6	1.7		
19	6.2	3.7	2.2	0.6	0.6	1.7	0.7	1.1
26	7.5	4.6	2.7	0.7	0.7	2.1	0.8	1.2
21	7.7	4.6	2.8	0.7	0.8	2.1	1.0	1.2
23	8.2	5.0	2.8	0.7	0.8	2.4	1.1	1.3
23	8.6	5.2	3.1	0.7	0.9	2.7	1.2	1.4
25	9.6	6.2	3.3	0.8	1.0	2.8	1.4	1.4
33	10.3	6.7	4.0	0.8	1.2	3.1	1.6	1.4
33	10.8	6.7	4.2	1.1	1.2	3.2	1.6	1.7
28	11.8	7.5	4.4	0.9	1.2	3.6	1.8	1.7
35	13.0	8.2	4.4	1.2	1.5	4.2	2.1	1.9
40	14.5	9.0	5.5	1.2	1.6	4.2	2.2	2.0
38	16.8	10.2	6.3	1.2	1.9	5.0	2.5	2.5
35	18.0	11.2	6.7	1.5	2.0	5.7	2.7	2.6

Specimens between dashed lines are undergoing notochord flexion.

by the heavy pigment over the trunk. Juvenile *P. maculatofasciatus* develop a strongly contrasting stripe that extends from the snout through the eye to the caudal peduncle.

Description. Morphometrics of *P. maculatofasciatus* are given in Tables 2 and 4. Early preflexion larvae of *P. maculatofasciatus* are similar to those of *P. clathratus* in having three dorsal contour melanophores and several rather large melanophores along the ventral midline of the tail (Figure 8A). The line of pigment is almost continuous along the ventral margin of the abdominal fin fold. At about 3.6 mm, the posteriormost dorsal midline melanophore is lost. In some specimens the anteriormost dorsal melanophore is also lost (Figure 8B). After this, no significant pigment changes take place until notochord flexion.

During notochord flexion, lateral pigment is added over the gut, along the horizontal septum, and below the developing dorsal fin (Figure 9A). Following notochord flexion, pigment is augmented over the anterior portion of the trunk, and a conspicuous line of pigment develops on the head from the snout through the eye onto the operculum (Figure 9B and C). At about 11 mm, the conspicuous dark line extends from the snout to the caudal peduncle. A second horizontal stripe broken by unpigmented areas forms along the dorsum from the nape to the second dorsal fin during transformation (Figure 10A). At this stage, a third stripe begins to form from the base of the pectoral fin to the lower base of the caudal fin. The juvenile pigment is characterized by the three prominent stripes, with a background of six vertical bars similar in position to those on *P. nebulifer*. In larger juveniles the bars become larger and more conspicuous and begin to mask the stripes (Figure 10C). Pigment areas begin to break up into spots, a feature that characterizes the adults (Figure 10C). The cheek and lower opercular region are covered with large spots, and the pigment pattern forward of the pectoral fin consists of three distinct spots arranged in a triangle.

DISCUSSION

We have used laboratory-reared larvae as the basis for these descriptions. Pigment in laboratory-reared specimens is often more heavily expressed and certainly better preserved than in field-collected specimens. Considerable variability in pigmentation was observed in the laboratory series. Because of abrasion in the net and differences in preservation, field-collected specimens often lack important characters. In particular, fin folds are seldom present on net-collected larvae. Therefore, some field-collected

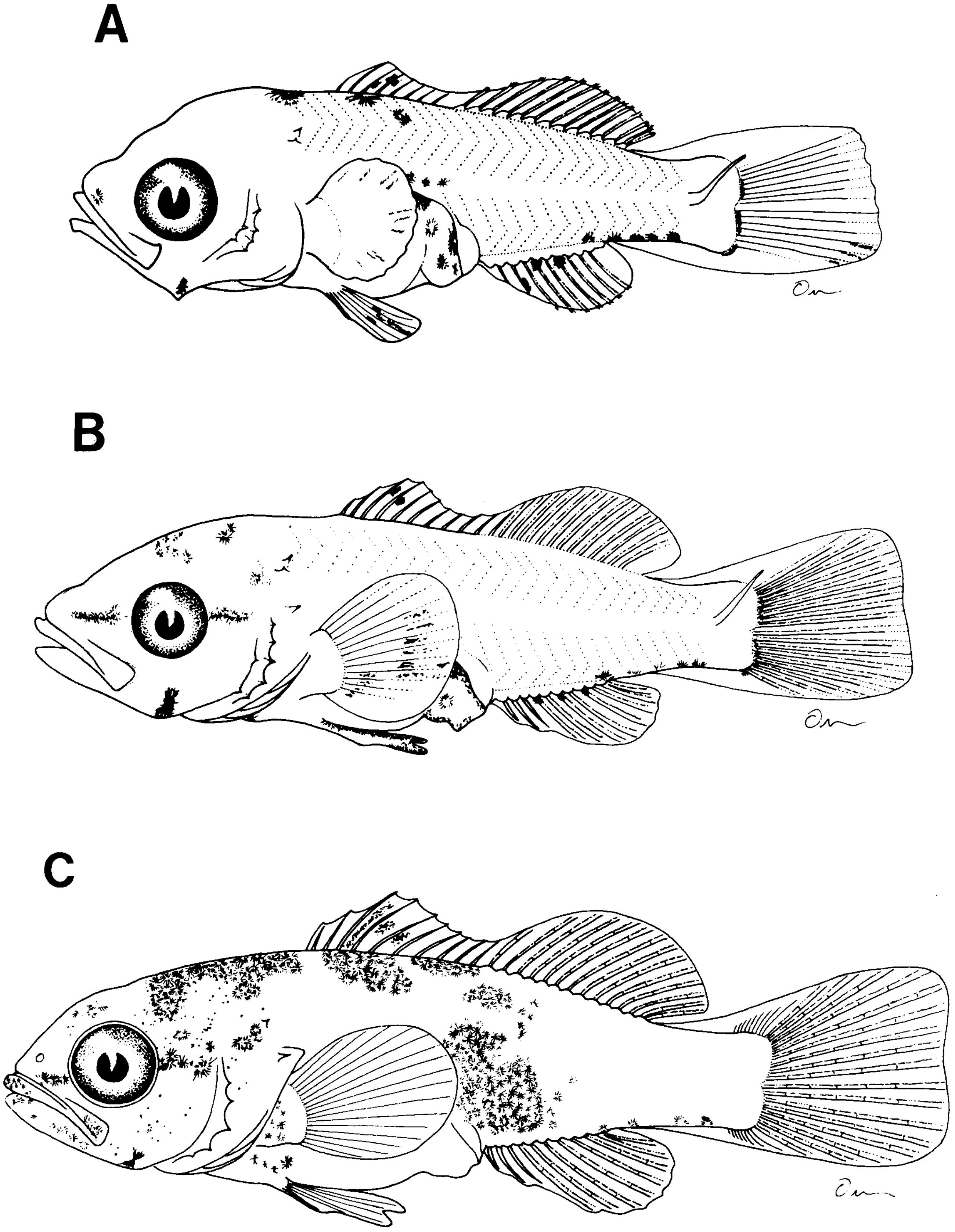

Figure 9. Larvae of *Paralabrax maculatofasciatus*: *A*. 5.8-mm flexion larva, 23 days; *B*. 7.9-mm postflexion larva, 26 days; *C*. 9.3-mm postflexion larva, 26 days.

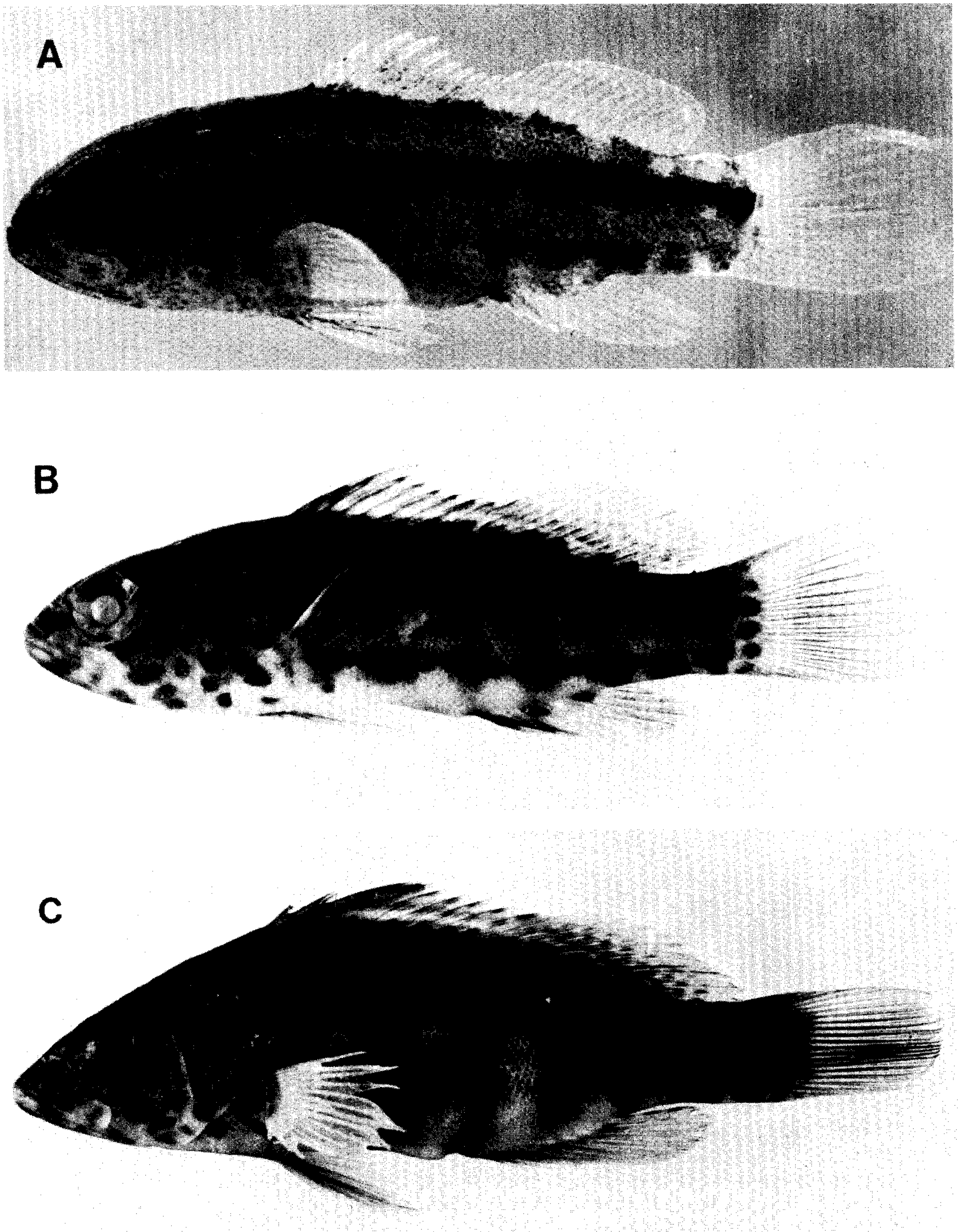

Figure 10. Juveniles of *Paralabrax maculatofasciatus*: *A.* 12.3-mm juvenile, 40 days; *B.* 29.5-mm juvenile, 49 days; *C.* 46-mm juvenile, SIO 73-345, Mission Bay, San Diego.

specimens often lack important characters. These descriptions are meant as an aid for identifying very similar larvae.

ACKNOWLEDGMENTS

Morgan Busby, Susan D'Vincent, Elaine Sandknop, Betsy Stevens, and Barbara Sumida MacCall sorted eggs from live plankton and assisted during numerous rearing attempts. We gratefully acknowledge their cheerful help and encouragement. Henry Orr drew the illustrations. Eric Lynn provided algal and rotifer cultures. Richard H. Rosenblatt, Scripps Institution of Oceanography, provided specimens of juvenile basses. Other sources of material were Marine Biological Consultants, Costa Mesa, California; Woodward Clyde Associates, San Diego, California; the Southern California Edison Collection, King Harbor, California; Marine Ecological Consultants, Solana Beach, California. Bill Watson of Marine Ecological Consultants, and Art Kendall of the National Marine Fisheries Service read the manuscript.

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OBSERVATIONS ON THE EARLY LIFE HISTORY OF THE MUSSEL BLENNY, *HYPSOBLENNIUS JENKINSI,* AND THE BAY BLENNY, *HYPSOBLENNIUS GENTILIS,* FROM SPECIMENS REARED IN THE LABORATORY

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ABSTRACT

Two egg masses of the mussel blenny, *Hypsoblennius jenkinsi,* with attending males, were collected in Mission Bay, California, and incubated in the aquarium. After hatching, the broods of larvae were reared to the benthic juvenile stage on a diet of the rotifer *Brachionus plicatilus* and brine shrimp. Juveniles of one of the broods were maintained in the aquarium to the adult stage. On day 141 after hatching, one of the females produced a viable egg mass from which larvae hatched in 22 days. A single egg mass of the bay blenny, *Hypsoblennius gentilis,* was collected and incubated in a similar manner, producing larvae that were reared to a length of 6.7 mm. This paper describes the eggs and larvae of *H. jenkinsi,* including growth rate, and provides characters for distinguishing the larvae of this species from *H. gentilis* larvae.

RESUMEN

En Mission Bay, California, se recolectaron dos nidadas de huevos del blenio *Hypsoblennius jenkinsi,* junto con los machos que las atendían, para ser incubadas en al laboratorio. Las larvas eclosionadas se criaron alimentadas con el rotífero *Brachionus plicatilus* y el crustáceo *Artemia salina* hasta que alcanzaron la fase juvenil bentónica. Los juveniles de una nidada lograron alcanzar la fase adulta, y una hembra de 141 días efectuó una puesta de huevos de los cuales eclosionaron larvas a los 22 días. Una puesta de huevos del blenio *Hypsoblennius gentilis* que también se recolectó, fué incubada bajo las mismas condiciones, obteniéndose larvas que alcanzaron 6.7 mm de longitud. En este trabajo se describen los huevos y larvas de *H. jenkinsi,* incluyendo su índice de crecimiento, y se discuten los caracteres distintivos de las larvas de esta especie y de *H. gentilis.*

INTRODUCTION

The family Blenniidae is represented off California and Baja California by three species of the genus *Hypsoblennius: H. gentilis, H. gilberti,* and *H. jenkinsi* (Miller and Lea 1972). The behavior of these species has been studied by Stephens et al. (1970) and Losey (1968), but descriptions of their larvae have not been published. Eggs and larvae of an Atlantic species, *H. hentzi,* were described by Hildebrand and Cable (1938). Balbontin and Perez (1979) described the eggs and larvae of a Chilean species, *H. sordidus.*

Although the species of *Hypsoblennius* are shallow-water demersal spawners, their larvae occur routinely in nearshore CalCOFI plankton collections, both in oblique and surface tows. Larvae of *Hypsoblennius* species are similar in morphology and pigmentation, and identifying them in ichthyoplankton samples has been an intractable problem. Developmental series obtained from eggs of captive adults have been useful in establishing characters for identification of larvae in other fishes. The purpose of this paper is to describe the larvae of *H. jenkinsi* obtained from egg masses of that species and to make comparisons with reared larvae of *H. gentilis.* Information on the reproductive biology of *H. jenkinsi* is also presented.

MATERIALS AND METHODS

Egg masses of *H. jenkinsi* and *H. gentilis* were collected by a diver in Mission Bay, San Diego, and reared in the experimental aquarium at the Southwest Fisheries Center, La Jolla. Brooding males were captured with each egg mass and preserved as voucher specimens after hatching was completed. In all egg collections, the nest was on the inner surface of the shell of the scallop *Hinnites multirugosus.* The shell and brooding male were placed in a plastic bag, taken to the laboratory, and submerged in a 20-liter bucket of filtered seawater. The bag was removed; an airstone was introduced; and the nest was left undisturbed until hatching began. As larvae emerged, they were dipped out with a 1-liter beaker and placed in 100- or 400-liter black fiberglass rearing tanks containing filtered seawater held in water tables at ambient seawater temperatures.

Initially the larvae were fed the rotifer *Brachionus plicatilus,* maintained at a concentration of 50/ml. A liter of a dense algal culture *(Tetraselmnis suesica)* was added daily as food for the *Brachionus.* When the larvae were 10-15 days old, *Artemia* nauplii were

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[Manuscript received January 20, 1982.]

added at a concentration of about 1 nauplius/ml. Large larvae, juveniles, and adults were fed frozen adult *Artemia,* supplemented with wild zooplankton when available.

Larvae were sampled regularly and preserved in 4 percent Formalin. Some were photographed before preservation to record xanthic pigmentation. Morphometric measurements were made according to the methods described in Sumida et al. (1979), except for the following measurements:

> Greatest body depth = body depth at the cleithral junction.
>
> Pectoral fin length = horizontal distance from the edge of the fin base to the posteriormost margin of the fin blade.
>
> Length of the longest preopercular spine = distance from the base of the spine to its tip.
>
> Snout length = horizontal distance from the anterior edge of head to the edge of the eye.

Meristic counts were taken from specimens cleared and stained using the alcian cartilage staining method of Dingerkus and Uhler (1977) and the trypsin-alizarin red technique of Taylor (1967).

Diameters of field-collected and aquarium-spawned eggs were measured with the ocular micrometer of a stereoscopic microscope. The number of eggs in aquarium spawnings was estimated by counting all eggs in a sample area estimated to be 10 percent of the total egg patch.

The growth curve for *H. jenkinsi* was computed from lengths of Formalin-preserved reared larvae, juveniles, and adults fitted to the Gompertz curve, using a canned program, PAR of BMDP-80 (Dixon and Brown 1979). Pooled lengths were used for larvae less than 40 days old.

Distribution data were taken from fish larvae identification records of CalCOFI collections from 1950 through 1972.

REARING CHRONOLOGY

The first collection of *H. jenkinsi* eggs was made on July 22, 1977. Both valves of the *Hinnites* shell were covered with eggs, estimated to number over 10,000 on one valve. The male measured 73 mm SL. Incubation temperatures ranged from 20.0° to 21.5°C. Subsequent examinations of the shell indicated that about 20 percent of the eggs hatched. The oldest survivors died on day 62, with the largest juvenile reaching 14.1 mm SL.

The second brood was obtained on July 14, 1978. The male measured 44 mm SL. Hatching began on July 16 and lasted for 4 days. Water temperature during incubation and rearing ranged from 19.0° to 23.0°C. Transformation to benthic juveniles was observed on day 53, when larvae had reached 10-13 mm SL. Shells, sponges, and concrete blocks were placed in the rearing tank to provide cover. On day 103 one male and three females, all of about equal size, remained; one, anesthetized with quinaldine, measured 32.0 mm SL.

On day 141 after hatching, a patch of about 450 eggs appeared on the bottom and sides of the rearing tank, covering an area of about 20-25 cm^2. The male fanned the eggs intermittently. A small section of the egg patch was excised from the side of the tank with a scalpel and incubated in a 10-liter pot. Incubation temperatures ranged from 15.2° to 18.0°C. Larvae began to hatch from the eggs after 22 days of incubation (day 163 for the adults). *Brachionus* was added to the rearing pot, but all larvae died within 3 days. On day 240 the male died and was replaced by a field-caught male. Spawning occurred 6 more times, on days 260, 264, 277, 281, 313, and 317 and resulted in clutches of 300-650 eggs, but none of the eggs survived to the hatching stage. The temperatures ranged from 16.0°-19.0°C. The three females died on days 296, 319, and 320 at lengths of 55, 65, and 64 mm SL.

The single egg mass of *H. gentilis* was collected in a *Hinnites* shell on August 9, 1977, along with an 86-mm SL brooding male. Hatching began on August 17 and continued to August 18. Water temperature during incubations was approximately 18.5°C. Larvae fed on *Brachionus* but suffered a high mortality; the last ones died 21 days after initial hatching at lengths of 6.7 mm SL.

DESCRIPTION OF DEVELOPMENTAL STAGES

Eggs

Wild eggs of *H. jenkinsi* reported on here are deposited in a single layer on *Hinnites* valves. They are slightly flattened in the plane of the substrate and are attached by an adhesive disc. The yolk is granular, and the perivitelline space is narrow. Diameters of 29 field-collected eggs from two broods ranged from 0.69 to 0.80 mm ($\bar{x}$ = 0.75 ± 0.029 SD). Diameters of 22 aquarium-spawned eggs from two masses ranged from 0.71 to 0.78 mm ($\bar{x}$ = 0.75 ± 0.023 SD). The aquarium-spawned eggs were used in the following description.

A striking feature of *H. jenkinsi* eggs is the presence of a clump of violet inclusion bodies and a clump of golden yellow oil globules within the yolk. As reported for the eggs of *H. hentzi* (Hildebrand and Cable 1938), the violet bodies disperse, shrink, and fade with development. They disappear before hatching. The oil globules have a similar fate, although some may persist in newly hatched larvae. After about 3 days of development the outline of the embryo is clearly visible in an equatorial position. After 7 days the embryo extends about two-thirds of the way around the yolk, and the heart is beating. The body axis is now located on the side of the yolk mass facing the substrate, and the head faces upward. By day 17 the body begins to twitch, and by day 19 the eyes are rotating. Hatching occurs at the end of the third week.

The first pigment to develop in the embryo is a covering of scattered melanophores over the upper and lower surfaces of the yolk mass. At the end of the first week the eyes begin to develop melanistic pigment. Midway through embryonic development, melanophores begin to form along the dorsal surface of the gut and on the medial surfaces of the pectoral fin buds. During the third week of the development melanophores appear at the bases of the otic capsules, and a medial series extends along the base of the cranium to the snout. Melanophores cover the medial surface of each pectoral fin. One or two melanophores are present on the ventral surface of the gut just anterior to the anus. A ventral midline series of small, evenly spaced melanophores extends from the anus to the posterior region of the tail. Melanophores are absent on the remaining yolk mass.

Larvae

Morphology. Development of *H. jenkinsi* larvae is illustrated in Figure 1. Body measurements of *H. jenkinsi* and *H. gentilis* are listed in Tables 1 and 2, and proportions are summarized in Table 3. Both species hatch at about 2.5 mm, with large heads, thin tapering bodies, and prominent functional pectoral fins. Both species are similar to the larvae of other species of the genus (Hildebrand and Cable 1938; Balbontin and Perez 1979). Snout-anus length and pectoral fin length are slightly greater in larvae of *H. jenkinsi* than in *H. gentilis*. In *H. jenkinsi*, three major preopercular spines develop, the upper two approximately equal in length (Figure 2). The middle spine is 15 percent of the head length in a 7.6-mm larva and undergoes a reduction to 3 percent of head length at 17.9 mm ($\bar{x}$ = 9.1 ± 4.15 SD for the series). Preopercular spines are absent in *H. jenkinsi* specimens larger than 18.0 mm SL.

TABLE 1
Average Measurements (mm) of Reared Larvae of *Hypsoblennius jenkinsi*

Body length	N	Range	Snout length	Head length	Snout to anus	Eye width	Greatest body depth	Pectoral fin length	Length of longest preopercular spine	Length of cirrus
2.5	1	-	.10	.56	.98	.28	.56	.28	<.02	
2.8	7	2.76- 2.82	.11	.61	1.0	.29	.62	.37	.02	
2.9	7	2.8 - 3.0	.12	.64	1.1	.28	.59	.39	.05	
3.2	6	3.0 - 3.4	.14	.67	1.2	.31	.64	.46	.04	
3.6	5	3.5 - 3.8	.15	.74	1.4	.34	.73	.48	.08	
4.5	6	4.0 - 4.6	.19	1.0	1.6	.44	.92	.82	.06	
4.7	7	4.7 - 4.8	.21	1.1	1.8	.47	.98	.92	.09	
4.9	6	4.9 - 5.0	.23	1.2	2.0	.51	1.1	1.1	.13	
5.2	12	5.0 - 5.2	.21	1.2	2.1	.52	1.1	1.2	.16	
5.7	7	5.3 - 6.3	.25	1.5	2.4	.66	1.3	1.5	.19	
5.8	5	5.6 - 6.0	.22	1.5	2.6	.74	1.4	1.7	.22	
6.2	5	6.1 - 6.6	.23	1.6	2.7	.75	1.6	1.8	.27	
7.6	3	7.2 - 7.9	.20	2.1	3.3	.92	2.1	2.3	.31	
8.9	3	8.6 - 9.6	.30	2.6	4.0	1.1	2.3	2.8	.32	
10.5	4	10.2 -10.8	.38	2.9	4.6	1.2	2.6	3.1	.38	.04
11.3	1		.30	3.1	4.6	1.3	2.6	2.8	.28	.35
12.6	1		.56	3.2	5.5	1.3	3.2	3.7	.48	.12
12.8	1		.40	3.7	5.8	1.5	3.3	4.1	.32	.43
14.1	1		.52	3.8	6.6	1.8	3.8	4.6	.24	.22
15.7	1		.68	4.9	7.3	1.7	4.2	5.1	.20	.69
16.8	1		.75	4.8	7.8	1.7	4.1	4.9	.25	.30
17.9	1		.80	4.8	8.1	1.8	4.8	5.8	.16	.56
18.2	1		.73	5.3	8.5	1.8	5.2	5.7	—	.72
18.6	1		.65	5.3	8.6	1.8	4.9	5.6	—	.52
19.7	1		.89	5.3	9.5	1.9	5.0	6.1	—	.80

Specimens larger than 11 mm are considered early juveniles.
Specimens between dashed lines are undergoing notochord flexion.

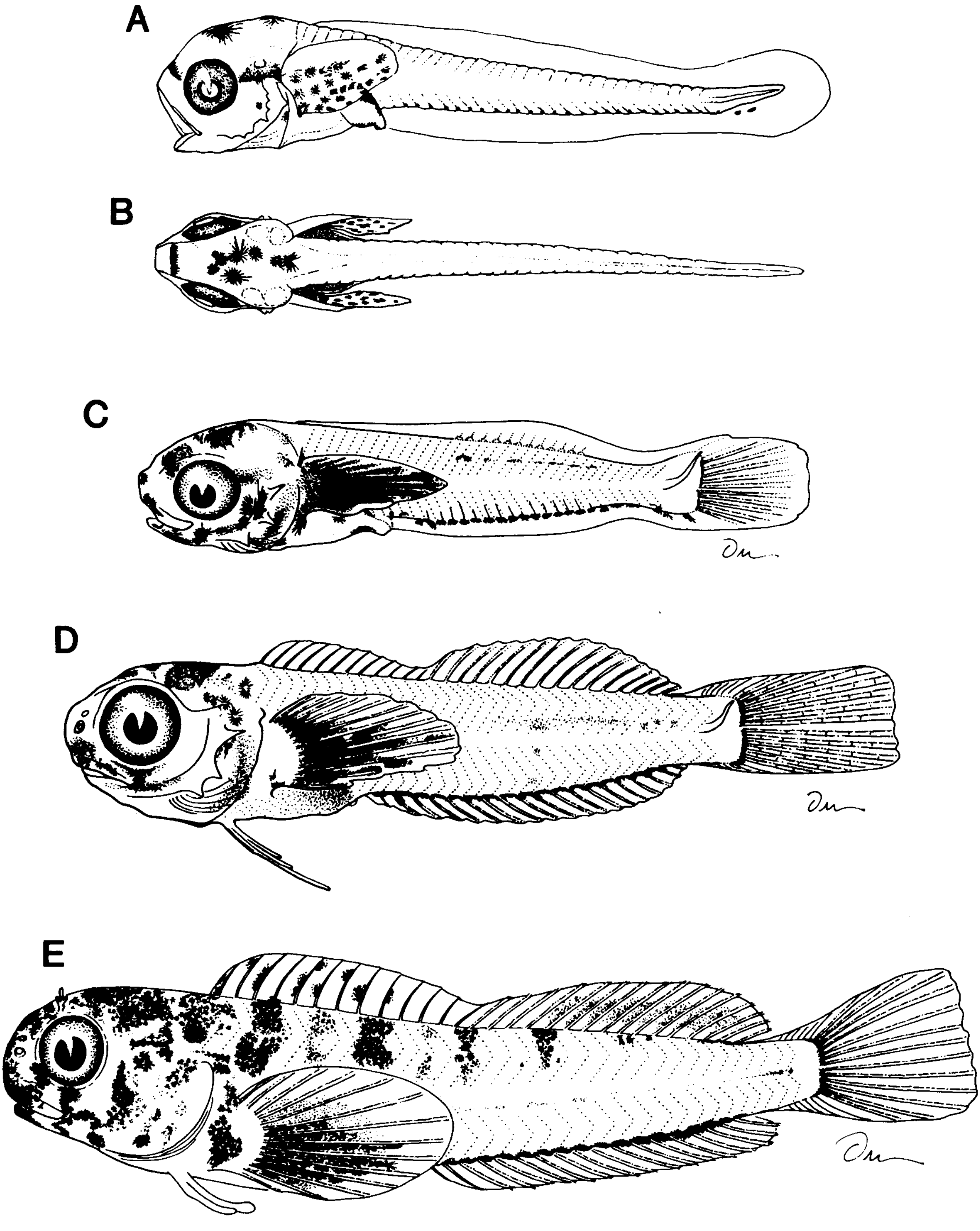

Figure 1. Reared specimens of *Hypsoblennius jenkinsi: A.* 4.3-mm larva (day 7); *B.* 4.3-mm larva, dorsal view; *C.* 5.3-mm larva; (day 29); *D.* 10.2-mm larva (day 34); *E.* 18.6-mm juvenile (day 58).

TABLE 2
Average Measurements (mm) of Larvae of *Hypsoblennius gentilis*

Body length	N	Range	Snout length	Head length	Snout to anus	Eye width	Greatest body depth	Pectoral fin length	Length of longest preopercular spine	Length of cirrus
2.5	7	2.4-2.6	.10	.52	.92	.25	.50	.33	—	
2.7	4	2.6-2.8	.12	.57	.96	.28	.55	.36	.02	
3.1	1		.12	.62	1.1	.28	.60	.46	.02	
3.5	4	3.4-3.6	.15	.77	1.4	.34	.76	.53	.08	
3.7	4	3.6-3.7	.20	.84	1.4	.35	.84	.58	.08	
3.9	5	3.8-3.9	.18	.90	1.5	.38	.80	.70	08	
4.1	1		.20	.94	1.5	.36	.86	.90	.06	
4.4	3	4.4	.19	1.0	1.6	.40	.93	.89	.09	
4.6	3	4.6-4.7	.21	1.1	1.8	.45	.87	.96	.12	
4.8	4	4.8	.20	1.1	1.9	.44	1.0	1.1	.12	
6.7	1		.28	1.9	2.9	.80	1.6	2.0	.20	

Specimens between dashed lines are undergoing notochord flexion.

TABLE 3
Comparative Morphometry of *H. jenkinsi* and *H. gentilis*

Body proportion	*H. jenkinsi*	*H. gentilis*
Snout-anus/body length		
A	37.4 ± 1.2 (33-40)	36.1 ± 1.3 (34-38)
B	40.4 ± 2.3 (35-47)	38.8 ± 1.9 (37-43)
C	44.1 ± 1.8 (42-49)	
D	45.6 ± 2.1 (41-48)	
Snout length/body length		
A	4.2 ± 0.6 (3-5)	4.2 ± 0.7 (3-6)
B	4.4 ± 0.6 (3-5)	4.6 ± 0.7 (4-6)
C	3.5 ± 0.7 (3-5)	
D	3.7 ± 0.7 (3-5)	
Head length/body length		
A	21.5 ± 1.2 (19-23)	21.0 ± 1.0 (19-22)
B	23.5 ± 1.8 (20-28)	23.0 ± 1.6 (18-27)
C	27.2 ± 2.2 (23-31)	
D	27.9 ± 1.8 (25-31)	
Eye diameter/body length		
A	9.8 ± 0.6 (9-11)	10.1 ± 0.6 (9-11)
B	10.2 ± 0.8 (9-12)	9.5 ± 0.6 (9-11)
C	12 4 ± 0.8 (11-14)	
D	10.6 ± 1.0 (10-13)	
Greatest body depth/body length		
A	20.7 ± 1.4 (19-24)	20.1 ± 1.0 (18-24)
B	21.6 ± 1.7 (19-26)	21.2 ± 1.9 (18-24)
C	25.5 ± 1.4 (23-30)	
D	25.8 ± 1.7 (23-29)	
Pectoral fin length/body length		
A	12.9 ± 2.9 (11-17)	13.4 ± 1.4 (11-16)
B	22.4 ± 4.0 (16-30)	18.8 ± 3.3 (14-25)
C	29.5 ± 2.0 (26-33)	
D	30.5 ± 2.3 (25-33)	
Longest preopercular spine/head length		
A	7.2 ± 3.9 (3-14)	2.8 ± 1.3 (1-5)
B	10.1 ± 3.9 (1-19)	10.1 ± 2.8 (6-15)
C	16.1 ± 2.4 (13-20)	
D	6.9 ± 5.7 (0-19)	
Cirrus length/head length		
C	2.4 ± 0.7 (2-3)	
D	10.3 ± 3.8 (3-15)	

A = preflexion, B = flexion, C = postflexion, D = juvenile (specimens > 11.0 mm). Values are mean, standard deviation, and range of percentage of body length or head length.

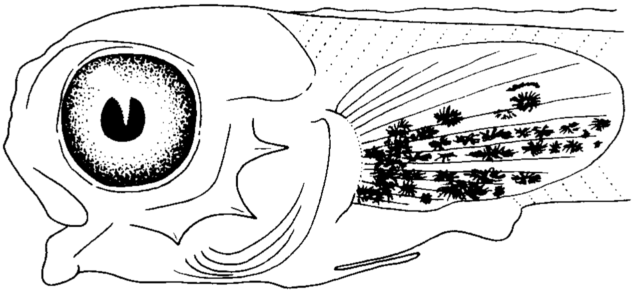
Figure 2. Preopercular spination of *Hypsoblennius jenkinsi* larva, 7.6 mm.

Fin formation. Pectoral fin rays begin to ossify at about 4.0 mm body length in both species, and the adult complements (12-15 for *H. jenkinsi;* 11-12 for *H. gentilis*) are formed during caudal fin flexion (Table 4). Principal caudal fin rays begin ossifying at about 4.0 mm in both species, and the adult complement of 7 superior and 6 inferior rays is present at the completion of notochord flexion. Dorsal, anal, and pelvic fin anlagen appear during caudal fin flexion, and the adult complements are present between 8.0 and 9.0 mm in *H. jenkinsi.*

Pigmentation. Newly hatched *H. jenkinsi* and *H. gentilis* larvae have four areas of melanstic pigmentation: the dorsal surface of the gut, with one or two preanal melanophores along the ventral midline; the medial surfaces of the pectoral fin base and blade; along the base of the cranium from the otic capsules to the snout; and along the ventral midline, with a series of melanophores extending posteriorly from just behind the anus to the tip of the notochord. In *H. jenkinsi* the number of principal postanal ventral midline melanophores ranges from 21-27 ($\bar{x}$= 23.6 ± 1.3 SD for 26 specimens counted). In *H. gentilis* the range was 22-26 ($\bar{x}$ = 24.1 ± 1.2 SD for 23 specimens).

TABLE 4
Meristic Characters of Cleared and Stained Larvae of *H. jenkinsi* and *H. gentilis*

Body length	Source	Vertebrae	Principal caudal rays	Procurrent caudal rays	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin
H. jenkinsi								
4.0	reared	35	5 + 6				12, 12	
4.4	"	10 + 24	5 + 3				11, 11	anlagen
5.0	"	35	5 + 6	0 + 2	12	16	12, 13	anlagen
5.7	"	10 + 24	7 + 6	1 + 2	12	15	13, 13	1, 1
6.1	"	10 + 25	7 + 6	1 + 3	14	17	13, 13	1, 1
7.3	"	10 + 24	7 + 6	5 + 5	XII, 15	I, 17	14, 14	4, 4
8.4	"	10 + 24	7 + 6	7 + 7	XIII, 16	II, 17	12, 12	I,3;I,3
9.8	"	10 + 24	7 + 6	7 + 8	XII, 17	II, 17	13, 13	I,3;I,3
10.3	"	10 + 24	7 + 6	7 + 7	XII, 16	II, 18	14, 14	I,3;I,3
12.1	"	10 + 24	7 + 6	8 + 8	XII, 15	II, 17	13, 13	I,3;I,3
17.1	"	10 + 24	7 + 6	7 + 6	XII, 15	II, 17	14, 14	I,3;I,3
H. gentilis								
3.7	reared	35						
4.1	"	35	2 + 2				11, 11	
4.6	"	10 + 25	4 + 4				9, 9	
4.8	"	10 + 25	4 + 4				11, 11	

Specimens between dashed lines are undergoing flexion.

There are 3-5 small, irregularly spaced melanophores at the tip of the tail.

In both species pigmentation increases during larval development primarily on the head, above the brain, on the nape, snout, jaws, operculum, and isthmus. Pigment descends laterally on the gut wall. During flexion, the irregular group of melanophores at the end of the notochord develops into a line of pigment on the posterior margin of the hypural plates. In postflexion *H. jenkinsi* the pectoral fin blade and median surface of the base remain heavily pigmented except for the dorsal region of the blade, which is unpigmented. *H. jenkinsi* above 18 mm SL develop melanophores on the lateral surface of the pectoral base. In early postflexion larvae of *H. jenkinsi* a series of melanophores develops on the dorsal surface of the vertebral column. At 10-11 mm SL, external dorsal pigment begins to develop. Pigment is arranged in a series of 5 to 7 saddles, beginning at the nape and eventually extending to the middle of the soft dorsal fin, with scattered melanophores on the dorsal margin posterior to the saddles. The saddles extend downward about one-fourth of the body depth. Paler saddles develop between the darker saddles. Concurrent with the dorsal pigment expansion a row of melanophores develops along the lateral line, beginning posterior to the pectoral fin and gradually extending to the tail.

Growth rate. The incubation time for *H. jenkinsi* eggs was determined from the laboratory-spawned egg mass, which began to hatch on day 21 and continued for about 2 days. During the 23-day period temperatures in the rearing tank ranged from 15.2-18.0°C. Hildebrand and Cable (1938) observed hatching of *H. hentzi* in 10-12 days at 24-27°C, and Hubbs (1965) recorded incubation times for *H. jenkinsi* of 14-21 days at 15-18°C and 6-8 days at 24-27°C in temperature-controlled experiments. In the field, eggs in one nest are deposited by several females over a period of time, and consequently hatching occurs over several days (Losey 1968).

The growth rate of the *H. jenkinsi* larvae was computed from lengths of 960 individuals in the two reared groups, fitted to the generalized Gompertz growth curve

$$Y_t = Y_o e^{\frac{\alpha}{\beta}(1-e^{-\beta t})}$$

where t = time in days, y = length in millimeters, α = the instantaneous rate of growth at age 0, and β is the change in growth rate. The resultant growth rate, $Y_t = 1.2845\ e^{3.92(1-e^{-.0177t})}$, is plotted in Figure 3. Sexual maturity, as shown by the laboratory spawning, occurs in the region of the upper break in the curve, at about 40-50 mm SL and 150 days of age. The length reached in 320 days by reared specimens, 60-65 mm, and the maximum length of *H. jenkinsi* reported by Stephens et al. (1970) as 89 mm, indicates that this species approaches its maximum length by the end of its first year.

DISTRIBUTION

Hypsoblennius larvae are not taken in great numbers but are collected over a wide latitudinal range, from CalCOFI line 73, just north of Pt. Arguello, California, to CalCOFI line 150, south of Magdelena Bay, Baja California Sur. They have also been taken in

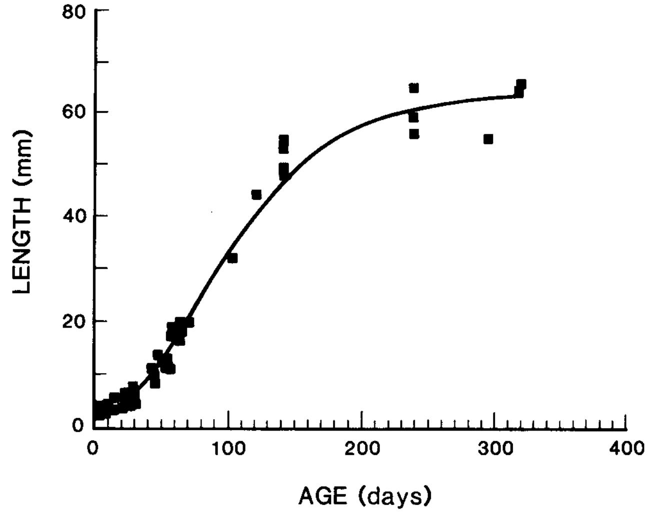

Figure 3. Growth curve for reared *Hypsoblennius jenkinsi*.

oblique tows in the Gulf of California. During October 1972 on CalCOFI Cruise 7210, when surface as well as oblique collections were made over an extended CalCOFI pattern, *Hypsoblennius* larvae were captured in greater numbers at the surface. *Hypsoblennius* larvae usually were collected close to shore but occasionally were taken well offshore, as at stations 107.70 and 133.70. The 781 occurrences of *Hypsoblennius* larvae in CalCOFI oblique tows from 1950–72 and the 13 occurrences in neuston stations in 1972 are plotted in Figure 4 and summarized in Table 5.

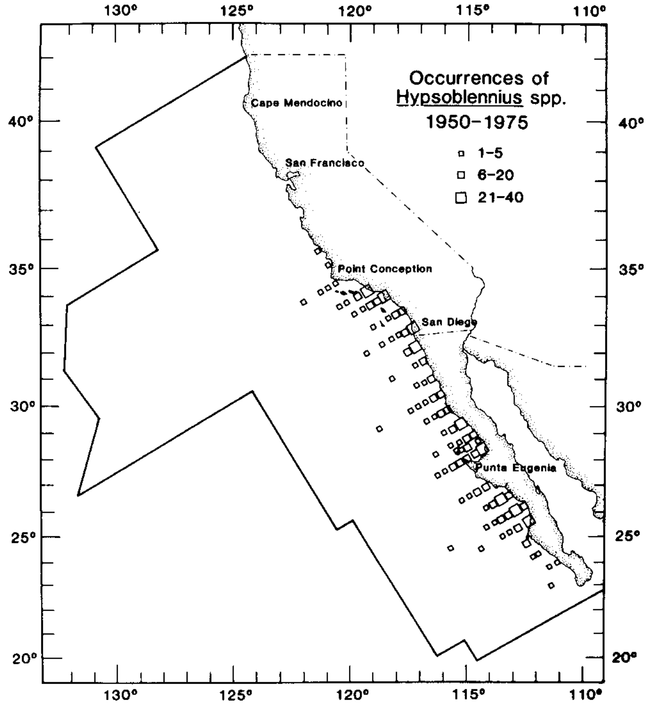

Figure 4. Occurrences of *Hypsoblennius* spp. larvae in CalCOFI plankton collections. Standard CalCOFI sampling pattern bounded by solid line.

TABLE 5
Areal and Seasonal Occurrences of *Hypsoblennius* ssp. Larvae in CalCOFI Collections

Area	% Occurrences	Month	% Occurrences
Lines 60- 77	0.3%	Jan.-Mar.	6.9%
80- 97	30.3	Apr.-June	12.4
100-119	22.2	July-Sept.	54.2
120-137	45.0	Oct.-Dec.	26.5
140-157	2.2		

Values are percent of total occurrences.

ACKNOWLEDGMENTS

We were able to undertake this project through the donation of field-caught egg nests by Dr. David Leighton, San Diego State University, and the Ocean Studies Division of World Research, Inc. Many people assisted with rearing: Jim Bodkin, Morgan Busby, John Butler, Susan D'Vincent, Dennis Gruber, Eric Lynn, Elaine Sandknop, and Bob Wytala. Ronald Leitheiser of Lockheed Center for Marine Research gave us specimens of juvenile *Hypsoblennius* spp. Susan D'Vincent and Henry Orr provided illustrations. Marianne Ninos Dawson of University of Southern California discussed problems of identification with us. Dr. Nancy Lo calculated the growth rate. Mary DeWitt typed the manuscript.

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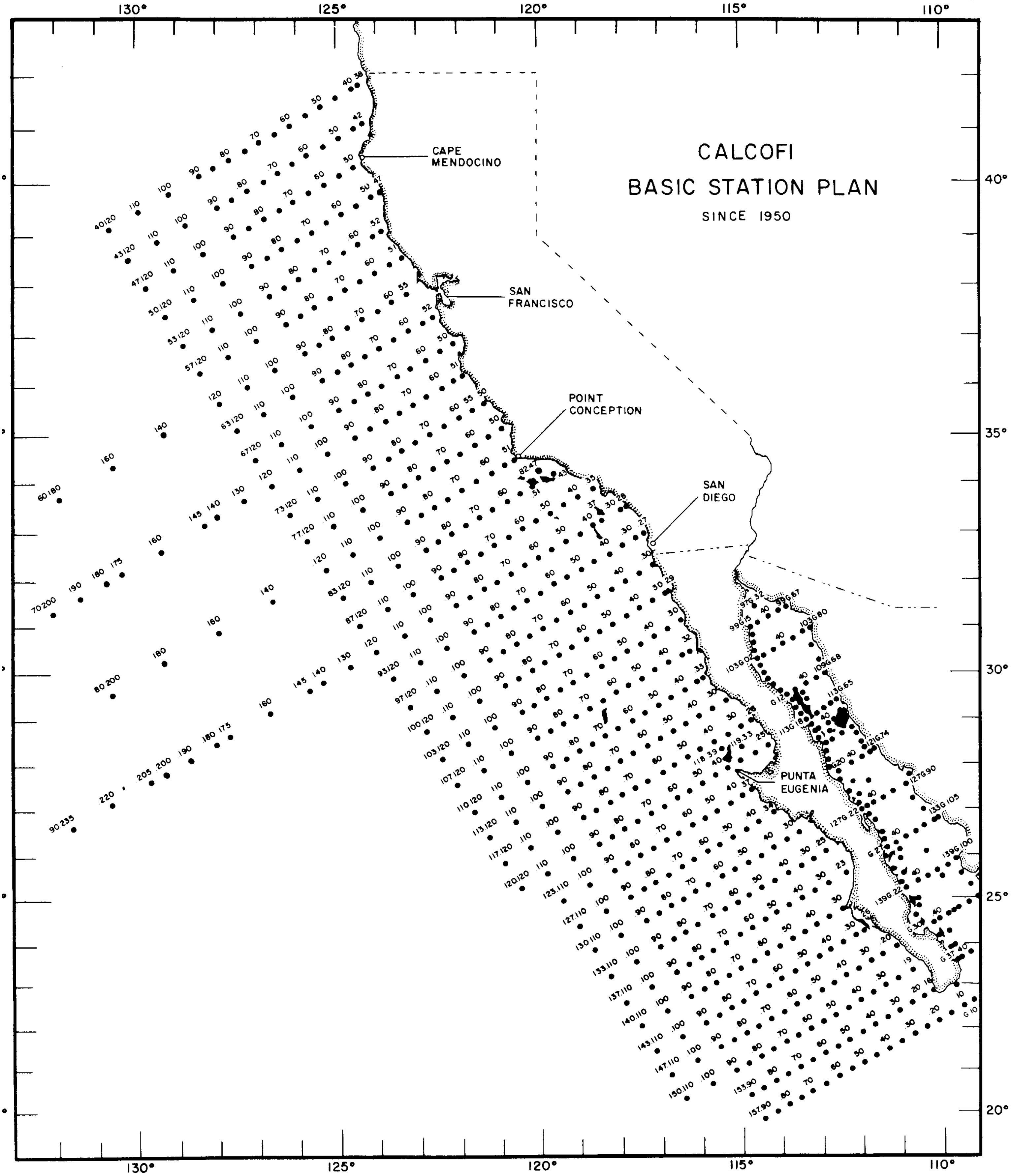

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