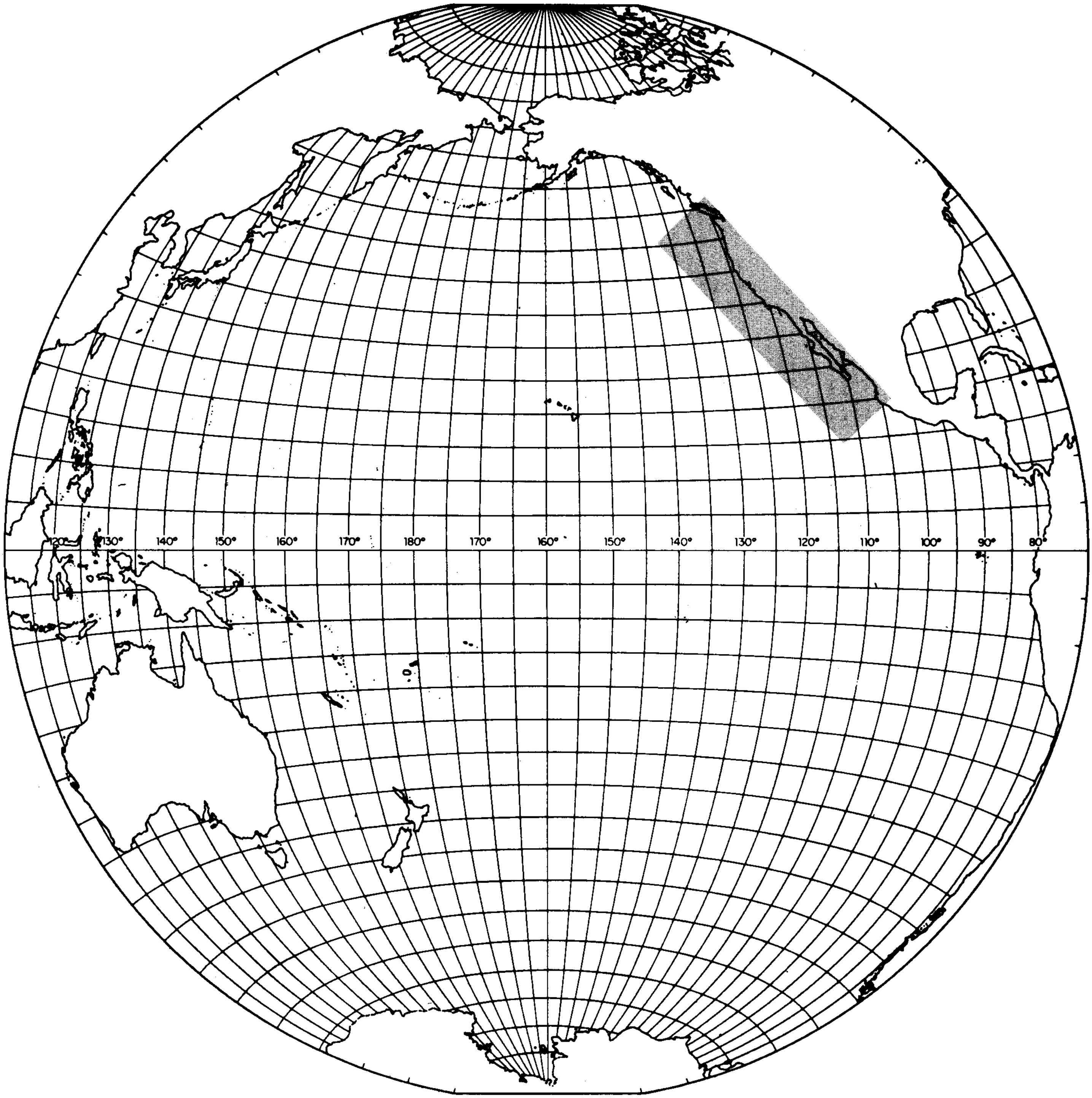

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

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NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL MARINE FISHERIES SERVICE

EDITOR Julie Olfe

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IN MEMORIAM

Martin W. Johnson

September 30, 1893–November 28, 1984

Dr. Martin W. Johnson, professor emeritus at the Scripps Institution of Oceanography, died on November 28, 1984, at Snohomish, Washington, at the age of 91. He had given up his 50-year association with Scripps only a few months earlier; he worked in his laboratory until the fall of 1984.

Johnson was particularly well known as one of the three authors of the landmark text and reference, *The Oceans: Their Physics, Chemistry and General Biology*. He further enhanced his stature with his World War II research, his postwar training of students, and his collaboration with them in describing the pelagic biogeography of the Pacific.

The "deep scattering layer" is probably his major wartime contribution. The use of acoustics, or underwater sound, was (and still is) the main method of detecting submarines. However, many properties of the ocean itself interfere with sound transmission and sometimes make submarine detection very difficult. An especially serious problem was the sound reflection that seemed to be coming from mid-depths. Research engineers spent a lot of Navy time and money trying to determine the source of these signals. Drs. R.J. Christensen, C.F. Eyring, and R.W. Raitt of the University of California Division of War Research asked Martin Johnson to investigate the problem because they had heard him lecture about deep layers of zooplankton and because of his earlier success in recognizing signals produced by shrimp.

It occurred to Johnson that ". . . if the layer was composed of organisms, it should behave as many marine animals do, especially the plankton, and undergo diurnal migrations . . ." He reasoned that the layer should begin an upward ascent around 5:30 p.m. (after engineers' normal quitting time) and migrate downward again around 6:00 a.m. (before shipboard work has normally started). Johnson's resulting hypothesis was tested at sea on the night of June 26-27, 1945. Thus the biological nature of the deep scattering layer was established.

In 1936 the faculty at Scripps had introduced a course in general oceanography in which it was "customary for those giving lectures to join the students as auditors in a following lecture given by some other faculty member." The principle of the interdisciplinary nature of oceanography led to the requirement that each graduate student at Scripps, no matter what his discipline, should take core courses in physical oceanography, marine chemistry, biological oceanography, and marine geology. Both Sverdrup and Johnson felt strongly about this issue, and their views prevailed until recently, when it was determined that the intellectual demands of certain subdisciplines are too great to require that all students be familiar with the whole of oceanography.

To follow through on their ecumenical notions and to provide a textbook for their courses, Sverdrup, Johnson, and Fleming collaborated on a book called simply *The Oceans*. It was, and still is, unique. Published in 1942, it initially received little attention, and some of that was not particulary complimentary. An early review in the *New York Times* read: ". . . this book shows that oceanographers have gone down in the ocean deeper, stayed down longer and come up drier than any other sailors." It is true that the writing style is distinctly reserved, Scandinavian, and in stark contrast to today's bated-breath, discovery-a-minute mode of expression. Nevertheless, the book has been in print and in demand for over 40 years; few authors of scientific tomes can claim that kind of record.

Scripps Institution and the science of oceanography grew rapidly after World War II, and Johnson felt that an increase in graduate student enrollment was "especially important." He played a significant role in establishing the California Cooperative Oceanic Fisheries Investigations and its Scripps branch, the Marine Life Research Group. Johnson put a group of graduate students to work studying the California Current and its plankton populations, with emphasis on determining which species were present and how their abundances varied in space and time. Only zooplankton were studied because other kinds of organisms could not be reliably and quantitatively sampled at the time (1949). It was typical of Johnson to employ students on such fundamental research as determining the nature and life histories of fauna rather than, say, energy flow through (mostly unknown) trophic levels, a field which even then was considered high fashion.

One of the results of these studies was the determination that much of the plankton fauna of the California Current seemed to comprise a mixture of species that had larger populations in other water masses outside the system. The central portion of the California Current is one of the few places where many of these species co-occur. This discovery of extensive stirring and mixing of populations led to the speculation that much population biology and community diversity here was to be understood in terms of the physics of water movement, rather than as biological function like food limitation, energy flow, or competitive interrelationships between populations. This was such a heretical idea at the time (1954) that Johnson and his students felt more data, particularly descriptive data, were required.

Because many of the species found in the California Current obviously had populations outside of it, broader-scale sampling was clearly necessary to establish the patterns of species abundance. That the major patterns were easily interpretable in terms of Sverdrup's water masses further indicates the predominant role of physics in regulating the biology of the ocean. This approach anticipated by over a decade terrestrial ecologists' renewed interest in biogeography. The large-scale patterns and the proximal reasons for their existence developed by Johnson and his students have stood the test of time.

During formal retirement in the 1970s and early 1980s, Johnson returned to his interest in larval development of the many Pacific lobster species. His descriptions of differing developmental sequences of these leaf-like "phylosoma" stages continued to include his superb illustrations. (He was more than an illustrator: his caricatures and doodles—often made during meetings—might have become legend had he cared to publicize them.)

Martin W. Johnson was born on September 30, 1893, in Chandler, South Dakota, in a sod-roofed farmhouse. Like many other young boys of Scandinavian ancestry, he worked the wheat harvests of Saskatchewan and the Dakotas. In the off-season, he rode herd and was a general ranch hand. When his family moved to Washington state, he worked as a logger and choker setter in the woods and as a guard to protect salmon traps from fish pirates. He has written that these early experiences stimulated his interest in "fundamental ecology" and sense of wonder at the basic differences in "the type of pasturage and resultant type of grazers of each." Thus the Great Plains, the virgin forests of the Pacific slope, and the sea strongly influenced him.

After serving in the army during World War I, he attended the University of Washington, graduating in 1923 at age 30. He was curator of the Friday Harbor biological station, served on the scientific staff of the Passamaquoddy International Fisheries Commission, and acquired a Ph.D. at the University of Washington. In 1934, T. Wayland Vaughan, Director of Scripps Institution, wrote him, offering a Research Associate position at $100 per month, saying "We have on the Institution's staff a few people who are not seagoing. I do not intend to add to the staff anybody else who will not work on water." Johnson was glad to get the low salary ". . . in view of the then nation-wide depression" and the sea-going stricture was, as he said, "not a deterrent to me."

Martin Johnson was, in spite of his adventurous childhood and youth, a quiet, diffident, dignified man. God had not granted him the gift of gab, and his lectures, for the most part, did not sparkle. Even private conversations were, at first, quite formal, somewhat strained. But he was actually an emotional man with a great sensitivity and awareness of the human condition and an intuitive feel for which scientific problems were important and which weren't.

In spite of his basic humaneness, he did not suffer fools gladly. There were events, situtations, and individuals of which he definitely disapproved. But never did he use his position and stature to impose his views. He was completely above academic politics, at which, in any event, he would have been a failure.

An outstanding trait, all who knew "D.J." will agree, was his absolute honesty and integrity. He was simply incapable of deviousness or manipulation. His death marks the end of an era of great growth in oceanography—one of openness and cooperation. Both he and the milieu in which he worked will be greatly missed.

John A. McGowan, Edward Brinton

Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

With deep regret the CalCOFI Committee reports the loss of long-time friend and colleague Martin W. Johnson of Scripps Institution of Oceanography. A memorial by John McGowan and Ed Brinton appears on the preceding pages.

Despite shrinking budgets and increasing pressures CalCOFI reached several important milestones during the year. We take great pride in the publication of the book *Ontogeny and Systematics of Fishes,* sponsored by the Southwest Fisheries Center, a member of CalCOFI, with H. Geoffrey Moser as chief editor. This volume is a memorial to Dr. Elbert H. Ahlstrom, former member of the CalCOFI Committee.

In November, CalCOFI was host to representatives from coastal South American nations to initiate proposals for a worldwide study on recruitment of sardines and anchovies (SARP: Sardine/Anchovy Recruitment Project). The meeting was convened by Reuben Lasker and jointly sponsored by the Intergovernmental Oceanographic Commission.

Studies initiated by CalCOFI during the 1982-83 El Niño event continued during the year with cruises headed by John McGowan and Thomas Hayward. The annual anchovy biomass estimate was completed in July 1984. The status of the sardine remained of great interest. In April-May 1985, a joint National Marine Fisheries Service/Scripps Institution of Oceanography cruise was made aboard R/V *David Starr Jordan.* Part of the mission of this cruise was the assessment of sardine spawning success.

The 1984 CalCOFI Conference was held in October in Idyllwild, California. This annual meeting continues to grow, with over two hundred scientists in attendance from eight countries, representing twenty-three research institutions and industries. Andrew Bakun convened the symposium entitled "Comparative Studies of Eastern Ocean Boundary Systems." Besides the eight symposium papers, of which seven are reprinted in this volume, sixty-two additional papers and fifteen posters were presented. Herbert Frey of the California Department of Fish and Game chaired a round table discussion on the state of California fisheries. A minisymposium of inshore papers was chaired by Edward DeMartini. We look forward to the 1985 conference.

In response to increasing financial pressures, CalCOFI has used the greatest number of volunteers in the history of its field sampling series: 67 volunteers, of whom 36 were Mexican nationals, were among the 122 people involved in seagoing operations in 1984-85. They contributed to a total of 4,000 person-days during 323 ship-days at sea; 966 hydrographic stations were sampled, and approximately 150,000 items of data (exclusive of weather) were obtained. To top this off, all data reports were published soon after the cruises. Finally, an ocean sampling program of quarterly cruises on a reduced grid commenced in 1985.

The reviewers and editorial staff of this volume, particularly Julie Olfe, are to be congratulated for their excellent work. This volume is the second, and last, of those edited by John J. Grant during his term as CalCOFI Coordinator. He has asked the committee to pass along his deep appreciation to everyone in the CalCOFI family for their assistance and support during the past two years. The committee wishes to thank John for his tireless efforts as CalCOFI Coordinator. George Hemingway of the Marine Life Research Group of Scripps Institution of Oceanography will be the coordinator for the next two years.

The CalCOFI Committee:
Izadore Barrett
Herbert Frey
Joseph Reid

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1984

California Department of Fish and Game
Marine Resources Region
245 West Broadway
Long Beach, California 90802

Total 1984 landings of fishes, crustaceans, and mollusks declined 13% from 1983 to a level that is 32% below the average for the last seven years.

Landings of pelagic wet fishes dropped for the third straight year; all species except Pacific mackerel exhibited declines (Table 1). Jack mackerel and Pacific herring landings declined by approximately 50%, and market squid were virtually unavailable along the entire California coast for most of the year.

Groundfish, pelagic thresher shark, and Dungeness crab landings remained at about the same level as in 1983. The ocean shrimp fishery off the north coast recovered moderately from the disaster of 1983, but declined dramatically off central California.

The brightest notes of 1984 were the record high landings of swordfish by primarily drift gill net vessels and the excellent early summer run of albacore for southern California recreational fishermen.

PACIFIC SARDINE

The moratorium on commercial fishing of Pacific sardines (*Sardinops sagax caeruleus*) remained in effect in 1984 because the spawning biomass was assessed as remaining below the 20,000 tons necessary to initiate a fishery. Good signs of a recovery of the resource continued to be evident. However, the trend of increasing occurrences of sardines appears to have slowed relative to last year.

Approximately 212 tons of sardines were landed incidentally with mackerel fishing in 1984, a considerable decrease from the high of 388 tons landed the previous year (Table 1). However, fishermen continued to report pure schools of sardines and sets on schools of mackerel with more than the allowable 15% by weight of incidental sardines. Sardines occurred in the southern California mackerel landings in all months of the year except July and December. At Monterey, sardines were landed incidentally to mackerel primarily during the last four months of the year. Sardines occurred in 30% of observed mackerel landings during 1984, about the same as observed for 1983. Preliminary analysis of length frequency and aging indicates that the 1983 year class (1-year-olds) was dominant; however, older fish were commonly sampled.

For the third consecutive year sardines appeared in record high frequency in midwater trawls during the annual California Department of Fish and Game (CDFG) recruitment survey off northern Baja California and southern California. Sardines were caught in

TABLE 1
Landings of Pelagic Wet Fishes in California in Short Tons from 1964-84

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	19,899	84,437
1979	18	53,874	30,471	18,300	4,681	22,025	129,369
1980	38	47,339	32,645	22,428	8,886	16,957	128,293
1981	31	57,593	42,913	15,673	6,558	25,715	148,483
1982	145	46,364	31,275	29,110	11,322	17,951	136,167
1983	388	4,740	35,882	20,272	8,829	2,001	72,112
1984*	212	3,203	46,482	11,930	4,241	622	66,690

*Preliminary

54% of the tows off southern California and 44% of the tows off Baja California. Although sardines previously (1966-82) were absent or rare in trawl surveys, they have become the second most frequently taken species during the last three years. Young-of-the-year fish in substantial numbers were taken for the second year in a row. Sizes this year ranged from 40 to 230 mm SL, with most fish in the 125-to-200-mm range.

The percent occurrence of sardines in live bait hauls during 1984 remained at about the same level as last year. Recently, logs were revised to allow fishermen to specify a quantitative estimate of sardines landed; however, these logs are submitted on a voluntary (and frequently incomplete) basis. Department observers on sportfishing boats were also estimating the occurrence of sardines in live bait. A preliminary estimate from these sources suggests possible 1984 live bait landings of sardines ranging from 70 to 250 tons. The live bait catch of sardines is considered to be greater in 1984 than 1983, but consists of more large and fewer small (young-of-the-year) fish than were seen in 1983.

Legislation was passed on September 4 that extends, until July 1, 1986 (an additional year), the sunset clauses on statutes regulating incidental catch tolerances for sardines mixed with other fish, and the allowable uses of sardines. This bill also requires CDFG to submit a report to the California legislature by January 1, 1986, on the effect of the regulations concerning the use of incidentally taken sardines. In addition, the bill allows 75 tons per year of sardines to be taken for live bait and requires a revocable permit and submission of logbooks. These provisions add to and continue statutes designed to alleviate and minimize the impacts of a resurgence of sardines on fishermen and dealers.

NORTHERN ANCHOVY

At the beginning of 1984 only 32 tons of northern anchovy, *Engraulis mordax*, had been landed for reduction purposes toward the 1983-84 season quota of 52,000 tons for the southern permit area (south of Point Buchon). The first 1983-84 season northern area landing (76 tons) occurred January 31, and was applied toward the 5,800-ton northern allocation. At that time, most of the northern area seiners were still fishing herring.

After the interseason closure (February-March), interest in anchovies for reduction remained low, with boats targeting primarily on mackerel. In the southern area, only a single landing was reported prior to the June 30 closure. In the northern area, only two seiners participated in the fishery. These boats made consistently good catches during April, May, and early June, and accounted for approximately 1,700 tons landed for reduction. During this period, the price dropped from $42 to $38 per ton. The 1983-84 season closed with preliminary landings of 1,765 tons in the north and 70 tons in the south (Table 2).

The National Marine Fisheries Service (NMFS) estimated a 1984 spawning biomass of 340,608 tons (309,000 MT). The optimum yield for the 1984-85 season was set at 12,346 tons, and the U.S. reduction fishery harvest limit was set at 6,944 tons. Allocations of 694 and 6,250 tons were established for north and south of Point Buchon, respectively. The 1984-85 season opened August 1 in the north and September 15 in the south. Only one landing, 78 tons in the south, occurred before the end of the year, even though a processor in each permit area had issued orders early in the fall. Fishermen in both areas concentrated efforts on mackerel and complained that only small anchovies were available during the fall.

The statewide reduction landings for 1984 were 1,896 tons. Nonreduction landings accounted for an additional 1,307 tons, whereas live bait catches were estimated at 5,726 tons.

JACK MACKEREL

For the sixth consecutive year, jack mackerel (*Trachurus symmetricus*) contributed less than Pacific mackerel (*Scomber japonicus*) to California's mackerel fishery. The 1984 landings of 11,930 tons constituted 20% of total mackerel landings. This ranks as the lowest proportion of jack mackerel in overall landings since this species began supporting a viable fishery in the late 1940s. Jack mackerel dominated landings

TABLE 2

Anchovy Landings for Reduction Seasons in the Southern and Northern Areas from 1966-84, 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	140,910
1976-77	101,434	5,007	106,441
1977-78	68,476	7,212	75,688
1978-79	52,696	1,174	53,870
1979-80	33,383	2,365	35,748
1980-81	62,161	4,736	66,897
1981-82	45,149	4,953	50,102
1982-83	4,925	1,270	6,195
1983-84*	70	1,765	1,835

*Preliminary

only one month of the year, in March, when interseason restrictions on landing Pacific mackerel were in effect. During most of the year, jack mackerel were largely unavailable off southern California, and made up only 15% of the mackerel catch. Jack mackerel were more available off central California, where they averaged 39% of the mackerel landings.

No explanation is readily apparent for the recent lack of availability of jack mackerel. Jack mackerel may be less abundant under conditions of high Pacific mackerel biomass, as has occurred in recent years. Although it is difficult to assess any impact of the recent El Niño on this species, behavioral patterns that may make jack mackerel unavailable may have been accentuated by this phenomenon, particularly with respect to southern California. In addition, during 1984 fishermen did not fish offshore areas that have traditionally produced large catches of jack mackerel.

A high incidence of young jack mackerel in midwater trawl catches during the 1984 CDFG anchovy recruitment survey suggests a relatively strong 1984 year class.

PACIFIC MACKEREL

The year began with approximately 1,000 tons remaining on the 1983-84 season quota of 22,000 tons. The trend of more northerly catches, which began during the summer of 1983 and persisted through December, continued during the first part of January, with mackerel being caught near Monterey and delivered to southern California by truck and boat. In late January the initial quota was increased to 26,000 tons, primarily on the basis of financial hardships facing the fishermen. Catches improved, with 100% Pacific mackerel available off the Santa Barbara Channel Islands. The season was closed on February 8, when the additional tonnage was landed. Interseason restrictions went into effect, limiting landings to 50% or less by number, or 3 tons of 100% Pacific mackerel. Fishermen were mostly unable to locate schools containing sufficient proportions of jack mackerel to comply with regulations, and this, together with limited cannery interest and poor weather, resulted in low landings during the rest of February and March. At this time fishermen were faced with no prospects of directed take of Pacific mackerel until July 1, poor availability of jack mackerel, squid, and anchovy, and poor market conditions for anchovy.

Urgency legislation (AB 384), which was signed and effective immediately on April 4, provided an additional 1983-84 season take of 7,500 tons, with 2,500 tons allocated for each month (April, May, and June) remaining in the season. In addition, this legislation authorized the California Fish and Game Commission (CFGC) to adjust the determined allowable catch for future seasons between February 1 and June 30. As a result of this legislation, the season was open from April 4-19, and during the first week of both May and June, with interseason restrictions in effect the remainder of the time. Pacific mackerel were more commonly available off southern California during the spring, with catch areas ranging from off Gaviota in April to off San Onofre in June. The season's catch reached 39,000 tons by the end of June—50% more than the adjusted allowable catch of 26,000 tons recommended by the CDFG. This represents an increased seasonal catch at a time when biomass levels appeared to be declining, and Pacific mackerel were entering their spawning season.

The 1984-85 season opened on July 1 with a quota of 16,000 tons based on a biomass estimated to range between 89,000 and 106,000 tons. Fishing got off to a slow start, because most southern California seiners fished for albacore during July. However, landings in August and September were brisk, with Pacific mackerel constituting 95% of the catch; some San Pedro boats fished as far north as Morro Bay. A permit amendment was enacted to limit landings per boat to 125 tons per week, or 375 tons per month, in an effort to distribute the quota more equitably among the fleet and discourage the waste of fish. The season quota was adjusted upwards by 5,000 tons in early October and by another 5,000 tons at the beginning of November, partly as a result of reevaluation of the biomass estimate then considered to range between 107,000 and 139,000 tons. On December 20, the Pacific mackerel fishery was closed when the 26,000-ton quota was reached, and interseason restrictions went into effect. The seasonal catch through December was 28,300 tons.

Landings of Pacific mackerel for the year totaled 46,482 tons. Slightly over 82% of the Pacific mackerel landings occurred in southern California, with Monterey accounting for 18%, or 8,312 tons. This is by far the largest recorded annual take of Pacific mackerel in Monterey since the beginning of the fishery in the 1920s. Landings of Pacific mackerel averaged 85% and 62% of the total mackerel catch in southern and central California, respectively. Jack mackerel continued to be largely unavailable, particularly in southern California.

Although eight year classes (1977-84) contributed to the Pacific mackerel fishery, the 1980 and 1981 year classes accounted for 72% of the tonnage landed in 1984, and fish 3 years of age and older accounted for 96% of the tonnage landed.

The assessment of the 1983 year class suggests that recruitment of these fish will be poor. The 1982 spawning season also produced a weak year class, resulting in two consecutive years of poor recruitment. The very weak presence of the 1982 and 1983 year classes in samples, less than 4% by weight, indicates a crucial need for a strong incoming year class. Preliminary indications suggest the 1984 cohort may be a moderate or even strong year class. Some observations of young-of-the-year fish have been reported, and during November, the 1984 year class contributed a surprisingly high 1% of the total month's tonnage.

MARKET SQUID

Both the central and southern California market squid (*Loligo opalescens*) fisheries fell far short of historical landings during 1984. Only 622 tons were landed statewide, the lowest catch since 1942.

The Monterey fishery produced only 538 tons, despite intense interest and scouting in other than traditional fishing areas. Although this is typically a summer-fall fishery, over half the tonnage, 57%, was landed in May. Prices offered reached record high levels, ranging from $250 to $900 per ton, but fishermen most frequently received $500 per ton.

Only 84 tons were landed in southern California; 87% of this was landed at San Pedro markets. This fishery, which normally has a fall-winter season, also landed over half the tonnage, 60%, in May. Prices paid ranged from $460 to $600 per ton.

Fishermen, processors, and some scientists are worried that the method and level of fishing may be affecting the abundance of squid. In Monterey, most lampara boat owners have proposed a prohibition of chains on nets (to reduce the number of egg cases torn from the bottom) and a limit on the number of boats that can fish on the spawning ground adjacent to the Monterey Peninsula. No known proposals have been made for southern California, which is a scoop boat and purse seine fishery.

Some central California fishermen have suggested that the poor availability of the last two years may reflect a coastwide decline in abundance; others feel that squid may be spawning on grounds inaccessible to the fleet. If squid were able to spawn successfully in deeper waters off Monterey or more northerly waters during the past two years of warm water, then they are expected to return to the Monterey Peninsula in abundance during the summer of 1985. However, if they were unable to spawn successfully, they should be in short supply, with recovery delayed or prevented by likely high exploitation rates.

PACIFIC HERRING

The cumulative effect of two consecutive warm-water years from 1982 to early 1984 had a devastating impact on the 1984 Pacific herring (*Clupea harengus*) fishery. The 1984 annual catch declined to 4,241 tons (Table 1), and the 1983-84 seasonal catch (December-March) was only 3,000 tons, representing a quota shortfall of over 8,000 tons—the poorest season since the fishery began in 1973.

In addition to the reduced catches in the 1983-84 season, herring in the catch exhibited below-normal growth characteristics and consequently were of poor quality. Data gathered from the catch indicated all age groups were 25% below normal weight. The base price for 10% roe recovery was $600 per ton during the season, but the poor condition of the fish caused the price to fall to $150 per ton in some cases.

Population estimates derived from surveying spawning grounds in Tomales and San Francisco bays also declined in 1984. In the 1982-83 season, the Tomales Bay population was estimated to be over 11,000 tons, the second highest estimate recorded. In the 1983-84 season, the Tomales Bay population declined to only 1,280 tons. It is believed that this sudden decline was a result of a northerly migration of the population rather than a sharp increase in mortality. The San Francisco population declined 30% from the previous season to approximately 40,000 tons. Most of this decline is attributed to the poor growth exhibited by herring during 1983.

The ocean temperatures off central California returned to normal during 1984, and both Tomales Bay and San Francisco Bay fisheries are expected to improve in the 1984-85 season.

As the 1984-85 season began, December catches were good in San Francisco Bay, but a lower quota, based on the population estimates from the 1983-1984 season, is in effect and will limit the overall season's catch for Tomales and San Francisco bays to about 7,500 tons. At the beginning of the season the base price for 10% roe recovery increased to $1,000 per ton, and good initial catches give hope for a quick economic recovery for the fishery during the 1984-85 season.

GROUNDFISH

California's 1984 commercial groundfish harvest was 40,030 metric tons (MT), with an ex-vessel value of $22,506,000. The 1984 harvest level represents an increase of 583 MT over 1983 statewide landings (Table 3). California's groundfish catch, which accounted for 20% of West Coast groundfish catches, is typically dominated by the rockfish complex (*Sebastes* spp), Dover sole (*Microstomus pacificus*), and sablefish (*Anoplopoma fimbria*). The majority of the catch (29,087 MT) was landed by trawl vessels. Set net, pot, and hook-and-line vessels accounted for the re-

TABLE 3
California Groundfish Landings (Metric Tons)

Species	1983	1984*	Percent change
Dover sole	8,402	9,744	16%
English sole	1,162	946	-19%
Petrale sole	563	582	3%
Rex sole	626	566	-10%
Thornyheads	1,675	2,105	26%
Widow rockfish	3,455	2,663	-23%
Other rockfish	14,200	14,491	2%
Lingcod	885	935	6%
Sablefish	6,509	4,707	-28%
Pacific whiting	980	2,335	138
Other groundfish	1,041	983	-5%
TOTAL	39,498	40,030	

*Preliminary

mainder. An additional 5,125 MT was estimated to have been captured by the recreational fishery.

First-quarter catches, averaging 1.8 MT per delivery, rebounded strongly from the previous year because of calm ocean conditions and favorable domestic markets. Catch rates declined to 1.4 MT per delivery during the second and third quarters, before rising again to 2.0 MT per delivery in the final quarter of 1984. The high fourth-quarter catch rates occurred despite frequent periods of hazardous ocean conditions, which restricted fishing effort.

Only two species, widow rockfish (*S. entomelas*) and sablefish, were regulated by Pacific Fishery Management Council (PFMC) catch quotas. A coastwide optimum yield of 9,300 MT was established for widow rockfish and enforced by a trip limit and frequency restriction of one landing per week between 3,000 and 50,000 pounds. Trip-frequency limits were not imposed on landings of less than 3,000 pounds. The industry soon adjusted to the new regulations by bringing more vessels into the fishery and extending the length of trips. The rapid pace of landings necessitated a reduction in the coastwide trip limit to 40,000 pounds per trip on May 6, 1984. By September 9, the PFMC was forced to order a cessation of directed fishing, for 9,200 MT of widow rockfish had been captured. An incidental landing limit of 1,000 pounds per trip was imposed on the industry until closure of the widow rockfish fishery at the end of September.

A coastwide acceptable biological catch (ABC) of 13,400 MT of sablefish was established for 1984 to achieve the OY of 17,400 MT. Harvest restrictions included continuance of the 22-inch size limit and a retention allowance of 5,000 pounds of undersized sablefish per trip. The ABC harvest guideline was not exceeded during the year, and no further restrictions were necessary. California's sablefish catch declined to 4,707 MT from the 1983 level of 6,509 MT. Several factors contributed to this decrease: notably, weak foreign demand, an absence of strong year classes of subadult fish, and the departure of two large trap-processor vessels from California waters.

Dover sole was landed in the greatest quantity of all groundfish species statewide: 9,744 MT. This species is typically harvested most intensively by trawl vessels near northern California ports. Yet in 1984 Morro Bay emerged as an important source of Dover sole: landings for this port increased from 350 MT in 1983 to 1,248 MT in 1984. The dominance in northern California landings of less desirable, deepwater dover sole, which have very soft, watery flesh, and better ocean conditions off Morro Bay are two probable reasons for this expansion. The set net fishery for rockfishes and lingcod continued to expand in central and southern California waters during the year. Conflicts with other user groups increased, as the fleet spread into fishing grounds traditionally exploited by trawl, troll, and sport vessels. Assessment of this important fishery has proved difficult.

In general, domestic demand for groundfish remained robust during the year, but fresh rockfish from British Columbia entered markets historically occupied by California rockfish, depressing wholesale prices. Weak ex-vessel prices and the stabilization of catches despite increased effort have created economic problems for a majority of the trawl fleet. By late 1984, many trawl fishermen were requesting a limitation on fishing effort through limited-entry or other alternative management measures.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings for the 1983-84 commercial season totaled 5.56 million pounds, slightly higher than 1982-83 seasonal landings of 5.33 million pounds.

December 1, opening day on the north coast, greeted fishermen with reasonable weather, a record opening price of $1.25 a pound, and low catches. By the end of January, 95% of the season's production was across the docks, and the price had risen to $1.85. Approval was given to extend the northern California season from July 15 to August 31. However, effort was minimal, and only 28,000 pounds were landed during this period. Fishermen noted that few sublegal crabs were in the traps, a sign that fishing might be poor for the 1984-85 season. Effort was slightly less than the previous season, when 432 vessels engaged in the fishery. Total landings for Crescent City, Trinidad, Eureka, and Fort Bragg were 3.21, 0.50, 0.79, and 0.20 million pounds, respectively.

San Francisco area Dungeness crab landings for the 1983-84 season were 0.86 million pounds, making it the best season of the past fourteen. The previous season's landings were 0.58 million pounds. Average landings for the past fourteen seasons are 0.50 million pounds. Bodega Bay, San Francisco, and Half Moon Bay landings were 0.25, 0.30, and 0.31 million pounds, respectively. Landings in this area were a little more evenly distributed throughout the 1983-84 season than during the previous season. In 1983-84, 57% of the season's total was landed in the first two months, compared with 76% for the same period in 1982-83.

The 1983-84 season opened November 8 in central California, with an ex-vessel price of $1.65 a pound. By mid-December, the price had reached $1.75, climbing to $2.00 by late January. By May, the price had reached $2.37, and fishermen expressed interest in extending the season from June 30 through the month of July. By the end of June, the price was $2.50 a pound, and there were about 20 boats fishing in the San Francisco area; because crab condition was reported to be good, the extension of the season through July was granted. Although many of the Half Moon Bay boats quit before the end of June, San Francisco landings increased, and 26,000 pounds were recorded during the season extension.

PACIFIC OCEAN SHRIMP

California's ocean shrimp (*Pandalus jordani*) fisheries reversed themselves during 1984 as ocean waters cooled to more normal temperatures. While the fishery off the north coast rebounded from record low landings in 1983, landings at the central California port of Morro Bay plummeted to a near-record low.

Shrimp landings from Area A (California-Oregon border to False Cape) totaled 1,107,266 pounds, a great improvement over the 568 pounds landed in 1983 but still well below the 1973-82 average of 4.6 million pounds. Although the season is from April 1 to October 31, no shrimp were landed until the last week in August. A total of 224,550 pounds caught in Oregon waters was landed in Crescent City during the season.

The price received by the fishermen was $0.45 a pound throughout the season. The number of vessels delivering shrimp to Area A ports was 35 (18 single rigged and 17 double rigged), the lowest number since 1977 (excluding 1983). Single-rigged boats had an average catch rate of 211.5 pounds per hour; double-rigged vessels averaged 381.6 pounds per hour for the season.

Shrimp landings in Morro Bay and Avila totaled 150,220 pounds, plus 4,113 pounds taken incidentally to spot prawn and ridgeback prawn fishing. This was the worst year since the fishery began off Morro Bay in 1979, with landings declining to only 15% of the nearly one million pounds landed in 1983. An ex-vessel price of only $0.40 a pound and declining catch per unit effort (CPUE) contributed to the low catch, because fishermen could not make enough money to continue targeting on shrimp. Readily available, low-priced, Norwegian frozen shrimp was a major factor in keeping the price down.

Only 10 vessels (3 single rigged and 7 double rigged) participated in the fishery. Individual vessels made from one to seven trips. Total hours fished fell to 597, down from 3,990 in 1983. Most of the catch came from the Point San Luis to Point Sal area, in water 80 to 120 fathoms deep, but tows were also made from 54 to 140 fathoms. CPUE started at over 200 pounds per hour for both types of vessels in April, but fell to less than 85 pounds per hour by June. No fishing at all occurred in July and August, because discouraged fishermen turned to other species. In September, two double-rigged boats found a bed of shrimp off Point Sal, and brought in two loads each. The fishery ended in early October with two landings totaling 17,000 pounds. Overall CPUE for double-rigged boats (242 pounds per hour) was higher than for single-rigged boats (141 pounds per hour). Total CPUE for all vessels was 201 pounds per hour. Most of the catch was transported to northern California for processing.

Average counts-per-pound ranged from 59 in April to 48 in October, and averaged 53 for the season. This was considerably lower than the 79 per pound in 1983, indicating the presence of older and larger shrimp in 1984. Two-year-olds constituted 66.2% of all shrimp sampled. Whereas transitionals were most abundant during 1983, females dominated the sex composition in 1984. If recruitment is poor, 1985 landings should be predominately 3-year-old females.

PELAGIC SHARK AND SWORDFISH

During 1984, 258 permits were issued to harpoon fishermen to take swordfish (*Xiphias gladius*), and 225 drift gill net permits were issued for taking pelagic sharks and swordfish. In addition, a special category of drift gill net swordfish permits, authorizing fishing north of Point Arguello only, was established by the California legislature. Of a possible 35 such permits, 30 were issued.

Harpoon fishermen met with moderate success in 1984, reporting 1,068 swordfish on logbooks. In October, an eight-year ban on the use of spotter aircraft as an aid to harpooning was repealed by the CFGC. That decision came too late to improve the 1984 season, but could add significantly to the harpoon success rate in subsequent years.

For the second consecutive season, drift gillnetters set a new record for reported catches of swordfish. Logbook submittals indicated 25,367 fish caught for the 1984-85 season (May through January). The previous record, set during the 1983-84 season, amounted to a reported 21,000 fish. The California-based drift gill net swordfish fleet continued to expand its area of operation during 1984. Waters adjacent to the escarpment, which borders the Southern California Bight, proved to be very productive fishing grounds. Other productive areas included the offshore Rodriguez and San Juan seamounts.

Preliminary 1984 annual landings of swordfish also established a new high. The estimated 4.4 million pounds with an ex-vessel value of $11.6 million easily eclipsed the previous highs of 2.6 million pounds in 1978 and 1983.

Common thresher shark (*Alopias vulpinus*) landings declined for the second consecutive year, with just over 1.5 million pounds having been taken. The final landings figures for 1983 indicated a total catch of 1.7 million pounds. Analysis of trends in the length composition, and continued declines in CPUE indicate that common thresher stocks may not be able to sustain current levels of harvest. Discussions are currently underway with representatives of the gill net industry concerning the need for reducing fishing effort. The main topic of discussion centers around the springtime fishery. This is the period when common thresher sharks are most available and swordfish are least available.

CALIFORNIA SPINY LOBSTER

Daily log returns from the 1983-84 commercial California spiny lobster (*Panulirus interruptus*) fishery documented the largest effort in the 11-year history of logbook submittal. The 221-boat fleet made almost 540,000 trap hauls, an increase of 9% over the previous season.

Log returns estimated that traps retained 486,000 sublegals ("shorts")—a 0.9 catch-per-trap (CPT) rate, which is the highest since sublegal escape ports were added to traps beginning in the 1976-77 season. This continuation of an 8-year trend of increased CPT on sublegals, even in the face of mounting effort, may reflect improved juvenile survivorship enhanced by the escape port addition.

A total of almost 324,000 legal-sized lobster were reported on logs during the season (first Wednesday in October to first Wednesday after March 15), with an estimated weight of 511,500 pounds and an estimated ex-vessel value of $1.9 million. This represents a catch almost double that reported for the 1973-74 season, when logs were first implemented. Still, total landing estimates for 1983-84 were only half that of the postwar bonanza of the early 1950s, which was the peak of historical annual landings dating back to 1916.

Comparing the 1983-84 legal CPT rates with the 11-year logbook record, the season could be considered average at 0.6 legals (0.956 pounds) per trap hauled.

As usual, fishermen expended most of their effort in the early season, with 37% of the season's trap-hauls made in October, 24% in November, and 15% in December. Effort continued to decline linearly thereafter, with only 4% of trap-hauls occurring in the closing month of March.

Catch success, averaging 1.7 pounds per hundred trap hours for the season, repeated a typical seasonal trend. Whereas nearly 3 pounds per hundred trap hours were recorded during the opening month, catch rates declined rapidly to 1.0 pounds in December, and then recovered well during the last half of the season, increasing to 1.8 pounds per hundred trap hours by March.

The southern California fishery was most concentrated along the mainland. Approximately 54% of the catch was taken by 68% of the effort (trap-hauls) in coastal waters south of Santa Monica Bay. Increased catch success occurred farther from port; fishermen at Channel Islands and Cortez Bank reported taking 34% of the catch with only 23% of the effort. Low trapping densities occurred in coastal waters from Malibu Point to Point Arguello, where fishermen trapped 12% of the catch with 8% of the effort.

Record effort levels in recent years have brought about increased friction, especially among the participants in the high trapping densities of crowded, productive, local fishing grounds. Veteran year-round lobster fishermen voiced increasing resentment over part-time "opportunists" who fish briefly at the season opening, when high catchability and availability of first-season recruits (brought on by summer molting) maximizes catch rates. Marginal operations, beset by the downward fluctuations of the fishery (initial log summaries indicate fall 1984 catches are 20% below average) have increased vocalization of this resentment. Limited entry and limitations on the number of traps per fisherman are management schemes often suggested by fishermen. Since preliminary evaluation of log returns gives no evidence of a persistent downward trend in CPUE, such management measures may not be biologically justifiable at this time.

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THE 1984 SPAWNING BIOMASS OF THE NORTHERN ANCHOVY

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ABSTRACT

The 1984 estimate of the spawning biomass of the central subpopulation of the northern anchovy (*Engraulis mordax*) is 309,000 metric tons (MT). The estimate was obtained using the egg production method, where biomass is defined as the ratio of the daily production of eggs found in the sea and the daily specific fecundity of the population.

In 1984, as in 1983, the central subpopulation of northern anchovy was geographically distributed more offshore and northerly than in previous years. Spawning was apparent throughout the southern portion of the Southern California Bight as far south as the latitude of Ensenada; no spawning was evident within 50 km of the coast between San Diego and Ensenada. A small amount of spawning was detected adjacent to the coast between San Francisco and Monterey bays, California, and between Cape Colnette and Punta Baja, Baja California.

RESUMEN

El valor estimado de la biomasa de desove de la subpoblación central de la anchoveta del norte (*Engraulis mordax*), para 1984, es de 309.000 toneladas métricas (TM). Esta estimación se obtuvo utilizando el método de la producción de huevos, en el cual la biomasa se define como el cociente entre la producción diaria de huevos colectados en el océano y la fecundidad específica diaria de la población.

En 1984, al igual que en 1983, la subpoblación central de la anchoveta del norte estuvo distribuída más lejos de la costa y más al norte que en años anteriores. A lo largo de la parte sur de la Bahia del Sur de California y, hacia el sur, hasta la latitud de Ensenada, hubo señales de desove. No se observaron evidencias de aquél hasta 50 km mar adentro entre San Diego y Ensenada. Pequeñas cantidades de desove se detectaron en la vecindad de la costa entre las bahías de San Francisco y Monterey, California, y entre Cabo Colnette y Punta Baja, Baja California.

INTRODUCTION

This report documents the 1984 spawning biomass estimate of the central subpopulation of the northern anchovy (*Engraulis mordax*), as required by the most recent version of the Anchovy Management Plan adopted by the Pacific Fishery Management Council (PFMC 1983). In recent years the anchovy biomass has been assessed using two ichthyoplankton-based methods: larval census (Smith 1972; Stauffer and Parker 1980; Stauffer 1980; Stauffer and Picquelle 1981) and egg production (Parker 1980; Stauffer and Picquelle 1980; Picquelle and Hewitt 1983, 1984). The larval census method assumes a constant proportionality between larval abundance and spawning biomass, whereas the egg production method measures and incorporates variability in the proportionality parameter. Only the egg production method was used to calculate the 1984 spawning biomass.

The egg production method defines spawning biomass as the ratio of the daily production of eggs and the daily specific fecundity of the adult population. The daily production of eggs was derived from the density of eggs sampled in an ichthyoplankton survey, and from egg development rates as measured in the laboratory. The daily specific fecundity of the anchovy population was derived from adult fish sampled during a trawl survey, which yielded estimates of average female weight, batch fecundity, sex ratio, and the proportion of females spawning each night. The two samples were obtained concurrently on a survey conducted during the seasonal peak of spawning.

This report describes the survey results, the egg production estimate of spawning biomass, and the variance of the estimate.

DESCRIPTION OF THE SURVEY

The 1984 survey was conducted by the NOAA ship *David Starr Jordan* from February 7 through March 30, 1984. The survey area extended from San Francisco, California (38°N), to Punta Baja, Baja California (30°N), approximately 250 km offshore in the main spawning region. The station pattern (Figure 1) was occupied from north to south, with the exception of the area between San Diego and Punta Baja. During the last portion of the survey, five station lines, spaced 40 miles apart and extending offshore, were occupied while the ship worked to the south, and twelve inshore lines, spaced 10 miles apart, were occupied while northbound to San Diego.

Planktonic eggs were sampled at 938 stations (Figure 1) using a 25-cm-diameter net of 150-micron

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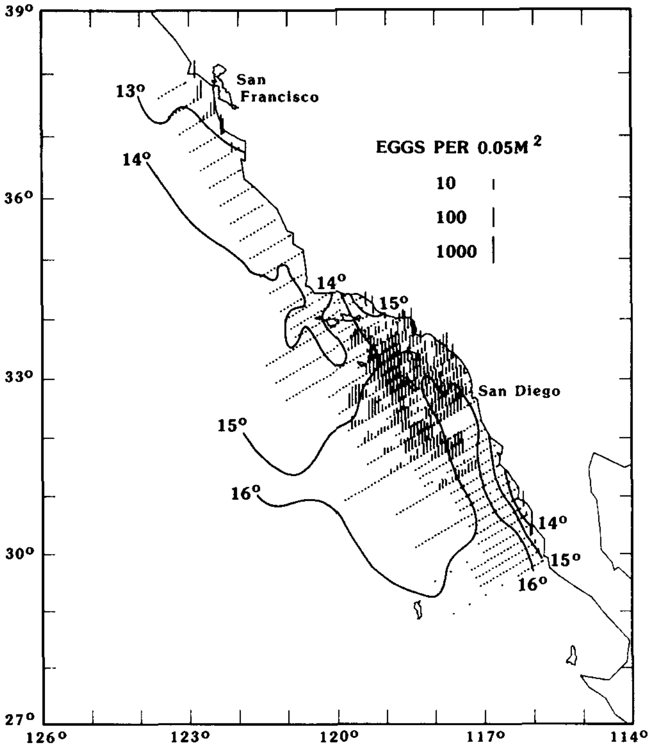

Figure 1. Geographic distribution of ichthyoplankton stations, anchovy eggs, and surface isotherms.

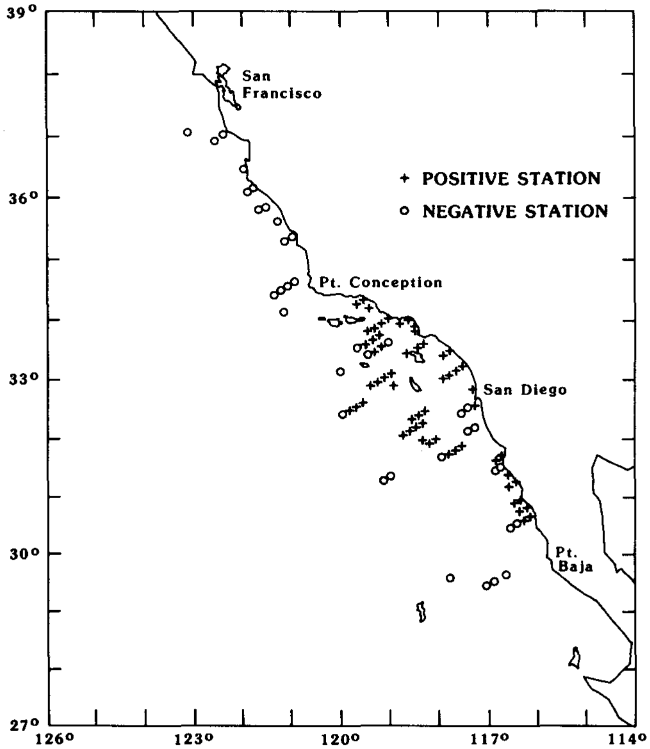

Figure 2. Geographic distribution of trawl stations.

mesh, retrieved vertically to the surface from a depth of 70 m; anchovy eggs were found in 384 of the 938 plankton tows. Planktonic samples were collected at all hours. Adults were sampled between 1800 and 0200 hours at 96 stations (Figure 2) using a 15-m^2 trawl with a 2-mm mesh liner; anchovies were caught in 66 of the trawl stations. (For a detailed description of field operations, see Cruise Report 8403-JD, dated May 31, 1984, William Flerx, Southwest Fisheries Center, La Jolla, California).

The geographic distribution of anchovy eggs was similar to that observed in 1983 and unlike previous years. In both 1983 and 1984 the range extended farther offshore, and a smaller proportion of eggs was taken off Baja California than in previous years. The distribution in 1984 was unique in that virtually no spawning was evident within 50 km of the northern coast of Baja California, although adult anchovies were caught in this area. Farther south and separate from the main spawning area, a few eggs were found very near shore between Cape Colnette and Punta Baja. Another inshore spawning area, separate from the main area, was detected extending from Monterey Bay to Point Reyes, north of the entrance to San Francisco Bay. This localized area of spawning has been evident in previous years. With the exception of northern Baja California, where the sampled fish were immature, the occurrence of positive trawls agreed well with the distribution of eggs. The egg and trawl surveys appear to have provided good sample coverage of the central subpopulation of northern anchovy in 1984.

There was an apparent correlation between the northern edge of spawning and the 14.5° isotherm; no correlation was evident along the southern boundary. A correlation between the range of the spawning population and temperature isotherms has been noted in previous years (Lasker et al. 1981; Picquelle and Hewitt 1983).

BIOMASS MODEL

The egg production estimate of anchovy spawning biomass and its variance is defined as:

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

$$\mathrm{Var}\,(B) \cong B^2 \times$$
$$\Bigg\{ \frac{\mathrm{Var}\,(P_o)}{P_o^{\,2}} + \frac{\mathrm{Var}\,(W)}{W^2} + \frac{\mathrm{Var}\,(R)}{R^2} + \frac{\mathrm{Var}\,(F)}{F^2} + \frac{\mathrm{Var}\,(S)}{S^2} +$$
$$2\Bigg[\frac{\mathrm{Cov}\,(P_o W)}{P_o W} - \frac{\mathrm{Cov}\,(P_o R)}{P_o R} - \frac{\mathrm{Cov}\,(P_o F)}{P_o F} - \frac{\mathrm{Cov}\,(P_o S)}{P_o S} - \frac{\mathrm{Cov}\,(WR)}{WR} - \qquad (2)$$
$$\frac{\mathrm{Cov}\,(WF)}{WF} - \frac{\mathrm{Cov}\,(WS)}{WS} + \frac{\mathrm{Cov}\,(RF)}{RF} + \frac{\mathrm{Cov}\,(RS)}{RS} + \frac{\mathrm{Cov}\,(FS)}{FS} \Bigg] \Bigg\}$$

where B = spawning biomass in metric tons,
P_o = daily egg production rate in number of eggs per day per 0.05 m^2,
W = average weight of mature females in grams (g),
R = female fraction of the population by weight,
F = batch fecundity in number of eggs,
S = fraction of mature females spawning per day,
A = area of survey in units of 0.05 m^2, and
k = conversion factor from grams to metric tons (10^{-6} MT/g).

These expressions were developed by Parker (1980) and Stauffer and Picquelle (1980) and were used by Picquelle and Hewitt (1983, 1984).

DAILY PRODUCTION OF EGGS

The parameter $P_o A$, the daily production of eggs, is the survey area multiplied by the number of eggs spawned per night per unit area, averaged over the range and duration of the survey. Eggs were enumerated by stage of embryonic development, and were aged using temperature-dependent development rates and assuming that spawning occurs at 2200 hours each night. An exponential mortality model was fit to the egg data by assuming constant instantaneous rate of mortality. The daily egg production rate was estimated as the value of the predicted curve at the time of spawning.

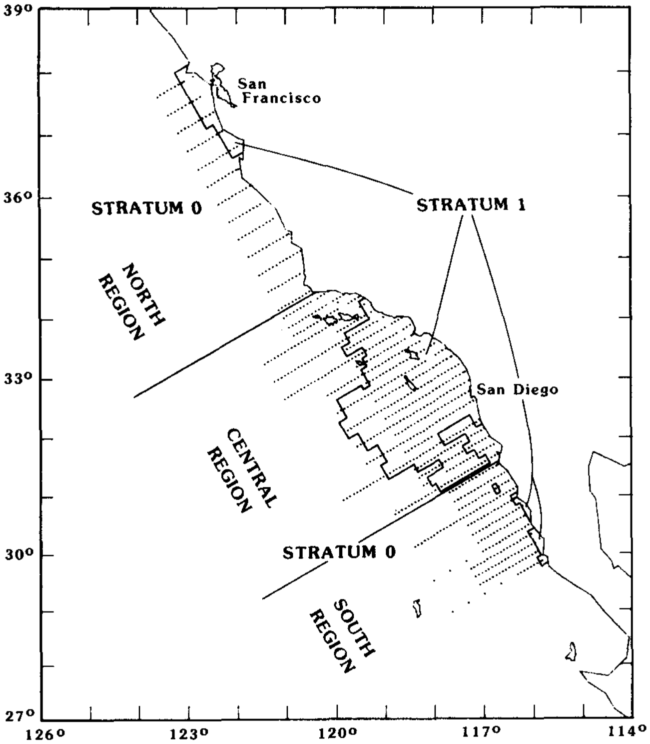

Figure 3. Subdivision of 1984 survey into strata (stratum 1 is the spawning area, and stratum 0 is devoid of eggs) and geographic regions (north, central, and south).

The egg counts were analyzed using a two-stage systematic sampling scheme (Picquelle and Hewitt 1983). First, each station was assigned a weight proportional to the area the station represents; second, the stations were stratified by location, where stratum 1 was defined as the geographic area of spawning, and stratum 0 was that area devoid of eggs (Figure 3). The exponential mortality model

$$P_{jt} = P_o^1 e^{-Zt} \qquad (3)$$

was fit to the data by a weighted nonlinear least squares regression,

where P_{jt} = the number of eggs from the jth station of age t,
t = the age in days measured as the elapsed time from the time of spawning to the time of sampling at the jth station (because spawning occurs once a day and because the incubation period was 3 days or less, as many as 3 cohorts of eggs could be found at each station),
Z = the instantaneous rate of mortality on a daily basis, and
P_o^1 = the daily egg production rate in stratum 1.

The data and fitted curve are described in Figure 4. The daily egg production rate in stratum 0 is zero, and the daily egg production rate for the total survey area

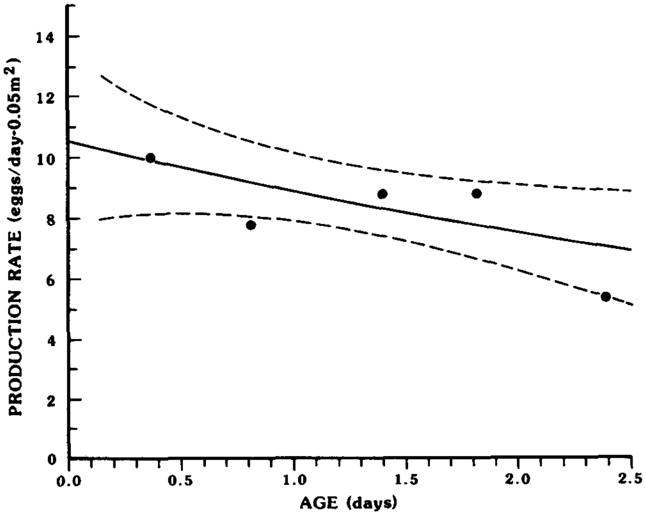

Figure 4. Egg production curve. The data is summarized as the mean abundance by half-day intervals, although the regression was fit to the individual data points. A 95% confidence region for the regression (broken line) is indicated.

TABLE 1
Parameters for Computing the Daily Production of Eggs

	Stratum 0	Stratum 1	Total survey
P_o	0	10.55	3.79
var (P_o)	0	1.66	0.60
Z	0	0.17	0.17
var (Z)	0	0.008	0.008
A	2.195×10^{12}	1.231×10^{12}	3.426×10^{12}
$P_o A$			12.98×10^{12}
var ($P_o A$)			7.02×10^{24}

and its variance (adjusted for postsurvey stratification; Jessen 1978) is:

$$P_o = \frac{A_1}{A} P_o{}' \tag{4}$$

$$\mathrm{Var}(P_o) = (1 + 1/n)[(A_1/A)\ \mathrm{Var}(P_o{}')] \tag{5}$$

where n = the total number of stations,
A_1 = the area of stratum 1, and
A = the total survey area.

The estimates for computing the daily production of eggs and their variances appear in Table 1.

ADULT PARAMETERS *W*, *F*, *S*, AND *R*

The parameters W, F, S, and R were estimated from a sample of adult anchovies collected by the midwater trawl. Each parameter was estimated by a weighted sample mean ($\bar{\bar{y}}$) with a weighted variance (Cochran 1963):

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

$$\mathrm{Var}(\bar{\bar{y}}) = \frac{\sum_{i=1}^{n} \left[\left(\frac{m_i}{\bar{m}}\right)^2 (\bar{y}_i - \bar{\bar{y}})^2\right]}{n(n-1)} \tag{7}$$

where m_i = the number of fish subsampled from the ith trawl,
$\bar{m}$ = the average number of fish subsampled per trawl,
n = the number of positive trawls,
$\bar{y}_i$ = the average value for the ith trawl = $\sum_{j=1}^{m_i} y_{ij}/m_i$ and
y_{ij} = the observed value for the jth fish in the ith trawl.

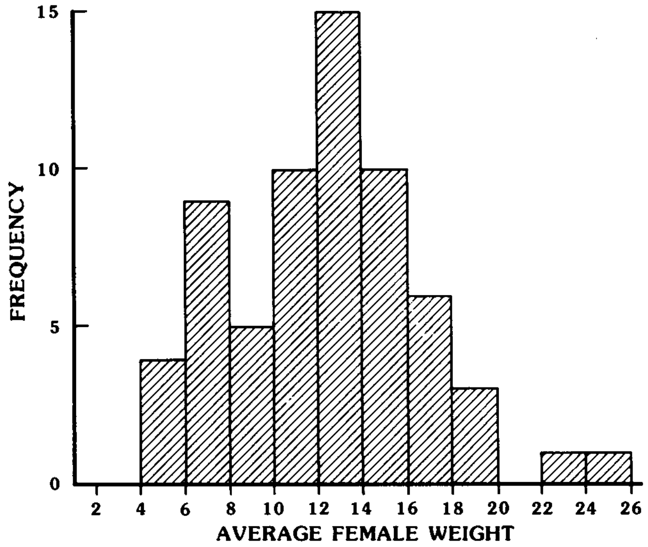

Figure 5. Frequency distribution of average mature female weight per trawl.

Average Female Weight

The average female weight was calculated using the above equations where $\bar{y}_i$ was the average female weight for the ith trawl. The desired subsample size was 25 fish from each trawl; however, this was not always possible for small trawl catches or for catches composed predominately of immature fish. The weight of females with hydrated eggs was adjusted for the extra weight of the fluid in their ovaries by measuring their ovary-free weight and estimating the whole-body weight of a female without hydrated eggs. The following regression, estimated from mature females without hydrated eggs, was used:

$$W = -0.176 + 1.06\,W^* \tag{8}$$

where W = estimated whole-body weight in grams, and
W^* = ovary-free weight in grams.

This regression had an $r^2 = 0.998$. The frequency distribution of average weight per trawl is described in Figure 5. the average female weight for the survey and its variance are listed in Table 2.

Batch Fecundity

Batch fecundity for each mature female was estimated from a regression of fecundity on ovary-free weight estimated from a sample of 75 hydrated females. The sample was selected so that the ovary-free weight distribution was similar to the ovary-free weight distribution of all the mature females (Figure 6). The regression model selected was:

$$F = -509 + 523\,W^* \tag{9}$$

TABLE 2
Estimates of Egg Production Parameters, Variances, and Coefficients of Variation

Parameter		Value	Variance	Coefficient of variation
Daily egg production (10^{12} eggs/day)	($P_o A$)	12.98	2.51	12.2%
Average female weight (g)	(W)	12.0170	0.21047	3.8
Batch fecundity (eggs)	(F)	5485.	96920.	5.7
Spawning fraction (day^{-1})	(S)	0.1597	0.00026	10.0
Female fraction	(R)	0.5820	0.00095	5.3
Daily specific fecundity (10^6 eggs/dayMT)		42.433		
Spawning biomass (MT)	(B)	306,000	2,547,706,812	16.5

where F = estimated fecundity for a female with W^* ovary-free weight (Figure 7). This regression had an $r^2 = 0.783$. Average batch fecundity for the survey was estimated using equation 6 where $y_{ij} = F_{ij}$ and the desired m_i was 25 mature females. The variance estimate (equation 7) was modified to include the extra source of variance from the batch fecundity/ovary-free weight regression (Draper and Smith 1966):

$$\mathrm{Var}(\bar{\bar{F}}) = \frac{\sum_{i=1}^{n} \left\{ \left(\frac{m_i}{\bar{m}} \right)^2 \left[\frac{(\bar{F}_i - \bar{\bar{F}})^2}{n-1} + \frac{S_h{}^2}{75} + (\bar{W}_i{}^* - \bar{W}_h{}^*)^2 \, \widehat{\mathrm{Var}}(b) \right] \right\}}{n} \tag{10}$$

where $S_h{}^2 = 2{,}291{,}706$ is the variance about the regression,
$\bar{W}_i{}^*$ = average ovary-free weight for the ith trawl,
$\bar{W}_h{}^* = 11.95$ gr, average ovary-free weight of the 75 hydrated females used in the regression,
$\widehat{\mathrm{Var}}(b) = 1041$, variance of the slope of the regression, and
n = number of positive trawls.

The average batch fecundity for the survey and its variance are listed in Table 2.

Spawning Fraction

The spawning fraction, S, and its variance were estimated using equation 6 where $\bar{y}_i = S_i$ was the proportion of mature females in the ith trawl that spawned one night prior to capture (day-1 spawners). The desired m_i was 25 mature females. Based on previous experience (Picquelle and Hewitt 1983), it was suspected that females spawning on the night of capture (day-0 spawners) were oversampled by the trawl, thus biasing the proportion of day-1 spawners. To compensate for the potential bias, it was assumed

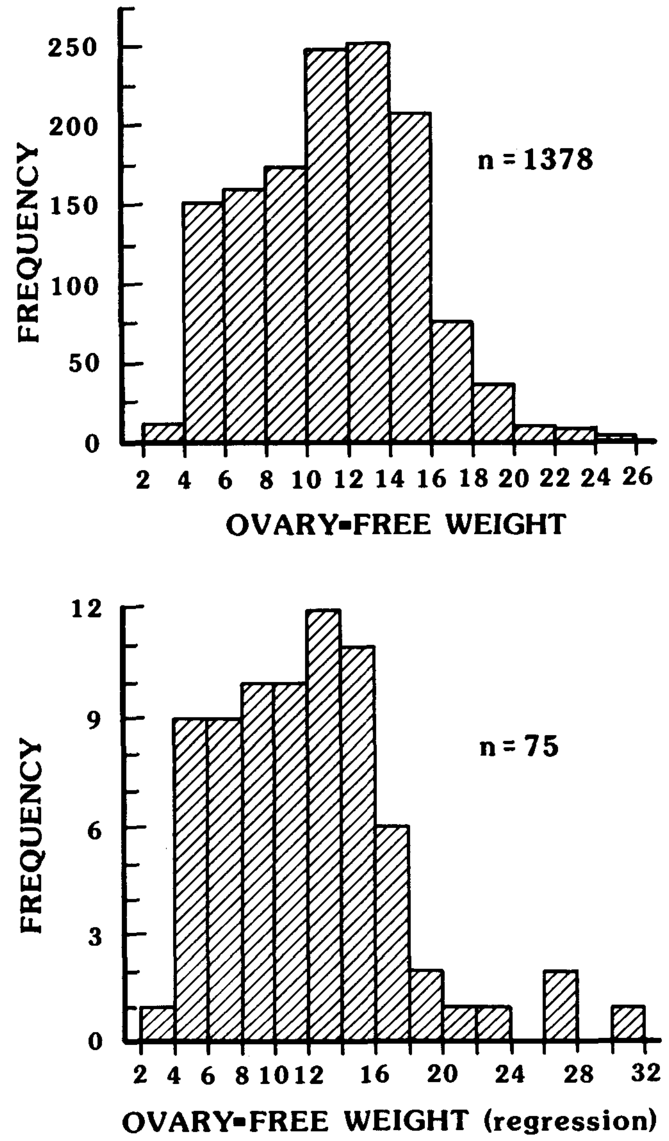

Figure 6. Frequency distributions of ovary-free weight for the entire survey (top) and for the females with hydrated ovaries used to estimate the batch fecundity/ovary-free weight regression.

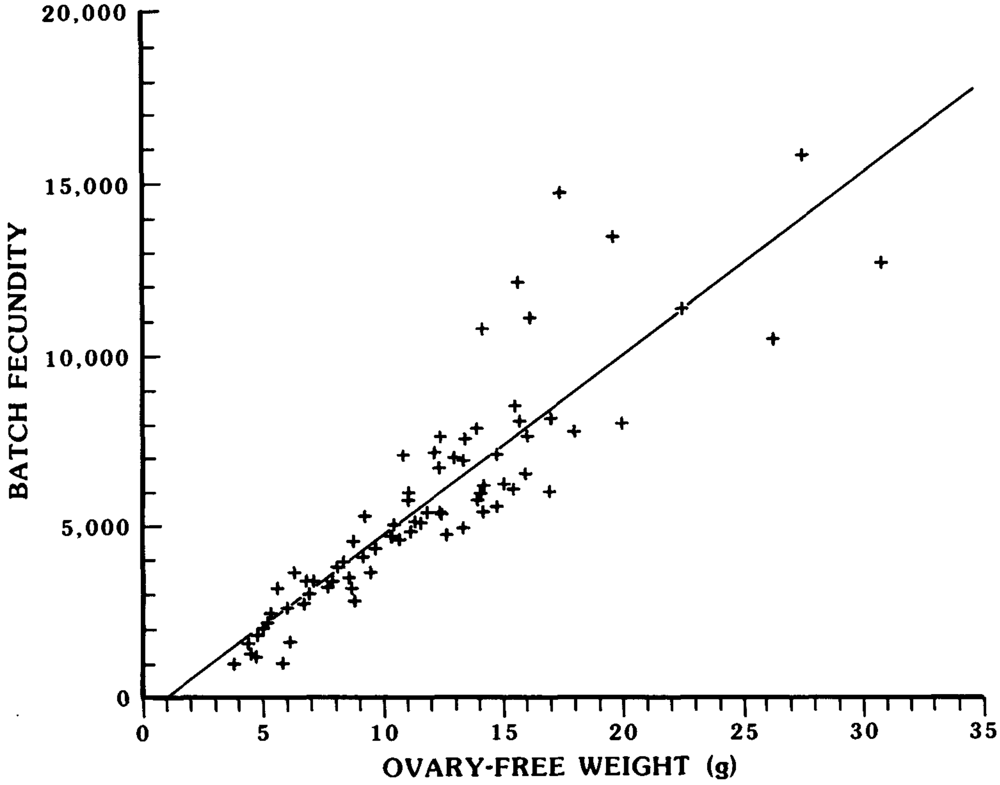

Figure 7. Linear regression of batch fecundity on ovary-free weight fit to 75 females with hydrated ovaries.

that the true proportion of day-0 spawners was equal to the observed proportion of day-1 spawners: the value of m_i in equations 6 and 7 is adjusted by deleting day-0 spawners from the sample and equating the number of day-0 spawners to the number of day-1 spawners, thus reducing the average subsample size, $\bar{m}$. The frequency distribution of the spawning fraction per trawl is described in Figure 8; the estimated spawning fraction for the survey and its variance are listed in Table 2.

Female Fraction

The female fraction, R, was measured as the fraction of females in the population by weight. Equations 6 and 7 were used by setting $\bar{y}_i = R_i$, where R_i is the estimated total weight of females in a subsample of 50 fish divided by the estimated total weight of the subsample; m_i was set equal to the total weight of the subsample. The average male and female weights for each trawl were estimated from 5 males and 25 females where the weight of any hydrated female was adjusted using equation 8. The frequency distribution of female fraction per trawl is described in Figure 9; the estimated female fraction for the survey and its variance are listed in Table 2.

BIOMASS ESTIMATE AND VARIANCE

The parameter estimates, their variances, coefficients of variation, and covariances are listed in Tables 2 and 3. The sample covariance terms were calculated only for the adult parameters. Because the daily egg production and the adult parameters were estimated from different samples, it was not possible to estimate their covariances, and they were assumed to be zero. The biomass estimate and its variance were

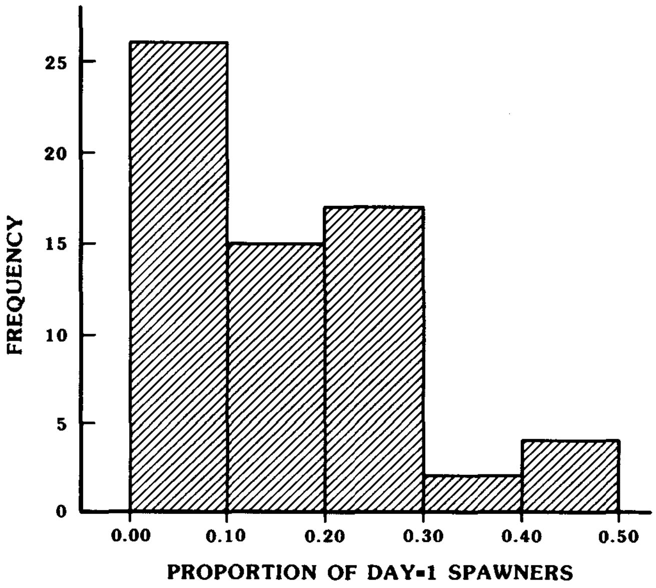

Figure 8. Frequency distribution of spawning fraction. Large portion of lowest class represents nonspawning fish from off northern Baja California.

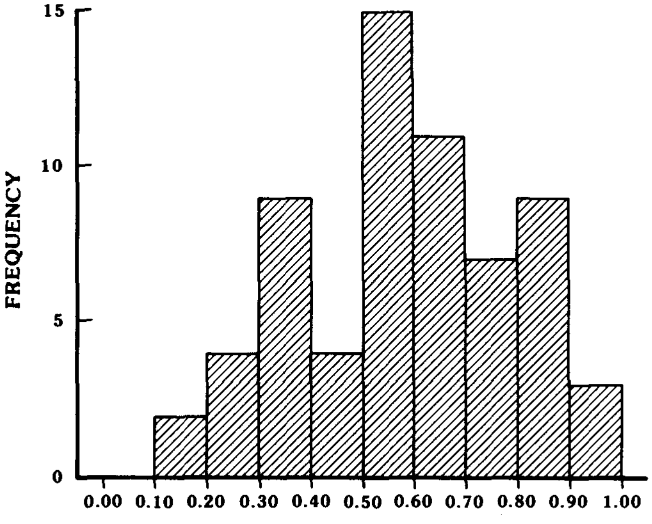

Figure 9. Frequency distribution of female fraction by weight.

calculated using equations 1 and 2. The estimate of spawning biomass was 306,000 MT, with a standard error of 50,475 MT.

The survey was subsequently divided into three geographic regions (Figure 3) corresponding to the three distinct spawning areas. Daily egg production and daily specific fecundity were calculated for each region (Table 4). Because of the small number of trawls in the north and south regions, the estimate of the female fraction by weight (*R*) was unreliable; *R* was thus estimated for the entire survey and was assumed to be similar among regions. Since the parameter values for the three regions were very different (Table 4), homogeneity could not be assumed. Biomasses were calculated separately for each region and were summed to produce the final estimate of 309,000 MT. This estimate is not very different from the unregionalized estimate but should be more accurate. I was not able to produce a corresponding estimate of the total variance because some of the variances and covariances could not be calculated for the individual regions.

TABLE 3
Covariances between Adult Parameters

	F	*S*	*R*
Female weight (*W*)	103.341133	0.00061	0.00085401
Batch fecundity (*F*)		0.30792	0.43871200
Spawning fraction (*S*)			−0.00009186
Female fraction (*R*)			

DISCUSSION

The 1984 estimate of the spawning biomass of the central subpopulation of the northern anchovy is less than half of the 1983 estimate (Table 5). Daily egg production by the population is down 25% from 1983, and the daily specific fecundity is up 75% from 1983. The daily specific fecundity is the highest ever estimated over the last five years and results from a high spawning fraction and a high female fraction by weight. Although the average female weight is slightly larger than the 1983 value, both years are low relative to the previous four surveys. Average batch fecundity is not unusual for the average female weight. This survey indicates that the spawning population comprises predominately small, young females with their center of distribution off southern California.

The geographical distribution of anchovies found in this survey agrees with an earlier report by the California Department of Fish and Game, (CDFG). K.F. Mais (Cruise Report 84-X-1, CDFG, Long Beach, California) conducted an extensive sonar and trawl survey from Point Conception, California, south to Punta Baja, Baja California, in February 1984. He reported that the anchovy central subpopulation was distributed more north and offshore than it was pre-

TABLE 4
Regional Estimates of Egg Production Parameters

Parameter		North region	Central region	South region
Daily egg production (10^{12} eggs/day)	($P_o A$)	2.00	5.42	0.14
Average female weight	(*W*)	14.18	12.57	9.06
Batch fecundity	(*F*)	6584	5752	4043
Spawning fraction	(*S*)	0.1052	0.1748	0.0891
Female fraction	(*R*)	0.5820	0.5820	0.5820
Daily specific fecundity		28.44	46.57	23.15
Spawning biomass	(*B*)	70,300	234,400	4,000
Total biomass		308,700		

TABLE 5
Time Series of Egg Production Parameters

		1980	1981 (Feb.)	1981 (Apr.)	1982	1983	1984
Daily egg production (10^{12} eggs/day)	($P_0 A$)	26.34	20.96	12.59	13.51	17.25	12.98
Average female weight	(W)	17.44	13.37	16.20	18.83	11.20	12.02
Batch fecundity	(F)	7,751	8,329	8,846	10,845	5,297	5,485
Spawning fraction	(S)	0.142	0.106	0.125	0.120	0.094	0.160
Female fraction	(R)	0.478	0.501	0.495	0.472	0.549	0.582
Daily specific fecundity (10^6 eggs/day-MT)		30.28	33.03	33.84	32.53	24.35	42.43
Spawning biomass (10^3 MT)	(B)	870	635	372	415	652	309
Calif. Dept. Fish and Game acoustic biomass estimate (10^3 MT)		498 to 598	493 to 591		233 to 247	461 to 504	479 to 560

vious to 1983. Mais estimated the biomass (including immature nonspawning fish) to be between 479,000 and 560,000 MT (Table 5). He also reported evidence of a relatively strong 1982 year class and weak 1981 and 1983 cohorts; fish of all ages were unusually small. Since 1980, acoustic abundance estimates have tended to be lower than those obtained by the egg production method (Table 5). This year's survey is unusual in that the acoustic survey results are substantially larger than the egg production method estimate. The young, nonspawning fish observed off northern Baja California, which were not included in the egg production method estimate, may account for some of this discrepancy.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

IDYLLWILD, CALIFORNIA

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COMPARATIVE STUDIES OF EASTERN OCEAN BOUNDARY SYSTEMS

COMPARATIVE STUDIES AND THE RECRUITMENT PROBLEM: SEARCHING FOR GENERALIZATIONS

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ABSTRACT

Empirical attempts to relate recruitment variation to variability in the environment or in the biological community have not been notably successful. This is due in part to the very short data series generally available for empirical analysis. Obviously, we must develop generalizations to provide a basis for unifying the available fragments of experience in a coherent framework.

The ecosystems of the four major subtropical eastern ocean boundary regions, i.e., the California, Peru, Canary, and Benguela current regions, appear to be controlled by similar environmental dynamics (characteristic late spring distributions of coastal temperature anomaly and Ekman transport for the four regional systems, supplementing previously reported winter and summer distributions, are presented). These regions contain very similar assemblages of exploitable pelagic fishes, and exhibit comparable histories of fishery growth and abrupt decline. The similarities suggest that fish communities in these different systems may function alike with respect to their environments and may have reproductive strategies for similar environmental problems. Because natural selection implies that reproductive strategies are responses to the most crucial factors regulating reproductive success, compelling patterns of correspondence among reproductive habits and environmental characteristics are likely to reflect important causal mechanisms. Such findings, which are independent of time series results, furnish a guide for selecting variables for time series modeling in a way that makes improved use of the minimal degrees of freedom that are available.

Beyond comparisons of spawning habitat climatology, it may be fruitful to compare actual time series relationships among similar regional ecosystems (a number of recent studies showing environmental/biological relationships for eastern boundary pelagic fishery stocks are cited). Under an assumption of analogy, weak empirical relationships having a similar general form in several systems could be assigned greater confidence than otherwise warranted. Conversely, a high correlation found in one system might be questioned if no suggestion of a similar linkage were found in other systems appearing to be analogous. Arraying identically formulated empirical models from different regional systems might yield patterns among model parameters that could provide insights for predicting effects of human actions or natural perturbations on a given system from the record of previous similar events in other systems.

RESUMEN

Los intentos empíricos de relacionar las variaciones en el reclutamiento con variaciones ambientales o en las comunidades biológicas no han sido demasiado exitosos. Ello se debe, en parte, a las series demasiado breves de datos que generalmente se dispone para los análisis empíricos. Es obvio que debemos desarrollar generalizaciones para proveer una base con el fin de unificar los fragmentos de experiencia disponibles en un marco de trabajo coherente.

Los ecosistemas de las cuatro principales regiones de corrientes de margen oriental, *i.e.*, California, Perú, Canarias, y Benguela, parecen estar controlados por esquemas dinámicos semejantes (se presentan las distribuciones primaveral tardía características de anomalías térmicas costeras y transporte de Ekman en los cuatro sistemas regionales, complementando la información previa acerca de las distribuciones invernal y estival). Estas regiones contienen conjuntos de peces explotables muy semejantes e historias similares en lo que se refiere al crecimiento y abrupta declinación de las pesquerías. Estas semejanzas sugieren que las comunidades de peces en estos sistemas diferentes pueden funcionar de manera semejante con respecto a sus ambientes, y pueden tener estrategias reproductivas para problemas ambientales similares. Dado que la selección natural implica que las estrategias reproductivas consistan en respuestas a los factores más importantes que regulan el éxito reproductivo, los obligatoriamente análogos modelos de hábitos reproductivos y de características ambientales pueden reflejar mecanismos causales importantes. Estos hallazgos, que son independientes de los resultados de las series temporales, proveen una guía para seleccionar variables para modelos de series de tiempo de manera tal que se optimiza el aprovechamiento de la cantidad mínima de grados de libertad disponibles.

Mas allá de la comparación de la climatología de los habitat de desove, puede resultar provechoso comparar las relaciones entre series de tiempo reales entre ecosistemas regionales similares (se mencionan varios estudios recientes que muestran las relaciones ambientales/biológicas en stocks pesqueros pelágicos en áreas de margen oriental). Asumiendo la analogía, podría asignarse mayor confianza a las relaciones empíricas débiles que poseen un formato general semejante en varios sistemas. Recíprocamente, una alta correlación en un sistema podría ser cuestionada si no se encuentra evidencia de una vinculación semejante en otros sistemas que parecen ser análogos al primero. El ordenamiento de modelos empíricos de formulación idéntica provenientes de sistemas regionales diferentes puede brindar patrones entre los parámetros de los models; estos patrones podrían suministrar información útil para predecir los efectos del accionar humano o de las perturbaciones naturales sobre un sistema dado, sobre la base del registro de eventos anteriores semejantes.

INTRODUCTION

The recruitment problem, which has been called the central problem of fish population dynamics (Beyer 1981), remains unsolved after decades of scientific interest and effort. The term "recruitment" refers to *the quantity of younger fish surviving the various egg, larval, juvenile, etc., stages to reach a size at which they become susceptible to fishing gear and thus begin to be sampled by the fishery.* The term therefore integrates the entire period during which the populations are invisible to humans, between the formation of reproductive products in the parental fishes and the later remanifestation of these products as progeny of harvestable size. It thus spans a lengthy continuum of susceptibilities to mortality involving a great range of processes by which the thousands of eggs spawned in the lifetime of a given female must, on average, be reduced to approximately two surviving adult fish.

As might be expected from such a tenuous chain of circumstances, recruitment is notoriously variable. In populations of fishes like anchovies, sardines, and mackerels, the ratio between parental stock size and resulting recruitment typically varies from year to year by factors up to several hundred. Such extreme variability, since it cannot be accounted for mechanistically, introduces a very large noise component into fishery population time series, and largely obscures the signals essential for managing human impacts on the biological system. These signals include evidences of stock-recruitment relationships, multispecies interactions, etc.—knowledge of which could govern fishery development and management strategies. Indeed, the need to account for quasi-random, large-amplitude variations in order to reveal essential mechanisms responding to human alterations of marine biological population structures probably presents, in many cases, a stronger argument for scientific efforts on the recruitment question than does the more often cited need for early prediction of a following year's recruitment. In recognition of the need for progress in this area, an International Recruitment Project (IREP) is the primary focus of the major new international program Ocean Science in Relation to Living Resources, cosponsored by the Intergovernmental Oceanographic Commission and the Food and Agriculture Organization of the United Nations (Anon 1985). For CalCOFI, in particular, the recruitment question could be considered the core scientific issue (Marine Research Committee 1950).

There seems to have been a remarkable lack of progress since the importance of the recruitment problem was recognized early in this century. However, when one considers the nearly total lack of direct information about the fairly complex series of events involving nutrition and associated growth or starvation; predation (which is size-dependent and therefore growth-dependent); transport processes (perturbations of which may disrupt well-tuned adaptations for placing large numbers of individuals in proper habitats for required life-cycle transitions); physiological stresses; etc., the problem's resistance to solution is not so surprising (Table 1). In addition, even where some data are obtainable, difficulties in coping with the interference of strong intrinsic annual periodicities has led to a conventional practice of pooling shorter-scale variations into annual composites; this has further exacerbated the difficulties of empirical analysis by (1) lowering the available signal-to-noise ratios in both environmental and biological time series, (2) severely limiting the number of data points available in reasonably stationary time series, and (3) scrambling together different causal mechanisms controlling different shorter-period survival variations within the same annual composite data point.

Because of the wide variety of possible linkages of environmental fluctuations to recruitment variations (Table 1), and because a variety of oceanographic, meteorological, or other proxy time series may be available to somehow be associated with one or more of these linkages, correlations with short available series of annually composited survival estimates can generally be found and readily justified according to some ecological mechanism. When such a correlation happens to be high enough to meet standard significance

TABLE 1
Some Hypothetical Controls on Survival of Early Life Stages of Fishes

I. Starvation hypotheses
- Turbulent mixing of fine-scale food particle strata
- Low productivity of system
- Wrong type of potential food organisms
- Dispersion of food due to divergent flow pattern
- Mismatch with seasonal food succession caused by anomalies in growth rate

II. Predation hypotheses
- Incidence of small planktonic predators
- Incidence of large planktonic predators (coelenterates, etc.)
- Incidence of predatory adult fish
- Incidence of predatory larval fish
- Variations in growth with size-dependent predation

III. Advection hypotheses
- Offshore transport (removal of drifting larvae from favorable habitat)
- Onshore transport (exposure of larvae to damage in surf zone, etc.)
- Disruption of normal current patterns to which reproductive habits are tuned

IV. Physiological stress hypotheses
- T, S, or $[O_2]$ conditions not within physiological range
- Effects of environmental pollution

V. Disease hypotheses
- Infectious outbreaks, etc.

criteria, it becomes publishable as an advance in scientific understanding, whereas slightly weaker correlations do not. This happens even though, given the complexity of the ecological systems involved, it may be quite unreasonable to expect such overwhelming control of survival by any single environmental variable or process as to yield significant (e.g., $P < 0.05$, etc.) nonspurious correlations from the very short data series typically available, particularly since the real degrees of freedom in both environmental or biological time series are often substantially fewer than the number of annual data points because of interyear serial correlation.

Thus, we have the situation that most of the published empirical environment/recruitment relationships are probably (at least to some degree) spurious, with others that may have represented realistic levels of linkage having been discarded as nonsignificant. Tacit recognition of this situation by the fisheries science community has led to a general low opinion of such relationships, with the result that they are not often used in serious decision-making procedures and thus presently are of little practical value.

The following sections of this paper attempt to illustrate a rationale for interregional comparative studies directed toward (1) providing a framework for systematizing fragmentary information and insights in order to foster useful generalities concerning physical, biological, and (most important for management activities) human impacts on recruitment, and (2) developing a basis for detecting spurious relationships and for increasing confidence in certain weak relationships by comparisons with similar situations in other regional ecosystems. Objections regarding the possibility of discrediting certain valid relationships in situations where the assumption of analogy may be faulty can be answered with the observation that such relationships are essentially useless anyway in a situation where the valid cannot be distinguished from the spurious.

The comparative method and the experimental method are the two great methods of science (Mayr 1982). The comparative method is particularly indicated in situations not amenable to controlled experiments, and it has underlain nearly all the revolutionary advances in evolutionary biology, to cite one example. It seems surprising that the method has not found wider use in the fishery-environmental field, which appears to have been preoccupied with diversity rather than synthesis, and prone to view each local situation as unique.

COMPARATIVE SPAWNING HABITAT CLIMATOLOGY

Parrish et al. (1983) presented maps of two-month (Jan.-Feb. and July-Aug.) long-term mean distributions of various environmental characters for the four major eastern boundary regions of the world: the California, Peru, Canary, and Benguela current systems. These maps generally represented seasonal extremes in each system; however, peak upwelling in the temperate areas is generally earlier toward the equator. The summer and winter maps of Parrish et al. are supplemented here by characteristic late spring (May-June, N. Hemisphere; Nov.-Dec., S. Hemisphere) distributions of coastal temperature anomaly (Figure 1) and Ekman transport (Figure 2).

Negative coastal temperature anomalies greater than 2°C (i.e., 2 degrees cooler than at the same latitude some 1,000 km offshore; stippled in Figure 1) delimit the major upwelling centers. Note the definite separation of the two distinct major upwelling regions off South America. Warm anomalies (areas of positive anomaly greater than 1°C are diagonally hatched in Figure 1), or areas where cold anomalies are less intense, often correspond to spawning regions of coastal pelagic fishes (Parrish et al. 1983). Ekman transport vectors illustrate the strong offshore surface transport that must be accommodated in reproductive

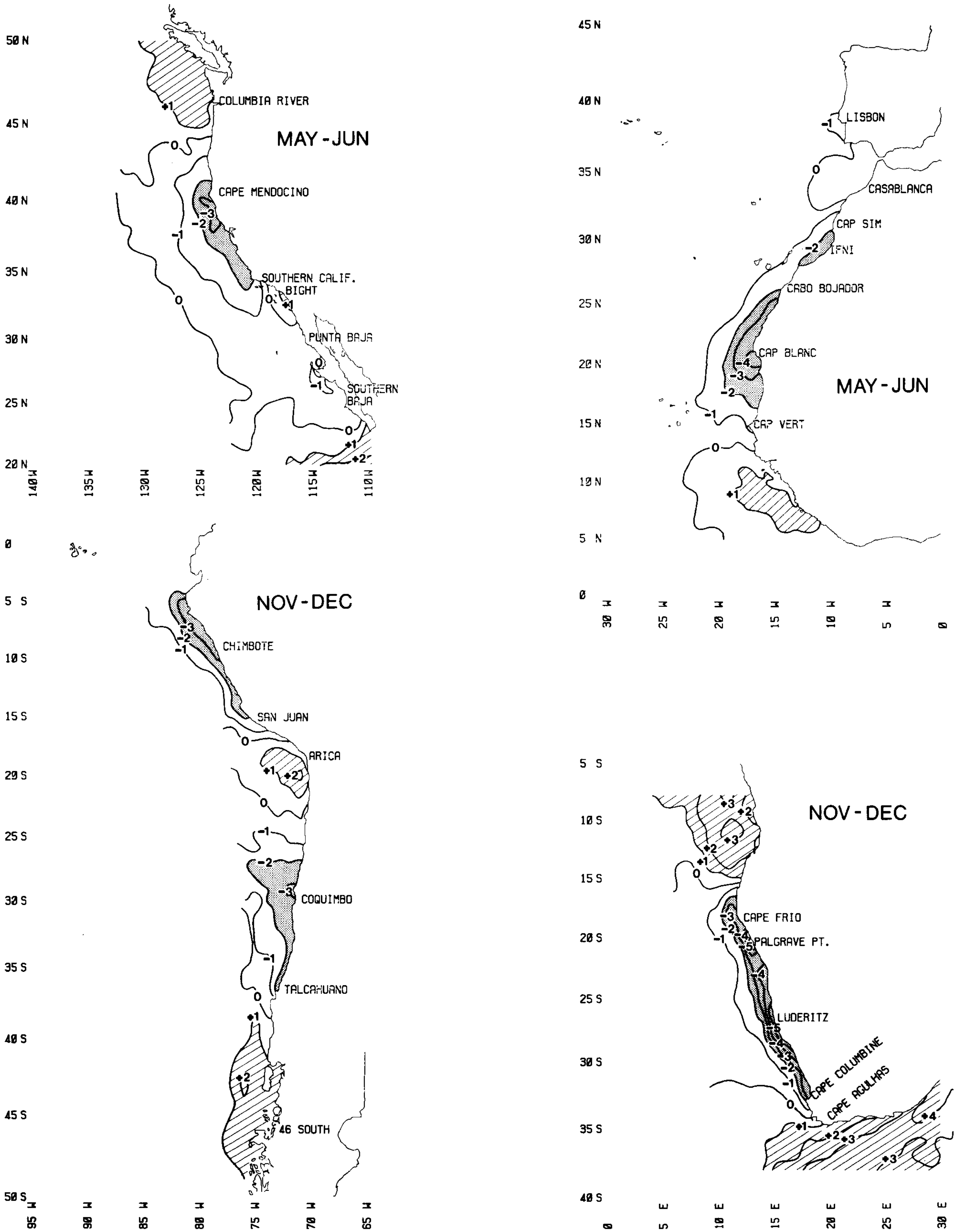

Figure 1. Coastal temperature anomaly (difference from characteristic temperature at similar latitude some ten degrees longitude offshore) distributions in the four major eastern boundary current systems, characterizing late spring conditions in the respective hemispheres. Units are degrees Celsius. Corresponding winter and summer maps, and details of their construction, are presented by Parrish et al. (1983).

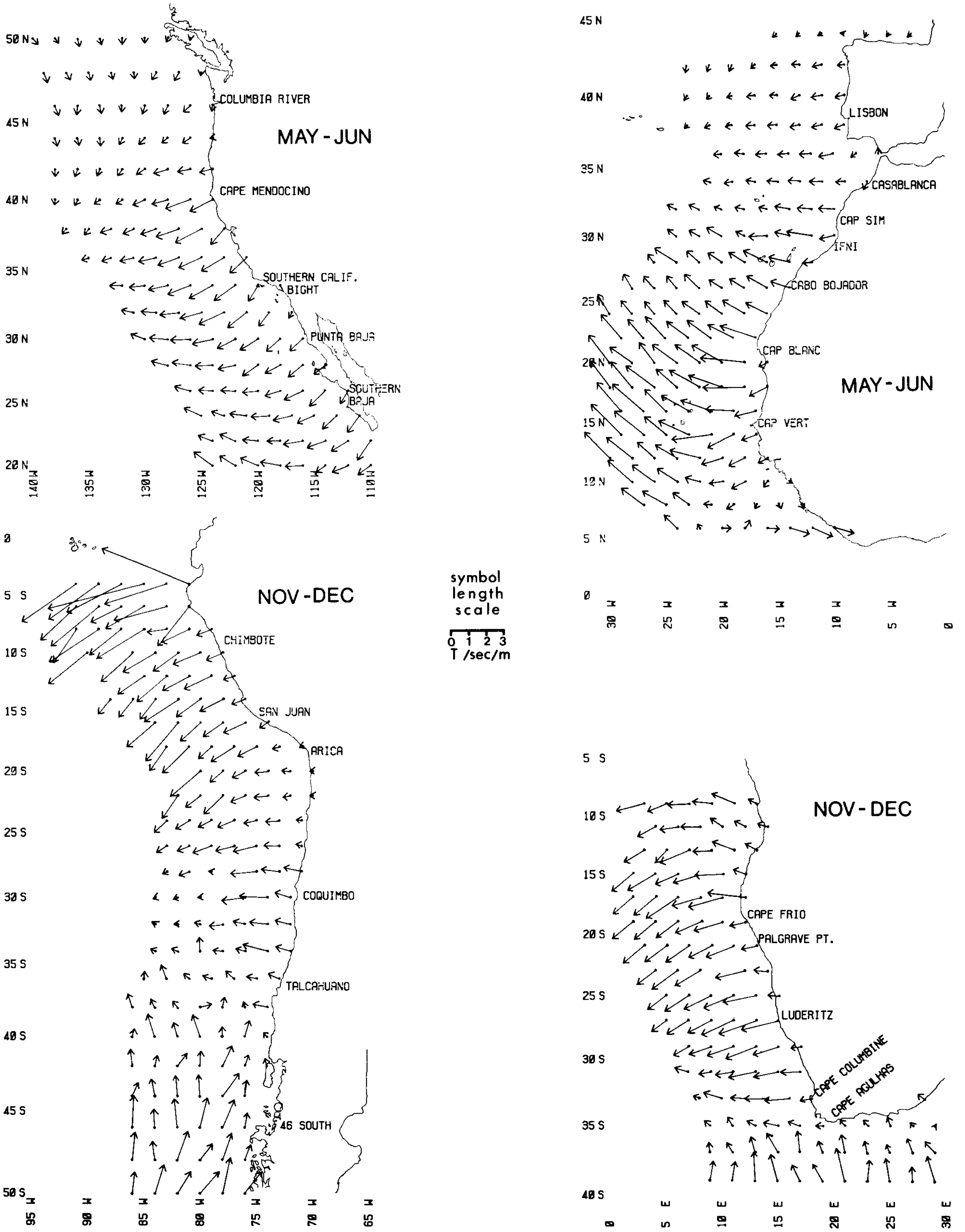

Figure 2. Surface Ekman transport distributions in the four major eastern boundary current systems, characterizing late spring conditions in the respective hemispheres. Transport is proportional to vector symbol length. A symbol length scale is provided; units are metric tons per second across each horizontal meter width. Corresponding winter and summer maps, and details of their construction, are presented by Parrish et al. (1983).

TABLE 2
Dominant Anchovy, Sardine, Jack (Horse) Mackerel, Hake, Mackerel, and Bonito in the Four Major Eastern Boundary Currents

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

After Bakun and Parrish (1980)

strategies of marine organisms inhabiting these regions (Figure 2). In addition, McLain et al. (1985) and Shelton et al. (1985) show that biological communities, not only in the Pacific systems but apparently also in the Atlantic, must cope with intermittent extreme warm episodes of El Niño-type intensity.

Very similar assemblages of dominant coastal pelagic fish species inhabit the four regions (Table 2). In each region there is a dominant anchovy, sardine, jack mackerel, hake, mackerel, and bonito. In several cases, the same nominal species inhabits more than one of the regions. In other cases, the species are so similar that their difference may be more a matter of assumption than of demonstration (R.H. Parrish, pers. comm.). There have also been similar regional experiences of rapid fishery expansions and precipitous declines (Parrish et al. 1983).

The various environmental and biological similarities suggest that fish communities in these different regional systems may function similarly with respect to their environments and may be solving similar problems in their reproductive strategies. Survival of offspring to the age of reproduction, which often approximates the age of fishery recruitment, is the direct causative factor in the selective process. Thus natural selection demands response to the most crucial mechanisms regulating recruitment. This implies that we can use the observed results of natural selection in terms of geographical and seasonal aspects of reproductive strategies to understand the causes controlling reproductive success. In other words, pervasive patterns of reproduction, with respect to environmental characteristics, may indicate the actual environmental mechanisms regulating recruitment success.

For example, Parrish et al. (1983) found a general pattern in the spawning habits of anchovies and sardines that seemed to point to a simultaneous minimization of both wind-induced turbulent mixing and offshore-directed transport. Thus the starvation hypothesis, as expressed in Lasker's (1981) scenario of turbulent dispersion of fine-scale food strata, and the transport hypothesis, involving detrimental transport of larvae away from favorable proximity to the coast, are implicated as important mechanisms to be considered in modeling and exploratory data analysis. Temperature of spawning showed much less coherent pattern, suggesting that selection of spawning habitat for any particular optimum temperature is less important than minimizing turbulent mixing or offshore transport.

Certain initially puzzling discrepancies from the general patterns have proved enlightening. For example, Bakun and Parrish (1982) reported that the Peruvian anchoveta, by far the largest fish stock on record before its collapse, stood out as an anomaly in that its spawning peak during austral winter occurred at the very season when offshore Ekman transport was most intense (Figure 3; Table 3), rather than when it was relatively weak, as is the general pattern. However, when mixed layer depth climatologies were produced for the various regions (Parrish et al. 1983), the discrepancy was apparently resolved. Seasonal variation of mixed layer depth off Peru proceeds in phase with that of transport but has greater amplitude (Figure 4), with the result that the thinner mixed layer of austral summer is apparently carried offshore some four times as fast as is the deeper winter mixed layer (Figure 5), even though the winter transport (by volume) is nearly twice as large. Thus the spawning season does indeed appear to be tuned to minimize the rate of offshore loss of eggs and larvae within the ocean's upper mixed layer. This resolution of what initially seemed a discrepancy of a single situation from the general pattern has thus pointed out the generality that, in treating the mechanism of offshore loss of reproductive products distributed in the mixed layer, estimates of wind-driven surface (Ekman) transport should ideally be divided by the effective mixed layer depth to yield an *Ekman velocity of the mixed layer*[1]. In this way we are able to combine two environmental variables to yield a

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[1] In the statement that these two variables should ideally be combined, the qualification "ideally" is important. Ekman transport is estimated from relatively abundant surface wind reports, which reflect the fairly large spatial scales of atmospheric variation. Mixed layer depth varies on much shorter oceanic length scales and must be determined from more sparsely distributed subsurface measurements. Thus there may be cases where the effective mixed layer depth is so imprecisely determined that the combined variable yields a less reliable indicator of interyear variation of offshore velocity than would be provided by the interyear variation in the Ekman transport estimate itself.

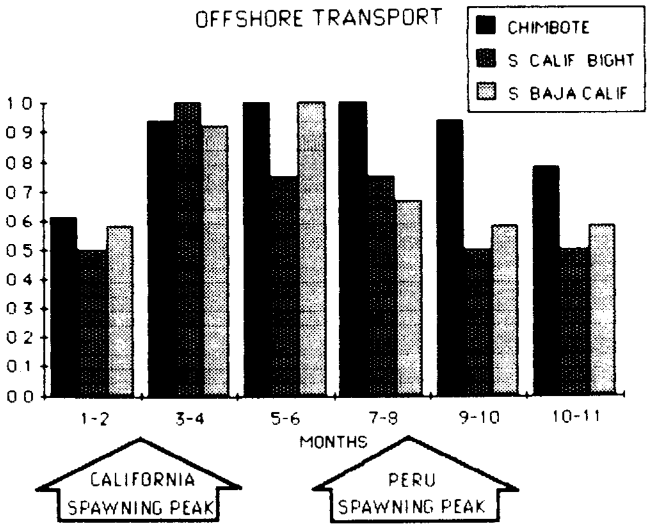

Figure 3. Offshore-directed Ekman transport within the spawning grounds of the Peruvian anchoveta (Chimbote) and within the spawning grounds of the central and southern subpopulations of (California Current) northern anchovy, by 2-month segments of the annual cycle. Units are scaled relative to the seasonal maximum in each area, which is assigned the value 1.0 in all three locations in order to scale them similarly (and thereby to emphasize seasonal timing rather than absolute magnitude). Timing of seasonal peak spawning in the two systems is indicated by the wide arrows. (See Table 3 for unscaled numerical values.)

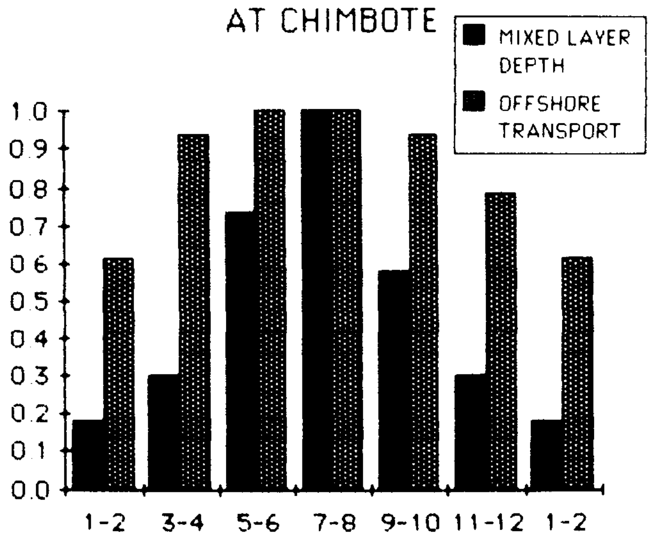

Figure 4. Offshore-directed Ekman transport and mixed layer depth within the spawning grounds of the Peruvian anchoveta, by 2-month segments of the annual cycle. Units are scaled relative to the respective seasonal maxima, which are assigned the value 1.0 in both cases in order to place both on a common scale (and to thereby emphasize seasonal timing rather than absolute magnitude). (See Table 3 for unscaled numerical values).

single more meaningful variable, thereby conserving degrees of freedom for improving the power of hypothesis tests.

The major point to be made is that such findings, which are based on patterns in the long-term composite averages, are independent of any results based on examination of the available time series data. Thus the findings provide a guide to selecting variables for time series analysis so that the selection process itself does not deplete the scarce degrees of freedom. One could say that the observed characteristic seasonality and geography of reproductive strategies results from a large number of "trial-and-error experiments" performed by the population over the period of development. Moreover, natural selection ensures that this observed result is the "most correct" one for the fish, at least in the long term (providing that we are observing truly long-term adaptations).

TABLE 3
Actual (Unscaled) Values Used to Construct Figures 3, 4, and 5

		Transport ($T\ sec^{-1}\ m^{-1}$)				
Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	1.1	1.7	1.8	1.8	1.7	1.4
S. Calif. Bight	0.2	0.4	0.3	0.3	0.2	0.2
S. Baja Calif.	0.7	1.1	1.2	0.8	0.7	0.7
		Mixed Layer Depth (m)				
Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	7	12	29	40	23	12
S. Calif. Bight	37	25	11	10	14	20
S. Baja Calif.	45	23	18	9	20	34
	Net Offshore Velocity of Mixed Layer ($km\ day^{-1}$)					
Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	13.6	12.2	5.4	3.9	6.4	10.1
S. Calif. Bight	0.5	1.4	2.4	2.6	1.2	0.9
S. Baja Calif.	1.3	4.1	5.8	7.7	3.0	1.8

Transport and mixed layer depth climatologies taken from Parrish et al. (1983); offshore velocities computed as the quotient of the two.

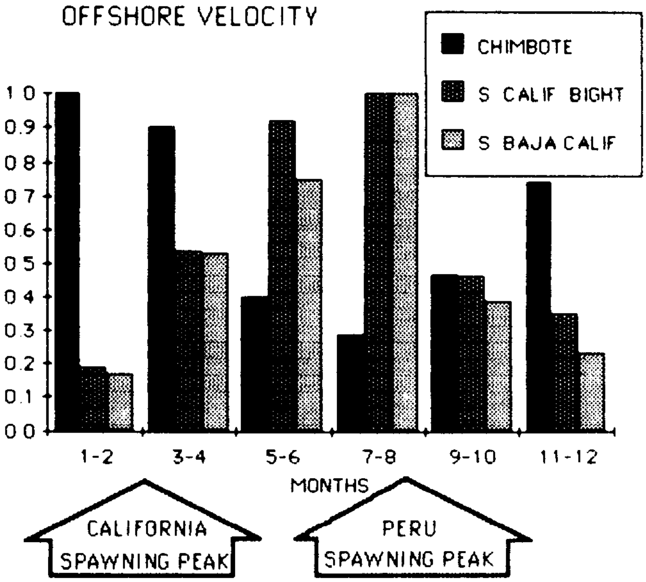

Figure 5. Offshore-directed velocity of the surface mixed layer (Ekman transport divided by mixed layer depth) within the spawning grounds of the Peruvian anchoveta (Chimbote) and of the central and southern subpopulations of (California Current) northern anchovy, by 2-month segments of the annual cycle. Units are scaled relative to the seasonal maximum in each area, which is assigned the value 1.0 in all three locations in order to scale them similarly (and thereby to emphasize seasonal timing rather than absolute magnitude). Timing of seasonal peak spawining in the two systems is indicated by the wide arrows. (See Table 3 for unscaled numerical values.)

Thus any empirical relationship based on short time series of recent data on reproductive success and on variations in some environmental characteristic, not corroborated by any apparent reproductive accommodation to that characteristic, might be of questionable validity. Conversely, an empirical relationship reflected in what seems to be an obvious adaptation in characteristic reproductive habits could be assigned increased confidence. This line of reasoning seems applicable even to a unique situation where no assumed analogues are available for comparison, but the comparative aspect introduces a more powerful test. For example, an apparent adaptation may be mere happenstance in a single situation. However, given the regional diversity introduced by varying coastline orientations, atmospheric regimes, advected characteristics, etc., it is unlikely that strong interregional correspondence of reproductive habits with environmental characteristics is due merely to happenstance. Therefore, recognition of such an interregional pattern provides much stronger confirmation of real mechanistic linkage. And, as noted in the Introduction, the present need in recruitment research is for any substantial error to be on the side of undue conservatism and rigor, if results are to be applicable to real problems.

At Pacific Environmental Group we are presently entertaining the notion that the coastal pelagic fishes of the more tropical eastern boundary areas (the sardinellas, etc.) may be playing the same basic survival "game" as those (sardines, anchovies, etc.) in the temperate zones, but at a warmer temperature range. If this is even partially true, the Angola, Guinea, and Costa Rica Dome coastal regions, the Ivory Coast-Ghana upwelling region, the Malabar Coast of India, etc., would provide another set of spawning habitat seasonalities and geographies with which to sharpen these interpretations. Other possibilities for instructive analogues include such western ocean boundary stocks as the Brazilian sardinella and the Japanese sardine; in these cases, basic differences in the environmental dynamics of the systems should be carefully evaluated.

COMPARATIVE TIME SERIES MODELING

Beyond comparisons of long-term mean characteristics of spawning habitats and biological consequences, it may be fruitful to compare empirical (time series) models among similar regional systems. There have been a number of published suggestions of environmental/biological relationships. (Some of the more recent examples for eastern boundary coastal pelagic fishery stocks are cited in Table 4.) Formulations and points of view have differed greatly among researchers concerned with the different regional systems. For example, I believe that Boyd's (1979) formulation in terms of sea-temperature variance, the results of which suggest Lasker's (1981) mechanism of turbulent dispersion of fine-scale food concentrations, has not been tried in the California Current or the other systems.

Systematic comparisons of identical empirical model formulations for all available "analogous" situations might yield suggestive patterns among model parameters to provide new insights into the processes controlling the biological systems. The comparisons could also yield information about the validity of attempts to transfer "experience" among systems (e.g., predicting consequences of human actions or natural perturbations in one system from the record of similar events in other systems, etc.). Under an assumption of analogy, empirical relationships having a similar general form in more than one system might be correctly afforded greater interest and confidence than otherwise warranted. Conversely, a correlation found in one system might be considered questionable if no suggestion of similar linkage were found in other systems appearing, in other respects, to function analogously.

For example, consider the following set of formulations (the variables illustrated in this example are perhaps most suitable to anchovies)

$$\log(R_i/S_i) = a_{1,i} + \mathrm{B}_{1,i}S_i^c \quad , \qquad 0 \leq c \leq 1$$
$$\log(R_i/S_i) = a_{2,i} + \mathrm{B}_{2,i}u_i$$
$$\log(R_i/S_i) = a_{3,i} + \mathrm{B}_{3,i}\tilde{u}_i$$
$$\log(R_i/S_i) = a_{4,i} + \mathrm{B}_{4,i}W_i$$
$$\log(R_i/S_i) = a_{5,i} + \mathrm{B}_{5,i}T_i$$
$$\log(R_i/S_i) = a_{6,i} + \mathrm{B}_{6,i}\tau_i$$

. . . .

. . . .

. . . .

$$\log(R_i/S_i) = a_{m,i} \quad + \mathrm{B}_{j,i}S_i^c \quad + \mathrm{B}_{k,i}\, u_i$$
$$\log(R_i/S_i) = a_{m+1,i} + \mathrm{B}_{j+1,i}S_i^c + \mathrm{B}_{k+1,i}\, u_i$$

. . . .

. . . .

. . . .

$$\log(R_i/S_i) = a_{p,i} \quad + \mathrm{B}_{q,i}S_i^c + \mathrm{B}_{r,i}u_i + \mathrm{B}_{s,i}\tilde{u}$$

. . . .

. . . .

. . . . etc.

where R_i is recruitment to a given fish stock "i",
S_i is adult stock size,
u_i is upwelling index coincident in time and space with spawning (we might generally expect strong upwelling to be a detrimental factor, involving loss of eggs and larvae via offshore transport),
$\tilde{u}_i$ is a properly space- and time-lagged upwelling index that would reflect longer time-scale nutrient inputs to the system at upstream upwelling centers,
W_i is wind-generated turbulence input to the larval habitat (motivation for the choice of variables u_i, $\tilde{u}_i$, and w_i can be found in Bakun and Parrish 1980),
T_i is an index of characteristic temperature,
τ_i is temperature variance as used by Boyd (1979), etc.

The dots indicate that other hypothesized factors and combinations of factors would also be considered.

The log (R/S) formulation simply connotes a multiplicative effect of the explanatory vari-

TABLE 4
Examples of Recent Studies Indicating Environmental/Biological Relationships for Eastern Boundary Current Pelagic Fishery Stocks

California Current

Lasker (1981)—northern **anchovy** (*Engraulis mordax*)—negative effect of wind-generated turbulence (wind cubed index) during spawning season.

Parrish and MacCall (1978)—Pacific **mackerel** (*Scomber japonicus*)—positive effect of upwelling (index) at spawning ground previous to spawning (one-month lag).

Bakun and Parrish (1980)—Pacific **sardine** (*Sardinops sagax*)—positive effect of upwelling (index) in upwelling maximum region upstream of spawning grounds (800-km spatial lag) integrated over previous calendar year (2- to 14-month spatial lag).

Bailey (1981)—Pacific **hake** (*Merluccius productus*)—negative effect of offshore transport (upwelling index) during planktonic larval period.

Collins and MacCall (1977)—Pacific **bonito** (*Sarda chiliensis*)—positive effect of upwelling (index) during spawning season.

Peru Current

Various authors—**anchoveta** (*Engraulis ringens*)—negative effect of El Niño (often attributed to lowered primary productivity).

Benguela Current

Boyd (1979)—Southwest African **anchovy** (*Engraulis capensis*) —negative effect of sea-surface temperature variance during spawning season.

Canary Current

Belveze and Erzini (1983)—**sardine** (Moroccan central zone; *Sardina pilchardus*)—positive relation of catches to upwelling (index) averaged over the three previous spawning seasons (catch is composed of one- two-, and three-year-olds).—**mixed small pelagics** (Moroccan northern zone; mostly *S. pilchardus*)—high catches in low-rainfall years.

Freón (1983)—**sardinella** (Senegal)—positive relation of CPUE to wind speed during upwelling season (previous winter); author suggests autocorrelation in wind series as explaining a recruitment effect.

Guinea Current

Bakun (1978)—Ghanain herring (**Sardinella** *aurita*)—negative relation of catch to rainfall and sea-surface temperature (related to upwelling).

Binet (1982)—**sardinella** (Ivory Coast and Ghana; *S. maderensis* and *S. aurita*)—positive effect of upwelling (temperature index) and negative effect of coastal runoff on catch.

Cury and Roy*—**sardinella** (Ivory Coast and Ghana; *S maderensis* and *S. aurita*)—positive effect on catch and on reproductive success of local upwelling (temperature index), which is related to remote forcing by wind stress variations in the western equatorial Atlantic (i.e., off Brazil).

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*Cury, P., and C. Roy. MS. Modelisation de l'abondance des especes pelagiques cotieres de Cote d'Ivoire integrant l'effort de peche et un indice d'upwelling ORSTOM, 24 Rue Bayard, 75008 Paris, France.

> ables; i.e., if an increase of a given variable were to double predicted survival per unit spawning biomass, then an equal decrease would halve predicted survival rather than reduce it to zero, as would be required by an additive (i.e., nonlogarithmic) formulation. The exponent c represents MacCall's (1980) suggestion for the incorporation of variable habitat dimension in a density-dependent mechanism such as adult cannibalism (where if $c = 1$, there is no habitat size variation and the result is a normal Ricker curve; if $c = 0$, the habitat size is proportional to stock size and therefore density does not increase with abundance, so that there is no stock-size dependence through the density-dependent mechanism; $0<c<1$ implies the less-than-proportional increase of habitat volume with stock size, which fits observation).

The set of formulations would then be fitted to the available data for various "analogous" stocks in similar environmental settings. Thus we fit univariate regressions, and then various multiple regression combinations of the selected explanatory variables, for each stock and spawning habitat. Then we array the total set of model parameters for the various stocks and look for informative patterns.

Obviously, among a large number of models like this, a certain number of fits satisfying significance criteria will always appear, if only by chance correspondence of unrelated variations. For example, if one does not find at least one fit at the $P = 0.05$ significance level out of twenty attempts, one is simply unlucky. But even if each researcher were limited scrupulously to a prior choice of a single formulation, it would not necessarily improve the utility of published results; we have no idea of how many unpublished failures to meet significance criteria may have occurred for each publishable success. In fact, given the multitude of possible interactions with growth, predation, transport processes, physiological stress, etc., at various life stages, it seems almost inconceivable that any one mechanism could so dominate total survival as to yield a strong univariate relationship that was not to some degree spurious. Thus, searching for "significant" empirical relationships may be an exercise in self-delusion. If the weaker relationships that may represent realistic levels of control by particular mechanistic linkages are to be usable, ways must be found to cull out the larger number of spurious chance fits resulting from relaxed significance criteria. If one finds patterns of similar form among relationships, similar signs of model parameters, etc., for analogous situations, even though the relationships are too weak individually to meet ordinary significance criteria, valuable insight may have been gained. If nothing is found but chaos suggesting unrelated random combinations, one might conclude that little confidence should be placed in any such models based on the really inadequate degrees of freedom represented by short autocorrelated recruitment time series.

CONCLUDING REMARKS

This paper is intended to serve as the convener's introduction to the invited papers for the Symposium on Comparative Studies of Eastern Ocean Boundary Systems at the 1984 CalCOFI Conference. Certain of these introductory remarks may seem negative; their purpose is to indicate that at this stage in the development of fisheries/environmental science, the likelihood that there is no such thing as an exact analogy among large marine ecosystems does not rule out interregional comparison as a useful deductive tool. In using interregional comparison as a gauge for validity of findings, inconsistency with an interregional pattern is of course no proof of spuriousness; however, interregional consistency may provide otherwise unavailable support for a statistically weak but potentially useful result.

In view of the great resources required for experiments covering the range of time and space in recruitment variability of a fish stock, the cost-effectiveness of the comparative approach deserves mention. In many cases the observational investment will already have been made. Maritime reports (such as those used in the construction of all the figures in this paper) are available, at varying density, for all the oceans of the world. Some fishery research studies will have been made in any area containing a substantial exploited fish stock. Thus the costs of a rudimentary comparative study may be little more than those involved in acquiring existing data and arraying them in similar formats.

Fishery/environmental science clearly needs generalities and unifying principles with broad applicability. Consider, for example, the situation at the FAO Technical Consultation to Examine Changes in Abundance and Species Composition of Neritic Resources (held in Costa Rica in 1983) where, at a major gathering of fishery scientists from all over the world, no consensus could be found (e.g., Bakun 1983) as to the probable consequences of continuing to take record sardine catches off northern Chile in the presence of the 1982-83 El Niño, even then recognized as the strongest environmental anomaly in the eastern Pacific for at least fifty years. We certainly expect that valid generalities do exist in the fishery/environmental field, as in other branches of science. Identifying them and making them available for fishery management and industrial decision making should be given high priority.

The following symposium papers present selected comparative aspects of the four major eastern ocean boundary ecosystems of the world and their associated fisheries. No attempt has been made to assemble a comprehensive and coherent comparative treatment. Our purpose is to provide some examples of ongoing comparative research, some useful insights into the degree of analogy presented by these four similar systems, and some basic information to aid comparative interpretation and deduction. Most important, we hope to stimulate fisheries scientists to maintain a comparative focus in their research efforts.

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MAJOR DYNAMICS AFFECTING THE EASTERN TROPICAL ATLANTIC AND PACIFIC OCEANS

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ABSTRACT

Despite their difference in size, the Pacific and Atlantic oceans have eastern tropical regions that are similar, especially in their dominant dynamics. Both regions are primarily influenced by remote wind stress effects through equatorial wave dynamics. However, the eastern equatorial Pacific is dominated by an interannual time scale (i.e., El Niño), whereas the eastern tropical Atlantic is dominated by a seasonal time scale. In both of these oceans, the Equatorial Undercurrent impinging upon the eastern boundary is associated with an important westward zonal pressure gradient—a gradient that is not in equilibrium with the local wind stress. Two other subsurface currents—the northern and southern equatorial undercurrents—play a role in the formation of the Guinea, Angola, and Costa Rica domes. All these common dynamic processes are important to the nutrient enrichment of both eastern boundary oceans.

RESUMEN

A pesar de sus diferencias en magnitud, los océanos Pacífico y Atlántico poseen regiones tropicales orientales semejantes, especialmente en lo que se refiere a sus características dinámicas más importantes. Ambas regiones están influenciadas principalmente por los efectos remotos de la perturbación del viento a través de la dinámica de olas ecuatoriales. Sin embargo, el Pacífico ecuatorial oriental está dominado por una escala temporal interanual (i.e., El Niño), mientras que el Atlántico tropical oriental está dominado por una escala temporal estacional. En ambos océanos la Corriente Ecuatorial Subsuperficial que avanza sobre el margen oriental está asociada con un importante gradiente zonal occidental de presión, gradiente que no está en equilibrio con la perturbación local del viento. Otras dos corrientes subsuperficiales, las ecuatoriales norte y sur, influyen en la formación de los domos de Guinea, Costa Rica, y Angola. Todos estos procesos dinámicos comunes a ambos sistemas son importantes para el aporte de nutrientes a ambos sectores oceánicos orientales.

INTRODUCTION

The eastern parts of the tropical Atlantic and Pacific oceans are among the most biologically active regions of the world oceans. This is because in these regions the thermocline is, on the average, very close to the surface and affected by strong vertical motions, which are fundamentally important in fertilizing the euphotic zones. The dramatic El Niño, now believed to be a large-scale ocean-atmospheric event, has its most spectacular effects in the eastern tropical Pacific. A similar phenomenon occurs in the eastern tropical Atlantic (hereafter referred to as the Gulf of Guinea) and despite its smaller oceanic signature can have devastating effects on the fisheries and climate of the surrounding countries (Hisard and Piton 1981).

Predicting such phenomena is the goal of numerous research groups, but this goal would be imperfectly reached without, first, a clear understanding of the mechanisms involved. A rational (cause-effect) approach is almost impossible in biological-ocean studies because of the complexity of the biological processes themselves and of their linkages with the physical environment. Medium- and high-latitude oceans are characterized by a predominance of thermodynamic effects in the surface layer and are dominated by the presence of highly energetic mesoscale vortices throughout the water column. Because of the high number of such vortices and the impossibility of linking them in a simple manner to any direct origin, an empirical approach appears more suitable at such latitudes. In the equatorial oceans the local thermodynamic effects are small compared to the dynamic ones, and these oceans have the outstanding property of responding clearly and coherently to the wind fluctuations. A rational approach is therefore much better adapted there.

In this paper I tentatively explain the major dynamics that affect the eastern tropical Atlantic and Pacific oceans. I have tried to concentrate on the cause-effect relationship, which necessarily involves some notion of the balance of forces involved. One fundamental aspect of the equatorial oceans—their ability to radiate energy quickly from one part of the basin to another—is explained through simple schemes. I hope to improve the understanding of the remote forcing

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theory, which has been applied with some success to the interannual El Niño in the Pacific and to seasonal upwelling in the Gulf of Guinea. The reversal of the zonal pressure gradient in the eastern equatorial oceans is also presented. It must be pointed out that although this reversal is not well known, it is indeed a general feature of these eastern oceans. Finally, the mechanisms involved in the formation of the highly productive thermal dome areas are discussed.

RESPONSE TO REMOTE FORCING

Most of the tropical Atlantic and Pacific oceans are under the influence of the northeast and southeast trades. In the eastern part of both oceans, the winds are predominantly from the south, with an eastward veering toward the coasts of the Gulf of Guinea and Central America. In the Gulf of Guinea the strong coastal and equatorial seasonal upwelling (Figure 1) does not seem related to the local wind via Ekman divergence (Houghton 1976; Berrit 1976; Bakun 1978; Servain et al. 1982), nor to heat exchange with the atmosphere (Merle 1980). In the same way, the interannual El Niño appearance of abnormally warm water along the coast of Ecuador and Peru is not clearly related to the weakening of the coastal southerly wind (Wyrtki 1975). Along the western coast of North America, sea level (representative of thermal variation over the water column) and local alongshore wind stress anomalies are poorly correlated south of San Francisco, but much better correlated farther north, where predominance of a local wind-driven response is suggested.

Bjerknes (1966, 1969) was the first to suggest that the El Niño phenomenon could be due to a large-scale ocean-atmosphere interaction in which the relaxation of the trades along the equator has a dominant role. Wyrtki (1975) emphasized the dynamical aspect of such an approach. The usually strong westward winds along the equator in the central and western part of the basin accumulate water in the west and build up an east-west sea-level slope (see next section for further explanation). A rapid relaxation of the trades in the central equatorial Pacific destroys the wind stress/sea-level slope equilibrium and excites an internal downwelling equatorial Kelvin wave. This wave propagates eastward and depresses the thermocline all the way to the eastern boundary. This remote forcing mechanism and its effect on the boundary has been studied analytically and numerically by Moore (1968), McCreary (1976), Hulburt et al. (1976), and Busalacchi and O'Brien (1981).

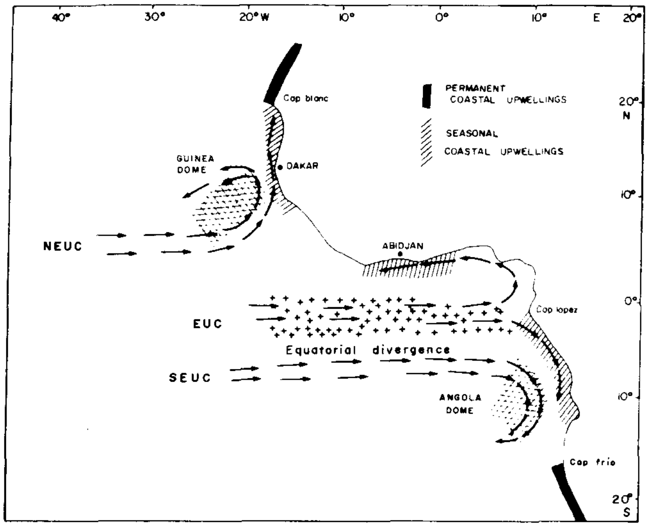


Figure 1. The productive areas in the eastern tropical Atlantic Ocean and the three branches of the Equatorial Undercurrent system (from Voituriez and Herbland 1982).

In the Pacific Ocean, the downwelling El Niño event occurs on an interannual time scale. In the Gulf of Guinea the strong upwelling signal occurs seasonally. In neither case does local forcing seem to be the main explanation. In view of such similarities, Moore et al. (1978) have suggested a similar mechanism for upwelling in the Gulf of Guinea, with the seasonal intensification of the trades in the western Atlantic at the origin of an equatorial upwelling Kelvin wave. Numerical models have also been used to detail this seasonal remote forcing mechanism (Adamec and O'Brien 1978; Busalacchi and Picaut 1983; McCreary et al. 1984).

In order to better explain this remarkable property of far-field forcing, which is characteristic of the equatorial oceans, I have extracted some figures from O'Brien et al. (1980). They represent the simplest numerical solution that clearly illustrates this Kelvin wave scenario. A reduced-gravity linear model is forced by an easterly patch of zonal wind stress acting on the western part of an idealized equatorial basin, which is limited on the east and west by solid boundaries and on the north and south by open boundaries. This model simulates the generation of an upwelling Kelvin wave in the Pacific, but has also been adapted to the Atlantic by O'Brien et al. (1978). A simple reversal of the wind direction could induce a downwelling Kelvin wave and therefore simulate, crudely, an El Niño event. Figure 2 represents the depth displacement of the pycnocline separating the two layers of the model. Initially the ocean is at rest. Within a few weeks after the easterly winds, west of 170°E, are switched on, a westward, wind-driven surface flow accumulates water against the western boundary. At the same time the Ekman divergence along the equator induces upwelling just west of 170°E. This patch of upwelling then propagates eastward along the equato-

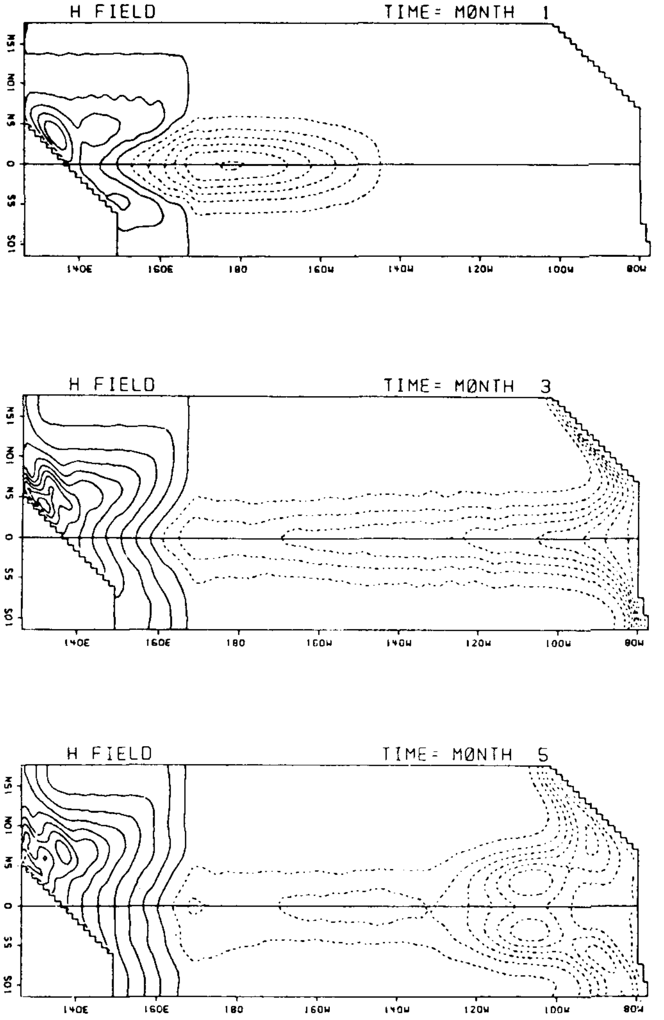


Figure 2. Interface displacement depicting the progression of an equatorially trapped Kelvin wave and resulting coastal Kelvin waves and Rossby waves. Contouring interval is 5 m, with dashed contours indicating upwelling (from O'Brien et al. 1980).

rial wave guide as a freely propagating equatorial Kelvin wave. When this upwelling disturbance reaches the eastern boundary, it reflects as packets of Rossby waves propagating westward symmetrically about the equator, and as two coastal Kelvin waves propagating poleward.

Such a scenario, where the westward equatorial wind (cause) could be easily related, a few months later, to an eastern boundary upwelling (effect) thousands of kilometers away, is one fundamental aspect of the equatorial region. At midlatitudes there is no wave mechanism to bring energy over long distances from west to east. Only Rossby waves exist, but they propagate westward so slowly, compared to their equatorial counterpart, that it is impossible to simply relate wind forcing with its effects in temperate oceans.

Reduced-gravity models assume that the ocean consists of a thin surface layer (50-200 m) of weak density overlying a deep lower layer (2,000-5,000 m) of greater density. Even if such an approximation is quite relevant in equatorial oceans, these models restrict the energy to traveling only horizontally. Figure 3, adapted from McCreary (1981), is a theoretical representation of equatorial waves in a continuously stratified model. The energy that appears east of the forcing area is the result of the radiation of many equatorial Kelvin waves. They superpose to form a beam of energy that propagates eastward but also downward. When this Kelvin beam arrives at the eastern boundary, it reflects as a collection of beams of Rossby waves that propagate energy westward and downward. This reflection may be completed, depending on the forcing frequency, by two coastal Kelvin beams, which propagate energy poleward and down-

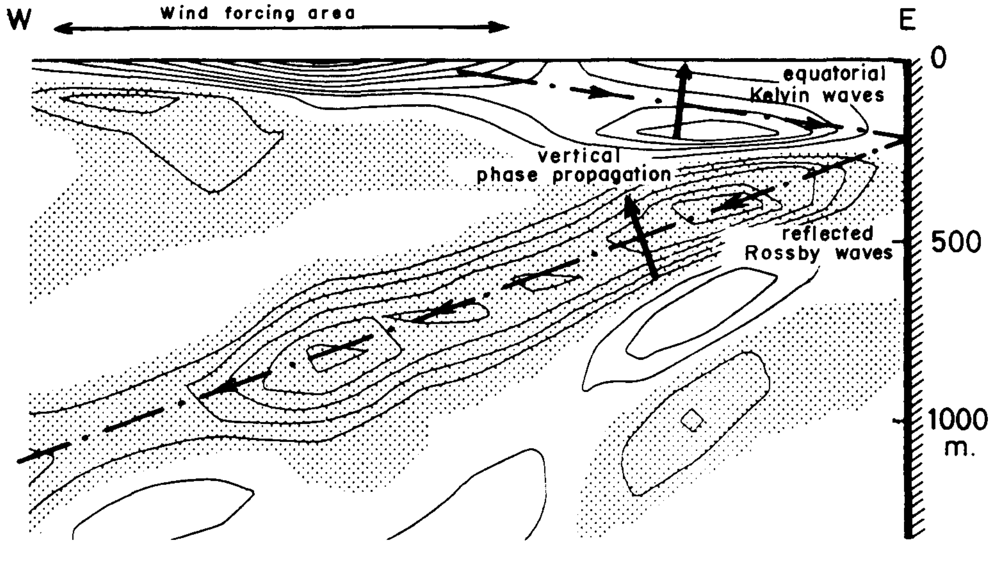


Figure 3. Vertical section of zonal velocity along the equator (contour interval = 5 cm s^{-1}, westward shaded) in a linear model forced by a zonal wind oscillating at the annual period. The response is shown at time of maximum eastward wind in the annual cycle. (from McCreary 1981).

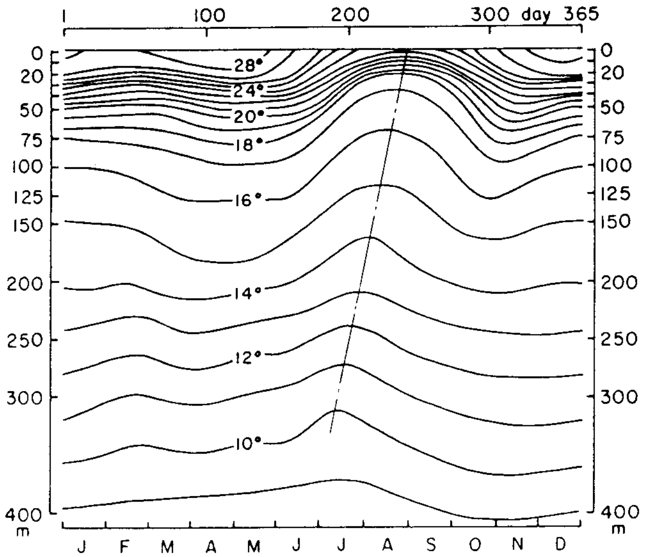


Figure 4. Mean seasonal cycle of isotherm depths deduced from 217 hydrological stations near Abidjan in the Gulf of Guinea. Straight line indicates vertical propagation of the seasonal upwelling signal (from Picaut 1983).

ward. As in the preceding example, the propagation of energy is expressed as an uplifting or a deepening of the isotherms, depending on whether the remote wind direction is westward or eastward. In addition, the downward propagation of energy implies that the energy penetrates in the deep layers faster than in the surface layers; therefore the thermal structure is displaced first in the deep layers, and then progressively toward the surface layers. This is clearly illustrated in Figure 4, where the observed seasonal upwelling signal, near the northern coast of the Gulf of Guinea, exhibits a vertical phase propagation from 300 m to the surface (Picaut 1983).

Horizontal and vertical phase propagation does not imply a mass transport from the forcing area to the eastern boundary, nor from the deep ocean to the surface. The reader has to keep in mind that many of the large-scale phenomena of the equatorial oceans are now explained in terms of wave dynamics, and the analogy to the well-known phenomena of tide and swell could improve understanding of this wave concept. The notion of phase propagation and of associated horizontal and vertical currents remains the same in both. Only the space-time scales are totally different; in these wave dynamics, the frequency is very low (periods from a few weeks to a few years) and the horizontal (vertical) wavelength is of the order of the ocean basin width (depth).

It is fascinating to note that most of the theoretical and numerical studies on El Niño and on the Gulf of Guinea upwelling were made at a time when there was no *in situ* wave evidence. Recently, Knox and Halpern (1982) have shown clear evidence in the Pacific of a pronounced pulse propagating eastward at 2.7 m/s along the equator from 150°W to 90°W; this pulse was apparently forced by an abrupt reversal of trades near 170°E. Eriksen et al. (1983) discussed propagation of such events in detail, and Lukas et al. (1984) presented direct evidence of equatorial wave propagation during the 1982-83 El Niño. In the Atlantic, Katz (1984) observed pulses of displacement of the thermocline that propagate eastward all along the equator. Enfield (1980) discussed evidence of poleward wavelike propagation of sea-level fluctuations all along the eastern boundary of the Pacific, and Picaut (1983) found poleward propagation of the seasonal upwelling along the coast of the Gulf of Guinea. In a study of 29 years of monthly sea level from Mexico to Alaska, Chelton and Davis (1982) showed that the interannual variability of all these records is closely related to El Niño phenomena in the eastern tropical Pacific and propagates poleward at a mean phase speed of 40 cm/s (Figure 5). But the interannual variability along the western coast of North America could not be explained solely by this wave-dynamical theory of El Niño. Large-scale and local atmospheric forcing are also important, especially (as previously noted) north of San Francisco. Lukas and Firing (in press) present evidence of an annual Rossby wave in the central equatorial Pacific; the wave propagates vertically from 900 m to the near-surface pycnocline. In the eastern equatorial Pacific, Lukas (1981) showed some evidence of remotely forced waves by discovering vertical phase propagation, from 500 m to 100 m, at semiannual frequency. Remote forcing of the seasonal upwelling signal along the Gulf of Guinea by zonal equatorial wind stress outside the gulf has been supported by the evidence of vertical (Figure 4) and horizontal phase propagation (Picaut 1983) and the SST-wind stress correlation of Servain et al. (1982). This remote forcing mechanism has been carefully detailed with the numerical models of Busalacchi and Picaut (1983) and McCreary et al. (1984).

WESTWARD ZONAL PRESSURE GRADIENT

Except in their eastern parts, the equatorial Atlantic and Pacific oceans are forced by the strong easterly trades. The westward wind stress appears to be roughly equilibrated by an eastward pressure gradient (Sverdrup balance), which appears as a descending slope of the sea surface from west to east (Figure 6a). This pressure gradient extends down into the subsurface layer and induces a descending slope of the isotherms (Figure 6b) from east to west (Lemasson and Piton 1968; Neumann et al. 1975). Just below the mixed layer this eastward pressure gradient is no longer in

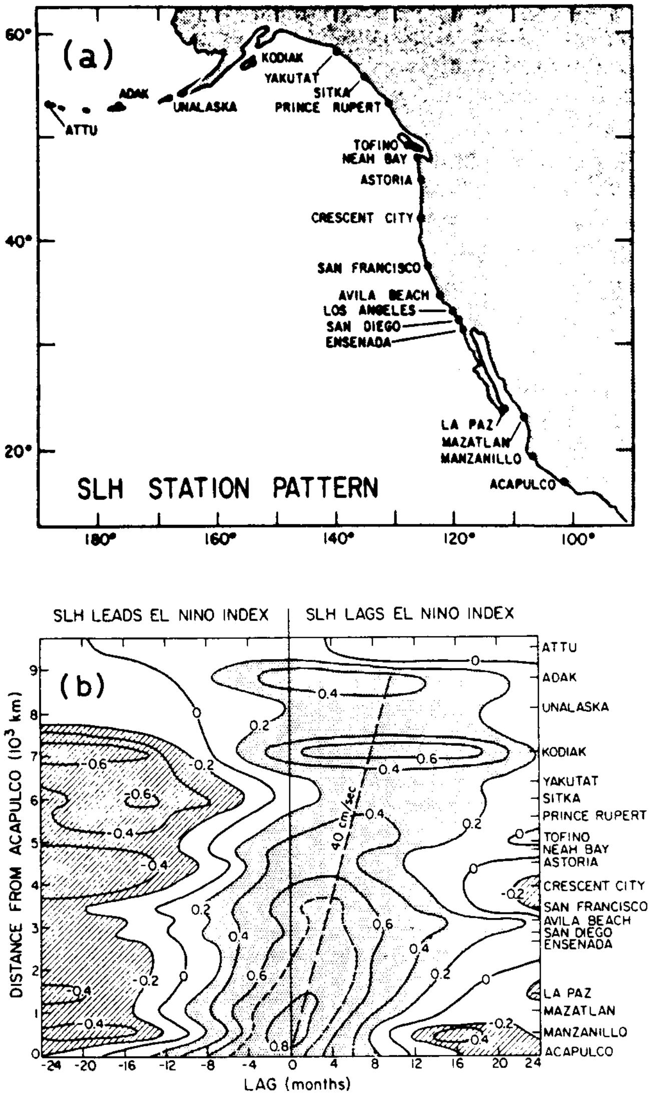


Figure 5. *a.* Location of the 50 sea-level height (SLH) tide-gage stations analyzed.
b. Contour plot of the correlation between low-frequency SLH at each of the 20 tide-gage stations and low-frequency eastern tropical Pacific SST. Dashed line represents approximately 40 cm s^{-1} northward propagation. The 95% significance level corresponds to correlations of ~0.35 (from Chelton and Davis 1982).

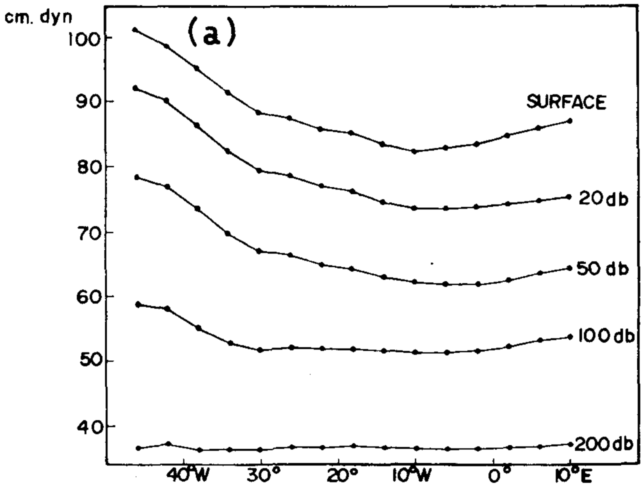
equilibrium with the zonal wind stress and therefore drives an eastward current, the well-known Equatorial Undercurrent.

A simple descriptive way to "explain" this zonal pressure gradient and associated isotherm slopes is to say that the westward winds accumulate water toward the western boundary (piling-up and downwelling), thereby elevating the sea level, while draining water from the eastern boundary and depressing the sea level (upwelling) there. Unfortunately, this common descriptive view lacks in physics, and the concepts of equatorial wave dynamics appear very useful in understanding that the zonal pressure gradient is established some time after a variation of wind in the wake of the propagating waves (Figure 2). If the wind varies regularly at low frequency, then an equilibrium between the zonal wind stress and pressure gradient could appear through a complex superposition of Kelvin waves and Rossby waves (Cane and Sarachik 1981). This appears to be the case at the annual frequency in the Equatorial Atlantic (Katz et al. 1977; Lass et al. 1982; Arnault 1984) but less so in the Equatorial Pacific (Tsuchiya 1979).

The eastern parts of both equatorial oceans are characterized by a clear reversal of sea level and thermocline slopes, which occurs east of 0°-5°W in the Atlantic (Figure 6a) and east of 90°-100°W in the Pacific (Figure 6b). This reversal is not confined to the equator but extends meridionally; for example, it appears all the way to the northern coast of the Gulf of Guinea (Verstraete and Picaut 1983). It is a permanent feature of both eastern oceans, although affected by important variations like the seasonal cycle (Neumann et al. 1975; Meyers 1979; Lukas 1981; Arnault 1984). As noted in the beginning of the previous section, in these eastern ocean regions the winds are predominantly from the south with a small westerly component. As in the central and western equatorial basins, it has been supposed that the eastward wind stress could balance the sharp westward zonal pressure gradient. Recent detailed calculations based on all historical data available, by Lukas (1981) for the Pacific and Arnault (1984) for the Atlantic, reveal that such equilibrium does not hold (by a factor of 3 to 6). In a Sverdrup balance the friction, thermodynamic effects, and nonlinear terms are neglected. Therefore, in the eastern parts of both oceans one or all of these terms must be important.

This could not be the case with the horizontal and vertical frictional effects, because they allow the Equatorial Undercurrent to run all the way from one side of the ocean to the other, and there is no specific reason why friction should increase suddenly when approaching the eastern boundary. Near this boundary, in both equatorial oceans and in their northeast parts, there is an accumulation of warm, low-salinity Tropical Surface Water (Wyrtki, 1967; Berrit, 1973). These light waters are due to heavy rainfall and freshwater outflow. They are present in, at most, the upper 20 meters of the surface layer, and their contribution to the increasing sea-surface height in the east does not appear important (Lukas 1981; Arnault 1984) even in the Gulf of Guinea where there is strong runoff from the Niger and Congo rivers. Finally, it appears that the nonlinear terms—i.e., inertia—probably are the most important contributors to the formation of this slope reversal. These terms are mainly expressed through a deceleration of the Equatorial Undercurrent as it approaches the eastern boundary.

Physically, we could summarize all these balances of forces as follows. In the western and central parts of the equatorial basin the eastward zonal pressure gradient, initiated in the surface layer by the westward winds, drives the Equatorial Undercurrent. When this current approaches the eastern boundary, it has to decelerate until it completely vanishes at the coast. This deceleration must be compensated by a new force, namely the observed eastward pressure gradient. In the first case the pressure gradient creates the current; in the second case the current creates the pressure gradient. According to the synthesis work of Khanaichenko (1974) and the dynamical investigation of McPhaden (1984), the Equatorial Undercurrent belongs to a set of triple-branched, zonal, eastward undercurrents. In the next section we will see that the northern and southern branches of these undercurrents might contribute to the formation of the highly productive tropical thermal domes.



THERMAL DOMES AND EQUATORIAL UNDERCURRENTS

According to Wyrtki (1964), the Costa Rica Dome, found in 1948 from BT observations, consists of a thermal dome situated near 9°N-89°W (Figure 7). It appears to be at the eastern terminus of a ridge in the topography of the thermocline, extending across the Pacific near 10°N, that corresponds to the northern side of the North Equatorial Countercurrent. When this eastward surface current reaches the eastern boundary, it turns north to form the Costa Rica Coastal Current. A cyclonic circulation is therefore completed with the westward North Equatorial Current. The divergence associated with this rotation creates an upward motion believed to be at the dome's origin.

The Guinea Dome, southwest of Dakar, near 10°N-22°W, was first noticed by Rossignol and Meyrueis (1964) and appears clearly, during the northern hemisphere summer, on the historical data analysis of

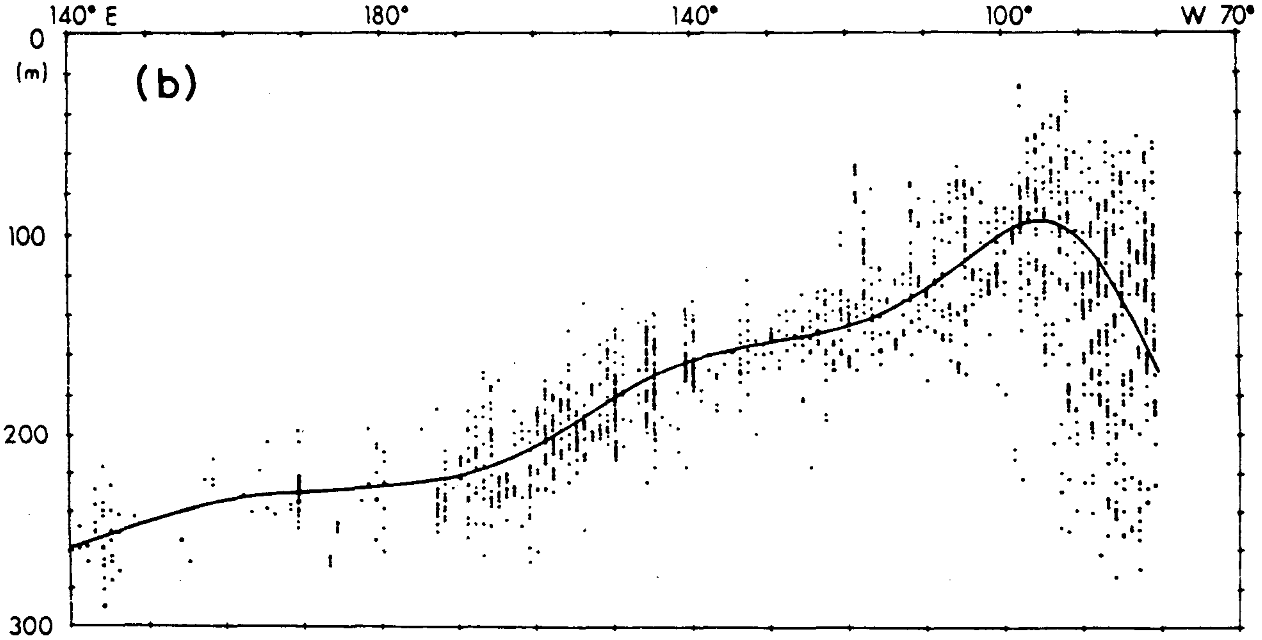


Figure 6. *a*. Mean dynamic height of the 0-, 20-, 50-, 100-, and 200-dbar surface relative to 500 dbar, calculated from a combination of all historical hydrological XBT and BT profiles along the Equatorial Atlantic and between 2°N and 2°S (from Arnault 1984).
b. Depth of the 14°C isotherm. The heavy lines fit all the scattered points obtained with all historical XBT and BT profiles along the Equatorial Pacific and between 1°N and 1°S (from Meyers 1979).

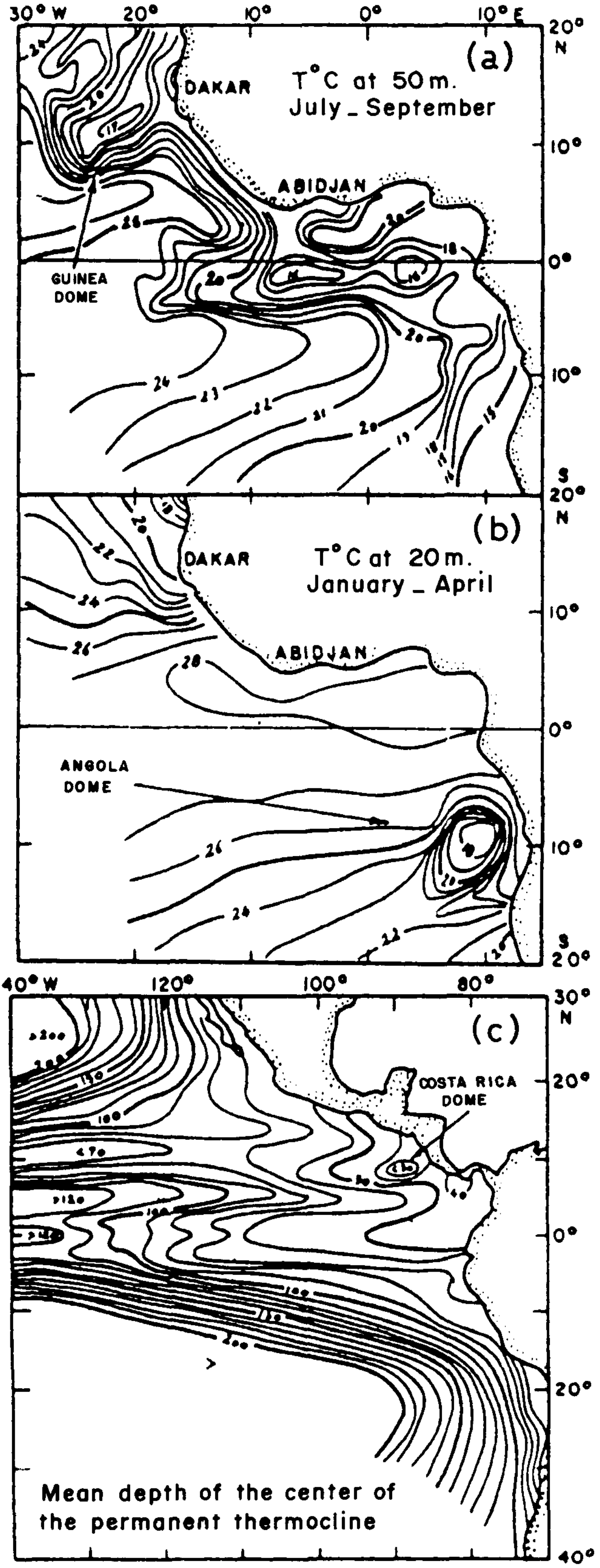


Figure 7. The thermal domes in the eastern tropical Atlantic and Pacific oceans: *a*. Guinea Dome (from Mazeika 1967); *b*. Angola Dome (from Mazeika 1967); *c*. Costa Rica Dome (from Wyrtki 1964).

Mazeika (1967). As in its eastern tropical Pacific counterpart, a cyclonic rotation induced by the surrounding current field seems associated with this dome. Such gyral circulation is not so well defined in the southeast part of the Gulf of Guinea, even though Mazeika's map indicates an Angola Dome near 10°S-9°E during the southern hemisphere summer. A hypothetical Peru Dome might exist near 8°S-85°W, but in the subthermoclinal layers (Voituriez 1981).

In a comprehensive review of phenomena associated with these domes, Voituriez (1981) contests the classical explanation. He noticed that the associated uplifting of the thermal structure is not limited to the thermocline layer but appears farther below (Figure 8). Therefore, the currents more probably involved in the formation of these domes are the North Equatorial Undercurrent (NEUC) and South Equatorial Undercurrent (SEUC). These two subthermocline undercurrents have been carefully documented in both oceans (e.g., Hisard and Rual 1970; Molinari et al. 1981). They take their energy from the Equatorial Undercurrent (McPhaden 1984) in the western and central parts of the equatorial basin and, like this central Equatorial Undercurrent, transport maxima of oxygen (Figure 8b). Near the eastern boundary they are completely detached from the central Equatorial Undercurrent, and when they impinge on this boundary they deflect poleward. Again, this turning motion creates a divergence and an associated upward movement that is probably a part of the domes' mechanism.

Divergence (or convergence) of water mass can also be produced by variations in space of the wind stress. For example, the associated Ekman transport could be greater in one area than in an adjacent area. This leads to a deficit of water mass at the boundary, which in turn is compensated by water from below, i.e., an upwelling. This phenomenon is known as Ekman pumping, and in a steady case is directly related to the wind stress curl ($\partial\tau y/\partial x - \partial\tau x/\partial y$) where τx and τy are the wind stress components. Maps of wind stress curl are therefore very useful in determining possible areas of open ocean upwelling or downwelling. The atlases of Hastenrath and Lamb (1977) and O'Brien and Goldenberg (1982) provide such maps for the entire tropical Atlantic and Pacific oceans, but the wind stress curl near the eastern ocean boundaries is more detailed in charts prepared by Bakun and Nelson[2], thanks to a finer grid resolution. These maps show that the Costa Rica and Guinea domes correspond to regions of favorable cyclonic wind stress curl, which is maximum from May to October. Near the Angola

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[2] Bakun, A., and C.S. Nelson. Wind stress curl in the California, Peru, Canary, and Benguela Current systems (Poster). 1984 CalCOFI Conference, Idyllwild, California, October 29-31, 1984.

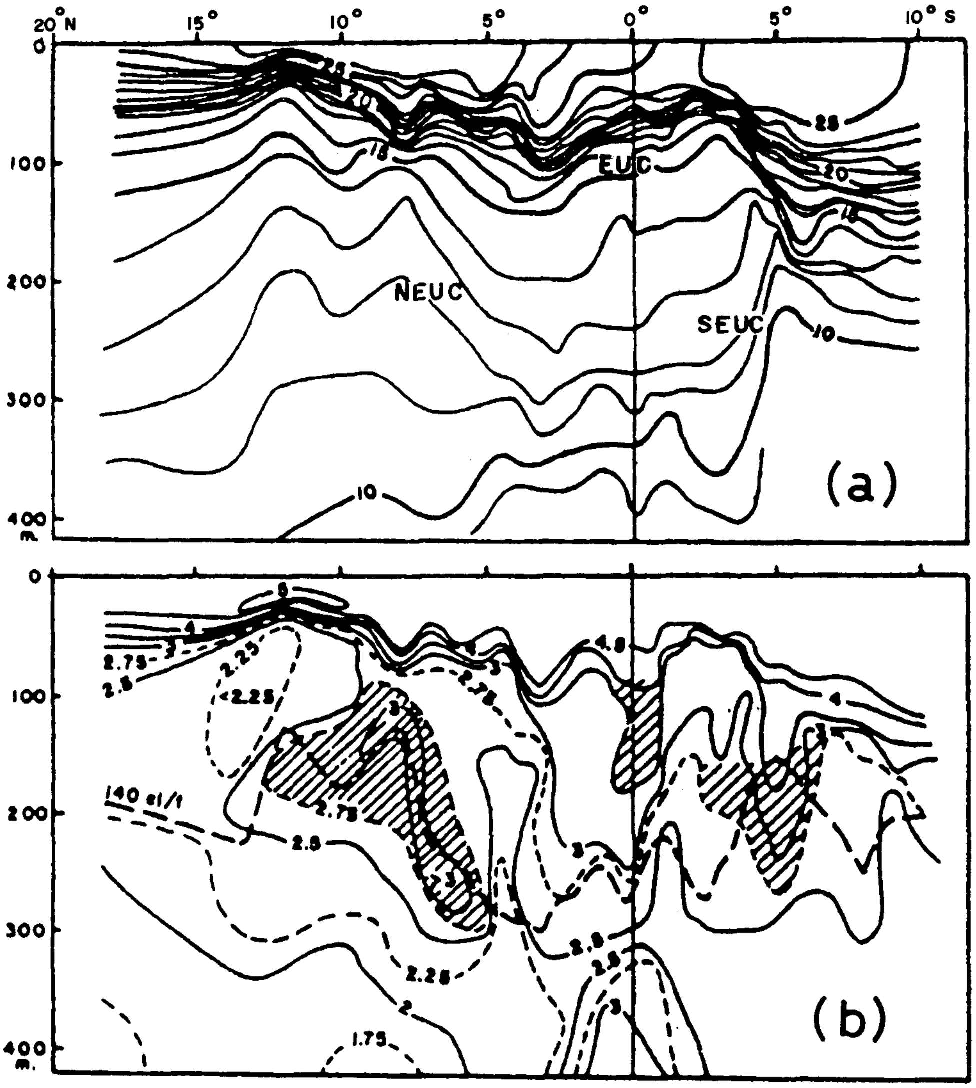

Figure 8. Transequatorial sections in summer 1964 in the Atlantic Ocean at 20°W (EQUALANT 2): *a*. temperature, *b*. oxygen. The high oxygen values of the three branches of the equatorial undercurrent system are shaded (from Voituriez 1981).

Dome the wind stress curl is also upwelling-favorable most of the year, but off Peru the wind stress distributions near the doming, noticed by Voituriez (1981) in the deep layers, are not favorable for upwelling development in the surface layer.

Simple models enable us to better understand the formation mechanisms of these domes. A simple mass transport model forced by wind stress was used by Hofmann et al. (1981) to obtain the gross features of wind-driven circulation in the tropical Pacific. The results do not indicate any surface cyclonic circulation in the Costa Rica Dome area and agree with the suggestion of Voituriez (1981) that surface currents are not necessarily the mechanism that forms these domes. The wind generation of the Costa Rica Dome was detailed by Hofmann et al. (1981) through the results of the reduced gravity model by Busalacchi and O'Brien (1980) that was forced by the observed mean seasonal wind stress. For the Atlantic, Busalacchi and Picaut (1983) discussed the results of a similar model in the Guinea and Angola dome regions. In the model, the simulated Guinea Dome appears to be governed only by Ekman pumping. The corresponding model pycnocline is shallow from August to October, and the associated upwelling-favorable wind stress curl is due, as in the Costa Rica Dome, to the northward movement of the Intertropical Convergence Zone. The contribution of Rossby waves in the seasonal variability is significant for the Costa Rica Dome and dominant for the Angola Dome.

CONCLUSION AND DISCUSSION

Thanks to a relatively clear causal relation resulting from particular equatorial dynamics, theoreticians have had great success in explaining the dominant processes at work in the eastern tropical Atlantic and Pacific oceans. Models like those presented in this paper appear to be tremendously helpful in such research. But we must bear in mind that their purpose is to explain, not to simulate. For example, the equatorial waves discussed in this paper, albeit important, are just a part of the chain that induces the global, large-scale phenomenon entitled ENSO (El Niño-Southern Oscillation). However, the recent model results of Busalacchi et al. (1983) clearly demonstrate the link between the changes of the zonal wind stress in the western and central Equatorial Pacific and the El Niño signature along the eastern boundary a few months later. The extension of the remotely forced theory to the Gulf of Guinea by Moore et al. (1978) and the predictive character of such causal relations have enabled Cury and Roy[3] to discuss a predictive model of fishery along the northern gulf coast. They first established a model using fishing effort and local upwelling index. Then they related this upwelling index with the zonal wind stress off Brazil, one month in advance (the time for an eastward Kelvin wave to cross the basin). Finally they discussed the ability of this wind stress to provide the basis for a predictive model of the fishery.

Another approach to prediction could be attempted through the upward phase propagation phenomenon. If the upwelling or downwelling event is remotely forced, we can expect that its signature will arrive first in the deep layer and then in the surface (Figures 3-4). But we must admit that even though observational evidence of horizontal phase propagations is still relatively rare, it is nonetheless more common than for upward propagation.

Most of the analytical and modeling equatorial studies have focused on purely equatorial mechanisms. As far as we know, only Hofmann et al. (1981) and Busalacchi and Picaut (1983) have looked at their model results near the dome regions. Apart from the modeling study of McPhaden (1984), little is known of the mechanism of the northern and southern branches of the equatorial undercurrents, and even less of their relation to the eastern boundary currents. Multilayer models, on a smaller scale than those usually used for large-scale studies, are needed to better understand some of the fascinating physics of the eastern tropical Pacific and Atlantic oceans.

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ANOMALOUS WARM EVENTS IN EASTERN BOUNDARY CURRENT SYSTEMS

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ABSTRACT

Monthly means of sea-surface temperature are computed for 3° blocks of latitude and longitude along the eastern coasts of the Pacific and Atlantic oceans from March 1971 to June 1984. Long-term mean, between-year standard deviation, and monthly anomaly values are computed and used to describe major anomalous warm events in the California, Peru, Canary, and Benguela eastern boundary current systems. Possible causes of warm events include anomalous local onshore transport, propagation of coastally trapped waves, and anomalous solar radiation.

RESUMEN

Se computan las medias mensuales de temperatura superficial del agua para sectores de 3° de latitud y longitud a lo largo de las costas orientales de los oceanos Pacífico y Atlántico desde marzo de 1971 hasta junio de 1984. Los cálculos de la media de este período, la desviación estándar interanual y las anomalías mensuales se utilizan para describir los principales eventos anómalos de calentamiento en los sistemas de corrientes de margen oriental de California, Perú, Canarias, y Benguela. Las causas posibles de los fenómenos de calentamiento incluyen transporte local anómalo hacia la costa, propagación de ondas retenidas por las costas, y anomalías en la radiación solar.

INTRODUCTION

The four major eastern boundary current systems—California, Peru, Canary, and Benguela—are characterized by equatorward surface flow; persistent coastal upwelling of cold, nutrient-rich waters; high biological productivity; and similar marine populations (Parrish et al. 1983). In certain years, anomalous warming events occur to disrupt the normal upwelling of nutrients and to reduce the surface water's productivity. Severe impacts on local fish populations may occur. In the California Current, warm events have occurred many times in the past, but major recent events have been in 1931-32, 1940-41, 1957-58, 1972-73, 1976-77, and 1982-83. Warm events have been studied intensely in the California Current (e.g., Sette and Isaacs 1960). This paper will describe anomalous events in the California Current and extend the analysis to the other eastern boundary current systems.

During warm events in the California Current, the surface layer warms and deepens and may remain warmer and deeper than normal for a year or more (Table 1). The greatest interannual variability of oceanic conditions off California occurs in winter. Thus, to compare conditions in different years, we computed winter quarterly means (December to February) using the years 1971 to 1984 as a normal. We chose these years because later we will present sea-surface temperature (SST) data for these years. During the winters of 1957-58 and 1982-83, the SST at Scripps Pier was 1.2° to 1.7°C above normal, and positive anomalies persisted into the following winter. Deepening of the surface layer can be represented by the depth of the 14°C isotherm, which is near the top of the thermocline off San Diego (Barilotti et al. 1984). During winter 1957-58, the 14°C isotherm was about 20 m deeper than normal off San Diego, and positive depth anomalies persisted into the following winter. During the 1982-83 winter, the 14°C isotherm was over 40 m deeper than normal and remained deeper than normal the following winter. Deepening of the thermal structure also causes sea level, as

TABLE 1
Winter Quarterly Mean Ocean Conditions During Warm Winters and Comparison with 1971-84

	December-February Quarterly Means				
	Mean winter 1971-84	1957-58	1958-59	1982-83	1983-84
SST at Scripps Pier (°C)	14.5	16.2 (1.7)	15.9 (1.4)	15.7 (1.2)	15.3 (0.8)
Depth of 14°C isotherm off San Diego (m)	48	69 (21)	65 (17)	91 (43)	58 (10)
Sea level at San Diego (cm)	201	204 (3)	203 (2)	215 (14)	202 (1)

Quarterly means were computed as means of monthly mean values for the months December to February. Quarterly anomalies from the mean winter 1971-84 are shown in parentheses. SST data from Scripps Pier, Scripps Institution of Oceanography, La Jolla, California. Depth of 14°C isotherm off San Diego computed from data of Fleet Numerical Oceanography Center (Barilotti et al. 1984). Sea-level data from National Ocean Service, NOAA, Rockville, Maryland.

observed at tide gages, to stand higher. Monthly mean sea level at San Diego was about 6 cm higher than normal in 1957-58 and up to 16 cm higher than normal in 1982-83.

Two biologically significant processes occur during warm events (McLain and Thomas 1983). One is an intensification of the normal seasonal poleward flow of undercurrents over and along the edge of the continental shelf. Current-meter observations in five winters off the central Oregon coast (Table 2) suggest that during winter 1982-83, the speed of poleward flow over the continental shelf (13.0 cm/sec) was almost twice the mean speed observed in the other four winters (7.5 cm/sec). This increased poleward flow advected warm southern water poleward, further increasing coastal temperatures. The strong poleward flows and warm coastal waters allowed warm-water fish species to extend their ranges poleward along the coast or inshore from warmer waters offshore. Occurrences of warm-water species in the California Current during warm years have been described by many authors (e.g., Radovich 1961). Bonito, barracuda, white sea bass, and others have been caught far north of their normal ranges during warm years. Whereas the larger animals may swim northward in the warm waters, many warm-water planktonic organisms also have been observed far north of their normal ranges, suggesting that poleward transport is a contributing factor in range extension.

A second major effect observed during warm events has been decreased biological productivity of the surface waters. The thickened and warmed surface layer reduces the ability of upwelling-favorable winds to cause upwelling of nutrients into lighted surface waters. Chelton et al. (1982) showed that zooplankton volumes observed on CalCOFI surveys during 1957-59 were much lower than on later surveys during the 1960s and 1970s. Although fewer observations of this type have been made in recent years, available data do suggest similar low zooplankton volumes and decreased productivity in the California Current in 1983 (McGowan 1984). Biological observations of poor reproduction of many species of fish and sea birds (Ainley 1983) and the extremely low harvest of kelp off southern California (Barilotti et al. 1984), for example, all suggest a sharp drop in biological productivity following the winter of 1982-83.

TABLE 2
Mean Poleward Speed of California Undercurrent Observed with Current Meters at Midshelf off Central Oregon

Winter	Poleward speed (cm/sec)
1973-74	7.5
1977-78	10.2
1981-82	5.8
1982-83	13.0
1983-84	7.0
Mean of four winters 1973-74, 1977-78, 1981-82, and 1983-84	7.5

Mean speeds are for the 93-day period October 30 to January 30. Current meters were about 25 m off the bottom in water depths of 90 to 120 m. Data from Dr. Robert Smith, Oregon State University, Corvallis, Oregon.

CAUSES OF ANOMALOUS WARM EVENTS

Two major hypotheses have been suggested to explain anomalous warm events in the California Current system: (1) propagating coastal waves in the ocean, and (2) atmospheric circulation changes. The ocean hypothesis suggests that during periods of strong trade winds over the tropical Pacific, warm surface water piles up in the western tropical Pacific, causing a rise in sea level there (Wyrtki 1975). When the trade winds relax or reverse, sea level falls and a pulse of warm surface water flows eastward toward South America, propagating as an equatorially trapped Kelvin wave. El Niño occurs as the warm water intrudes against the South American coast, causing a rise in sea level, and depressing the thermocline along the coast. The depression of the thermocline may be as large as 150 m (at 0°N, 85°W in October 1982, Toole 1984).

Wave theory (Gill 1982) suggests that the depression can propagate in two ways: (1) westward along the equator as equatorially trapped Rossby waves, and (2) poleward along the coast as both coastally trapped waves and coastal Kelvin waves. Since the trapping distance of coastal Kelvin waves is limited to the Rossby radius of deformation, they narrow as they proceed poleward and eventually become coastally trapped waves. Therefore, we will refer to the two types of poleward-propagating waves as coastally trapped waves. As they propagate poleward the coastally trapped waves lose energy by numerous processes, including generation of very slow, westward-propagating planetary Rossby waves. As the depression of the thermocline propagates poleward along the coast, it geostrophically forces an intensification of normal poleward coastal countercurrents. After the depression passes a point on the coast, the countercurrent may reverse to equatorward. The poleward flows commonly occur in winter, and the reversals, called spring transitions, are most intense following warm winters (Breaker 1983).

One shortcoming with the ocean hypothesis is that it does not explain the very wide expanse of anomalously warm water observed off the West Coast in early 1983 and the simultaneous formation of a pool of colder than normal water in the central North Pacific. Published SST anomaly charts for winter 1982-83 (U.S. Dept. Commer. 1983) show that SSTs were above normal for over 800 km seaward of the California coast. A coastally trapped wave would be restricted to within about 50 km of the coast and thus could cause positive anomalies only near the coast, leaving the offshore cold pool unexplained. Simpson[1] suggests that the westward-propagating Rossby waves generated by the poleward-propagating coastally trapped waves cannot explain the offshore cold anomalies observed in winter 1982-83.

Coastally trapped waves of higher than annual frequency are generated by tropical storms and have been observed off Central America in hourly sea level records (Christensen et al. 1983). As these waves propagate poleward, they become trapped in the Gulf of California and do not propagate poleward past the tip of Baja California. Evidently, coastally trapped waves must be of very large spatial scale and of several months' or longer duration to propagate past the Gulf of California.

Subsurface temperature data provide empirical evidence for the existence of poleward-propagating thermal depressions. Brainard and McLain (in press) computed anomalies of temperature at 100 m for areas along the west coast of North and South America. They analyzed over 115,000 temperature profiles from the files of Fleet Numerical Oceanography Center for a series of 3° blocks of latitude along the coast from 30°S to 50°N from 1951 to 1984. Anomalies of monthly mean temperature at 100 m computed from these profiles show that regions of anomalously warm water at 100 m occurred along the coast during 1957-58, 1972-73, 1976-77, and 1982-83. The regions appeared to expand poleward from near the equator, with their leading edges occurring progressively later in time with distance away from the equator. Although this could be evidence of a poleward-propagating coastally trapped wave, the leading edges of the anomalies traveled at speeds of 6 to 44 km/day, much less than the theoretical speeds of coastally trapped waves. Likewise, other authors (e.g., Enfield and Allen 1980; Chelton and Davis 1982) have found relatively low speeds of coastally propagating disturbances. The low propagation speed of the anomalies suggests that changes in advection may also occur (Chavez et al. 1984). Brainard and McLain (in press) also showed a general warming trend along the whole coast at 100 m beginning in 1976 and culminating in the extremely strong warm event in 1982-83. This warming trend was described by McLain (1983) and is similar to that described by Huang (1972) for the years 1958-69 relative to the years 1948-57.

Sea-surface temperature observations are more abundant than subsurface profiles and show the same general pattern of anomalies. Figure 1 shows the locations of 39 3° blocks of latitude and longitude in the Pacific, and 37 3° blocks in the Atlantic where monthly mean SST was computed. The SST reports used were received in real time by Fleet Numerical Oceanography Center from March 1971 to June 1984. The monthly means of SST were made for the 3° blocks by first averaging the reports by 1° blocks each month and then making 3° means of the 1° submeans. The number of observations in each 1° block varied widely from 0 to over 50 reports per month. Thus, making the 3° means from the 1° submeans reduced the spatial bias of sampling. A 3° mean was made if there was at least one 1° submean available. Because of the inhomogeneous distribution of the reports, this may have caused spurious 3° means in areas of sparse data. The number of reports used in each 3° block (shown in Table 3) varies from over 40,000 in the California and Canary currents to fewer than 100 in the Peru Current. Anomalies of SST were computed relative to the long-term mean for the period March 1971 to June 1984.

The long-term mean annual cycle of SST in the California Current region (Figure 2, left) is dominated by seasonal migration of a region of closely packed SST isotherms along the coast of Mexico between 18° to 28°N (Blocks 27 to 31 in Figure 1). This region represents a frontal zone between the colder water to the north (where the seasonal cycle of heating and cooling is strong) and the warmer water to the south (where seasonal fluctuations are small). A similar frontal region migrates seasonally in the Peru Current region from 0° to 10°S off Ecuador. The two frontal regions lie at the equatorward end of the California and Peru eastern boundary currents where the currents leave the coast and turn to the west.

Interannual variability of SST is described by between-year standard deviations of the individual monthly mean SST values (Figure 2, right). The greatest interannual variability of SST along the coast is in the Southern Hemisphere, with between-year standard deviations of over 1.0°C from the equator to at least 40°S. Peak variability (over 2.0°C standard deviation) occurs in a region from 15°S to 25°S from November to February, representing El Niño fluctuation. This

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[1] Simpson, J.J. MS. The Aleutian Low teleconnection between equatorial and mid-latitude "El Niño-type" events. Submitted to J. Geophys. Res.

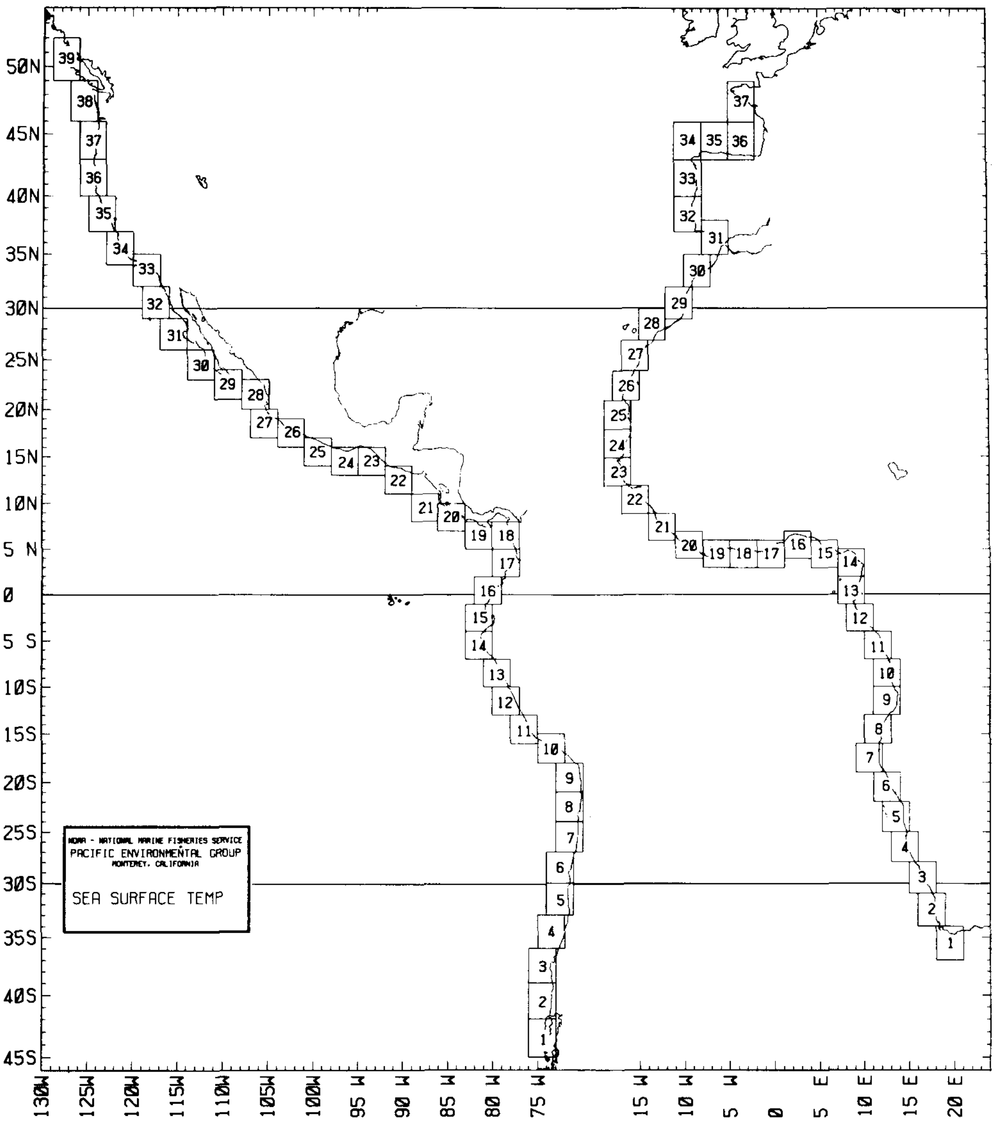

Figure 1. Locations of 3° blocks of longitude and latitude along eastern boundaries of Pacific and Atlantic oceans where monthly mean sea-surface temperature was computed for the period March 1971 to June 1984.

region is somewhat south of the region off Ecuador and Peru where El Niño is normally thought to be strongest. Perhaps the extreme scarcity of reports off Peru and Chile caused the apparent center of greatest interannual variability to be shifted southwards. Interannual variability in the California Current is lower than in the Peru Current and has between-year standard deviations of 0.5° to 0.8°C. The standard deviation is locally highest near the frontal zone off Mexico, representing interannual changes in the seasonal migration of the zone.

The computed anomalies of SST along the eastern Pacific were very noisy, with many small regions of positive and negative anomaly. Anomalies in the Peru Current were particularly noisy, perhaps because of the extreme scarcity of reports there. To smooth the array of SST anomalies, we applied two filters to the array in succession. First, we eliminated spikes with a 3 × 3 nonlinear or median filter in which the central value of each 3 × 3 subarray was replaced by the median of the 9 values in the subarray. Second we passed a 3 × 3 linear smoother with an arbitrarily chosen smoothing factor of 0.5 over the array. After this filtering, only the major anomalies remain.

Regions of positive anomaly of great coastwise extent occurred in the eastern Pacific in 1972-73 and 1982-83 (Figure 3), with peak values of about +4.0°C in December 1982 and January 1983 off Ecuador and Peru, and smoothed values of greater than +2.5°C. A positive coastwise anomaly of lesser magnitude and extent occurred in 1976-77. Because these coastwise anomalies are contemporaneous with major tropical El Niño events, they are probably of tropical origin. Negative coastwise anomalies occurred from 1973 to

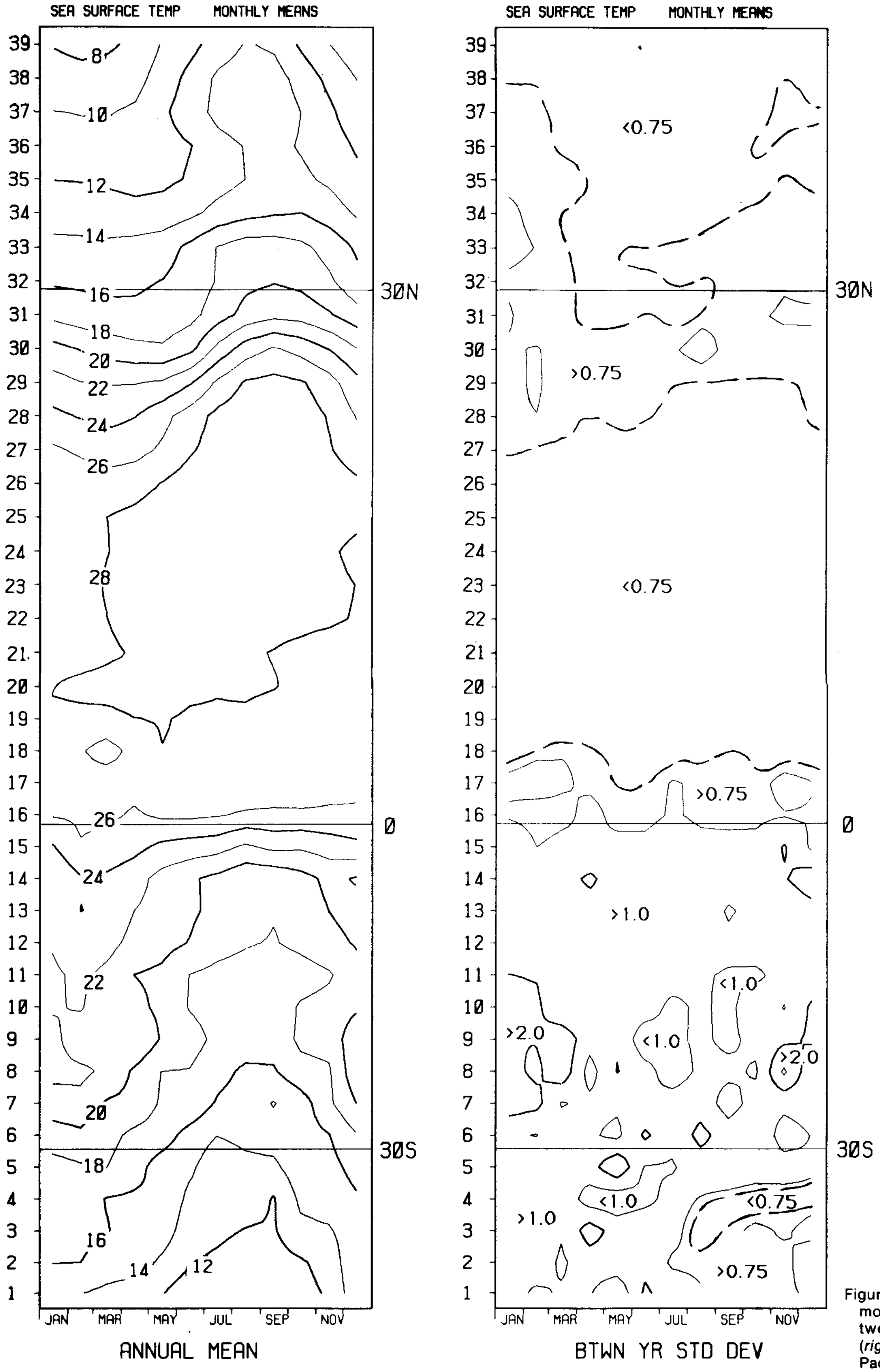

Figure 2. Annual cycle of long-term monthly mean SST (*left*) and between-year standard deviation (*right*) along eastern boundary of Pacific Ocean. Contour intervals are 2°C for the annual means and 1°C for the standard deviations (dashed line is 0.75°C).

TABLE 3
Total Number of SST Observations in 3° Blocks in the Eastern Atlantic and Pacific Oceans from March 1971 to June 1984

Block number	Pacific	Atlantic
39	5,710	—
38	47,092	—
37	20,581	15,980
36	30,149	5,415
35	82,058	14,797
34	42,885	46,279
33	35,568	46,759
32	8,107	30,665
31	8,956	21,035
30	10,559	10,817
29	10,020	6,510
28	5,427	11,503
27	8,886	19,488
26	9,763	59,190
25	9,103	32,198
24	8,600	24,063
23	5,592	22,255
22	7,126	9,426
21	8,016	15,075
20	8,067	5,466
19	7,122	5,030
18	1,475	3,825
17	332	2,201
16	985	1,121
15	673	930
14	879	553
13	636	456
12	477	452
11	305	1,453
10	120	5,946
9	62	4,659
8	70	1,661
7	73	12,238
6	150	15,424
5	115	6,113
4	81	3,269
3	115	7,258
2	110	10,693
1	198	8,440
Total	386,243	488,643

1975. Because of the large coastwise extent of these anomalies, the California and Peru current systems may have had similar anomalies simultaneously.

Large positive anomalies occur in regions such as off Baja and Alta California, where SST normally decreases rapidly with distance poleward along the coast. Stronger than normal poleward coastal flow during anomalous warm events would tend to cause positive SST anomalies in these regions. In contrast, off Central America, reduced positive or even negative SST anomalies occur as gaps in the coastwise positive anomalies. Negative SST anomalies also appear in maps of SST anomaly off Central America during February 1983 (U.S. Dept. Commer. 1983). A possible explanation for negative SST anomalies off Central America at a time when one might expect positive anomalies is that the mean coastwise SST gradient is small or negative in this region. A stronger than normal poleward flow along this coast would have little tendency to cause positive SST anomalies. Other possible reasons for gaps in positive coastwise SST anomaly might be: (1) wind mixing by Tehuantepec and Papagallo winds, which occur in this region and cause local cooling, and (2) upwelling of cold waters off Costa Rica. Douglas and Englehart (1983) found that cold anomalies off Mexico and Central America were correlated with alterations in the paths of tropical hurricanes.

In contrast to the coastwise warm events of 1972-73, 1976-77, and 1982-83 and the cold events of 1973-75, other anomalous periods occurred locally in the California Current and were not associated with tropical warm events. These included positive anomalies in the winters 1977-78, 1979-80, and 1980-81, and the negative anomalies in the winters of 1970-71, 1971-72, and 1978-79. Near-zero anomalies occurred in winter 1981-82. Similarly, many local SST anomalies occurred in the Peru Current that were not related to the major El Niño tropical warm events.

The second major ocean warm-event hypothesis—atmospheric circulation changes—suggests that the local anomalies in the California Current are caused by variations in wind-induced, onshore transport in midlatitudes. Recent work of Simpson (1983, 1984a, 1984b) and others emphasizes the importance of onshore transport of warm surface waters during local warming events. Horel and Wallace (1981) showed that a particular pattern of midlatitude upper atmospheric circulation, the "Pacific/North America" pattern, is associated with, or "teleconnected" to El Niño warming events in the Pacific. When there is anomalous warming in the tropical Pacific, there often is an associated shift in the upper atmospheric circulation, which causes a trough over the central North Pacific, a ridge over western Canada, and a trough over the eastern United States. This pattern of upper-atmospheric circulation is associated on the surface with an intensification of the Aleutian Low. Emery and Hamilton (in press) present maps of the winter mean surface atmospheric pressure over the North Pacific and show that years with a strengthened Aleutian Low are often associated with anomalous warmings in the tropics. During winter 1982-83, the Aleutian Low was several standard deviations deeper than normal and was shifted 10° to 20° of longitude east of its normal position over the central Aleutians, causing

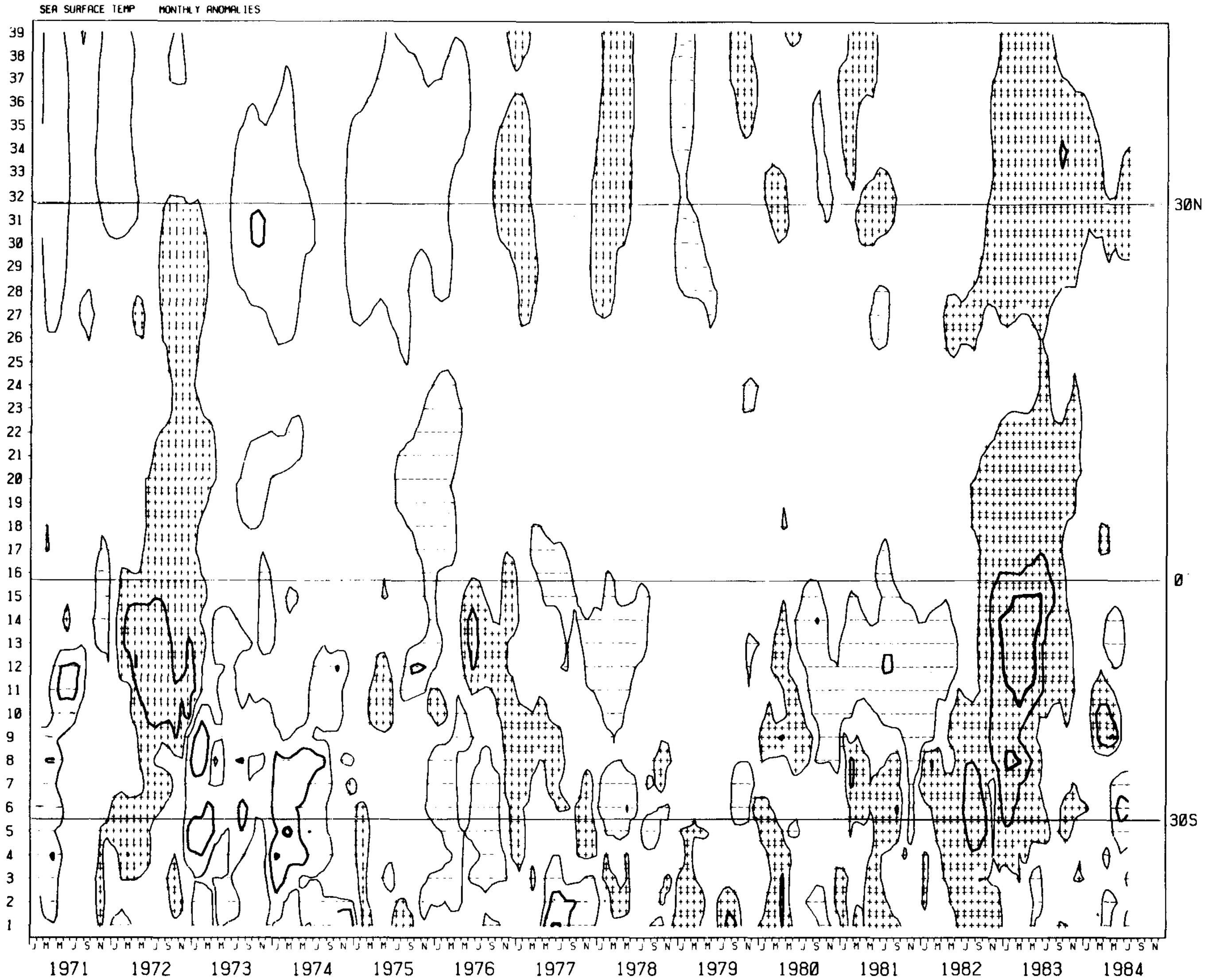

Figure 3. Anomaly of monthly mean SST along eastern boundary of Pacific Ocean. Small plus and minus signs represent anomalies before smoothing of greater than +0.5°C and less than −0.5°C, respectively. Contouring was performed after median and linear filtering. Light contour lines represent +0.5° and −0.5°C; dark contour lines represent −2.5°, −1.5°, +1.5°, and +2.5°C.

a very strong negative pressure anomaly over the Gulf of Alaska. The strong Aleutian Low combined with a weakened North Pacific High to cause a change in surface winds that resulted in very strong onshore transport of surface waters against the California coast.

Evidence of the importance of onshore transport in causing anomalous warm events off California can be seen in indices of upwelling intensity computed for 15 points along the west coast of North America (Figure 4) using methods of Bakun (1973). The strong upwelling off central California in summer has peak upwelling index values of greater than +200 m^3/sec/100 m coastline (Figure 5). During winter, tongues of negative upwelling index, representing onshore transport or downwelling, intrude southward along the coast from the Gulf of Alaska, where onshore transport occurs during much of the year. The tongues of onshore transport did not generally extend south of about 36°N in the early 1970s except in winter 1972-73. From 1976 to 1980, however, onshore transport extended south to about 33°N each winter. Increased frequency of onshore transport of warm surface water off central California in winter may thus have been a cause of the general warming along the coast during 1976-80.

During winter 1982-83, there was an extremely strong pulse of onshore transport with upwelling index

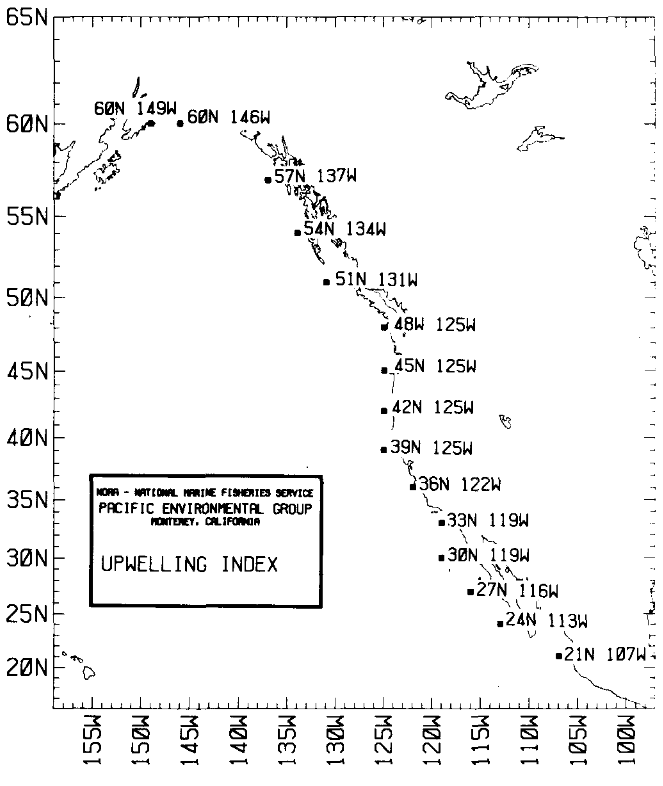

Figure 4. Locations of 15 points along west coast of North America where upwelling indices were computed by methods of Bakun (1973).

values of less than −200 units for two consecutive months. Onshore transport in the California Current region is not normally less than −150 index units in any one month. The largest total onshore transport (sums of negative index values at 42°N) of any winter in the period of record, 1946-84, occurred in 1982-83 (Norton et al. in press). There were −765 total units of negative upwelling index that winter, three times the normal of −251 index units. During the warm winter of 1957-58, there was also strong onshore transport, with a total of −544 index units. During the warm winter of 1972-73, however, strong onshore transport did not occur (−219 index units), suggesting that warming in 1972-73 was primarily a tropically related phenomenon. Lack of local reinforcement of the tropical warming in 1972-73 prevented positive SST anomalies from extending as far north as in 1982-83 and from persisting as long. During the more normal winter of 1981-82, the total onshore transport was −215 index units, and SST anomalies were near zero. Only very weak onshore transport occurred off California in winter 1978-79 (−99 index units), and negative anomalies (Figure 3) resulted.

The mechanism of onshore transport can explain a number of other features of anomalous coastal events. For example, it can explain the large offshore extent of the warm water along the coast in 1982-83 and the

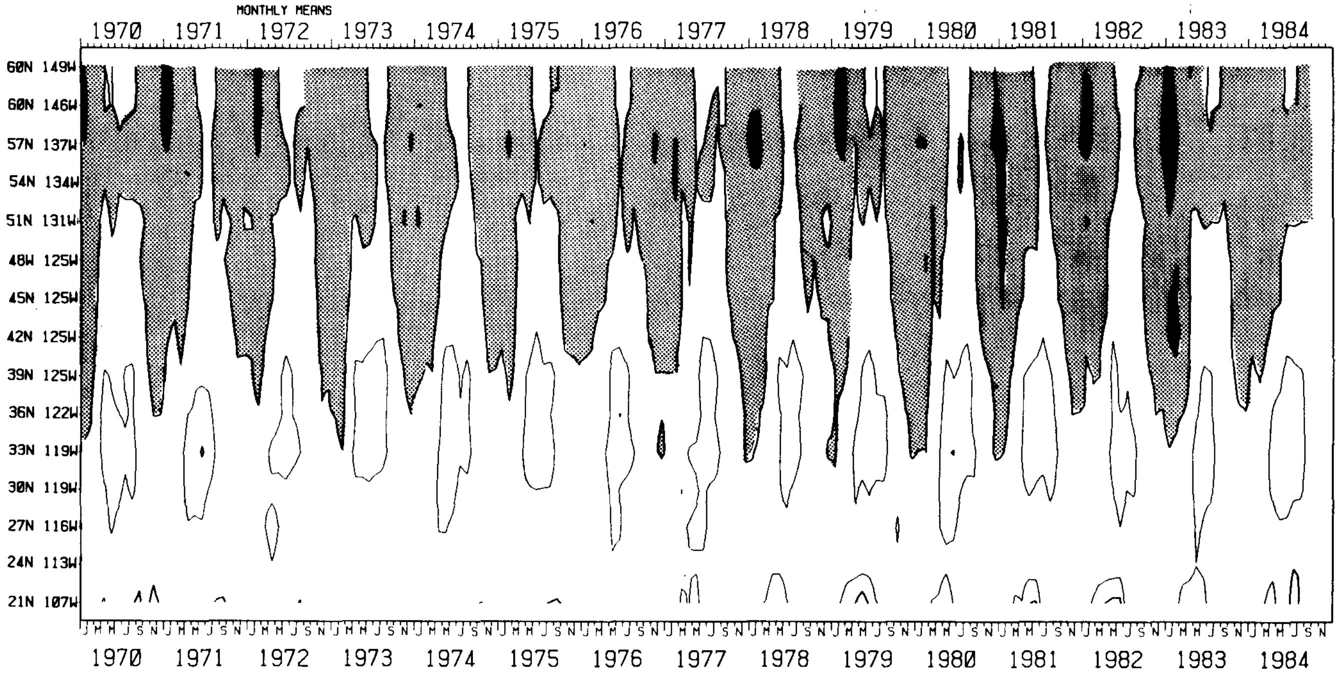

Figure 5. Monthly mean indices of upwelling intensity computed for 15 points along the west coast of North America. Units are m³/sec/100 m of coastline. Heavy contour lines are zero index and enclose tongues of onshore transport or negative upwelling index. Black areas are less than −200 index units. Fine contour lines are +200 index units and enclose areas of strong upwelling off central California in summer.

simultaneous formation of a pool of anomalously cold water in the central North Pacific. The onshore transport mechanism can also explain the low-salinity, high-dissolved-oxygen water observed in early 1983 on CalCOFI line 90 off San Diego (Simpson 1984a). Low-salinity waters have also been observed at frequently occupied coastal monitoring stations after periods of onshore transport (McLain and Thomas 1983).

In some years, local heating may contribute to anomalous warming events. In 1976-77, a blocking high-pressure system persisted over much of the western United States, causing record drought. The many warm, calm days associated with this high-pressure system probably caused increased solar radiation and warming of the surface waters. Solar heating cannot, however, explain the 1982-83 subsurface temperature anomalies, which were larger than those at the surface.

Thus it appears that anomalous warming events in Pacific eastern boundary current systems may be either—or both—tropical or locally forced events. El Niño events in the tropics can cause poleward-propagating coastally trapped waves, but because they narrow and lose energy, these waves do not seem to explain the large coastwise SST anomalies. Both processes may occur in the same year, and when they occur together, local onshore transport can reinforce the effects of coastally trapped waves to create the observed large anomalies in midlatitudes. Interannual variations in local onshore transport can cause local warm and cold events in the California Current. Onshore transport itself could generate coastally trapped waves, which would propagate the effects of the onshore transport poleward. To an observer at a point along the coast, both tropical and local processes would cause apparent depression of the thermal structure and intensified poleward coastal currents. When local reinforcement occurs, these effects may be additive. During 1982-83, for example, both processes were unusually intense, and combined to cause an extremely strong warm event in the California Current: warming in the tropics was the greatest in many decades, and local onshore transport was the strongest of any winter during the period of record 1946-83 (Norton et al. in press). The resulting depression of the thermal structure and poleward currents along the coast were very large (Tables 1 and 2). In contrast, during the tropical warm event of 1972-73, when local reinforcement was not strong, SST anomalies in the California Current were of short duration and did not extend far up the coast. Local reinforcement by onshore transport in the Peru Current has not been demonstrated (Fonseca 1984).

SST FLUCTUATIONS IN THE EASTERN ATLANTIC

The long-term mean annual cycle of SST fluctuations in the eastern Atlantic (Figure 6, left) is dominated by seasonal migration of frontal zones between 10°N and 20°N between Cape Vert and Cape Blanc in the Canary Current (Wooster et al. 1976) and between 10°S and 20°S near Cape Fria in the Benguela Current (Wooster, in Picaut 1983). As in the Pacific, the frontal zones represent regions where the eastern boundary current turns offshore. Seasonal heating and cooling is strong poleward of the frontal zones, and seasonal variations are weak equatorward of the zones.

Interannual variability of SST in the eastern Atlantic (Figure 6, right) is similar to that of the Pacific, with low values of between-year standard deviation in the Northern Hemisphere and large values in the Southern Hemisphere. Local, weak maxima of variability occur in the Canary Current near the frontal zone. Interannual variability in the Benguela Current is high, and between-year standard deviations range up to 2.2°C near 10°S, reflecting large interannual variations in the front. A band of high interannual variability occurs from 25° to 30°S as a result of multiyear anomalous periods.

The anomalies of SST in the eastern Atlantic (Figure 7) appear somewhat similar to those of the Pacific, except that no large coastwise anomalies occur. Anomalies in the Canary Current are weak and of local nature. There was a general warming trend evident during 1971-84 in the Canary Current; it was cool in 1972 and 1974 and then warming in 1976 and remaining generally warm thereafter, with positive anomalies occurring in 1978, 1979-80, 1981-82, and 1983-84.

SST values in the Benguela Current were above normal from 1971 to early 1979 and below normal from 1979 to 1983. Greatest negative anomalies (less than −1.0°C) occurred off Namibia from November 1981 to May 1982, in rough agreement with the cold period observed there during February to September 1982 by Boyd and Agenbag (1984). The persistence of these anomalous periods is unusual. Whereas in the other eastern boundary current systems, SST anomalies are more coherent with distance along the coast than in time (causing the generally vertical features in Figures 3 and 7), in the Benguela Current, anomalies were very persistent in time (causing the more horizontal features at the bottom of Figure 7). This suggests that the upwelling-related winds over the Benguela Current must be very persistent, but Picaut (1983) mentions that south of about 20°S in the Benguela Current the correlation between winds and SST anomalies is low. Perhaps the large persistence of the

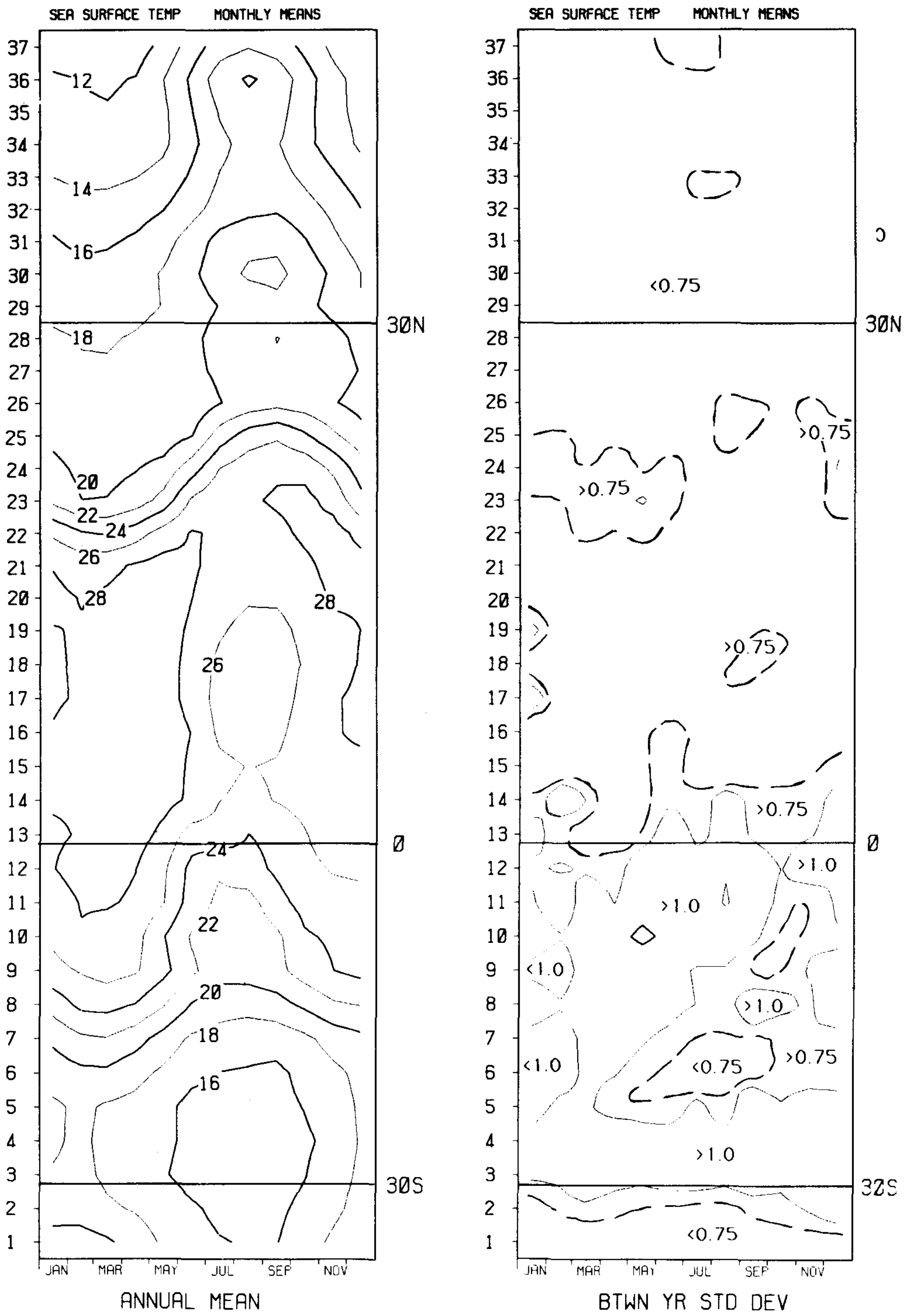

Figure 6. Annual cycle of long-term monthly mean SST (*left*) and between-year standard deviation (*right*) along eastern boundary of Atlantic Ocean. Contour intervals are 2°C for the annual means and 1°C for the standard deviations (dashed line is 0.75°C).

anomalies in this region is related to very slow changes in advection in the South Atlantic gyre.

An intense local warming occurred in the Benguela Current from March to at least May 1984. SSTs greater than 29°C intruded as far south as latitude 15°S. The warm event started along the coast near Cape Fria (12° to 19°S) and expanded equatorward, becoming most intense near Point Noire, Congo (5° to 10°S), in June 1984, with anomalies of up to 3.5°C. In contrast, Boyd and Thomas (1984) examined hydrographic data taken within 1° of the coast from 18° to 26°S and found water up to 6°C warmer than normal, particular-

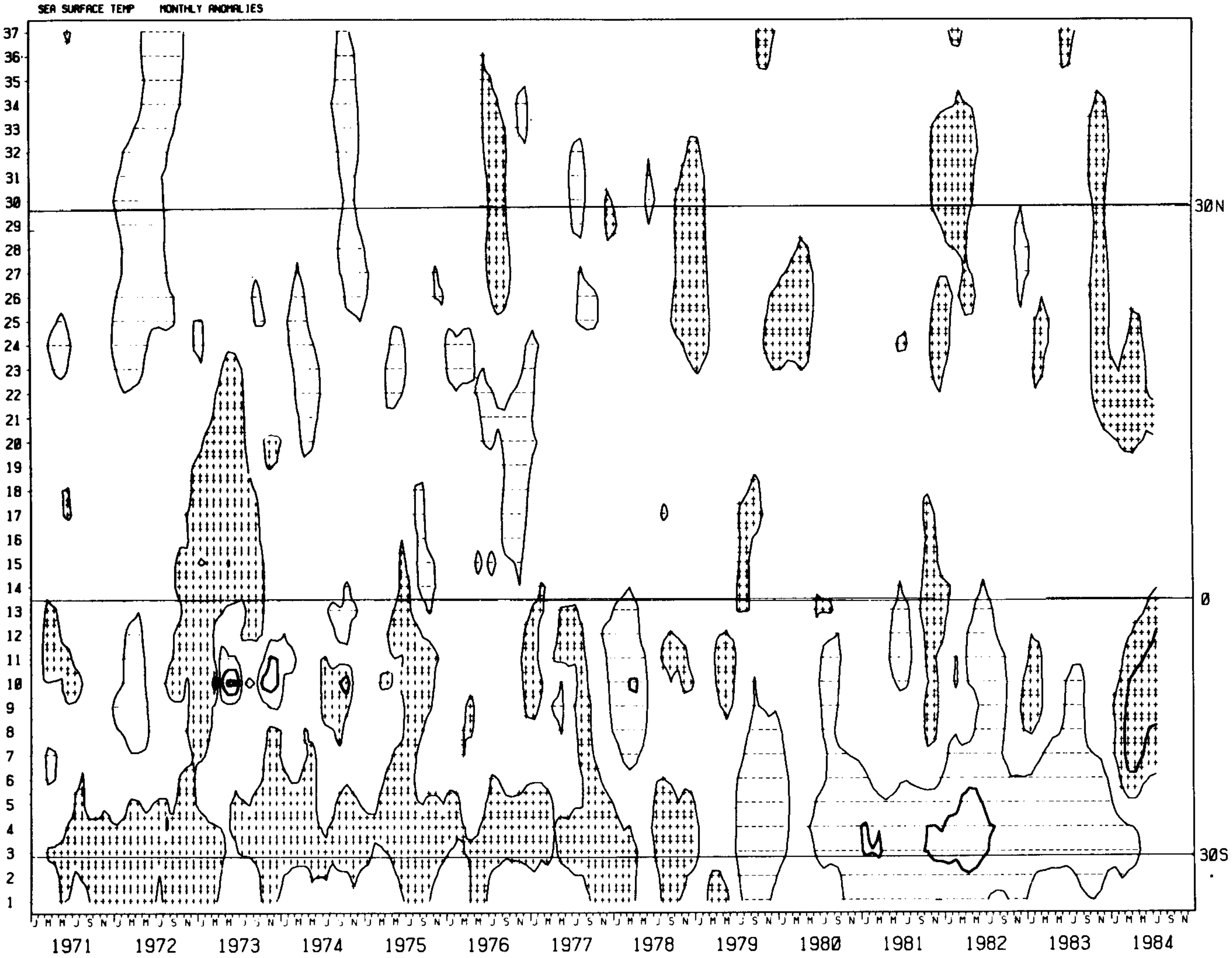

Figure 7. Anomaly of monthly mean SST along eastern boundary of Atlantic Ocean during the period March 1971 to June 1984. Small plus and minus signs represent anomalies before smoothing of greater than +0.5°C and less than −0.5°C, respectively. Contouring was performed after median and linear filtering. Light contour lines represent +0.5° and −0.5°C; dark contour lines represent −2.5°, −1.5°, +1.5°, and +2.5°C.

ly near the coast. They suggest that the warm event was caused by a southward intrusion of equatorial water. If so, the intrusion may have come from offshore, reaching the coast near Cape Fria, and then expanding generally northward, as seen in the 3°-block SST data. It may also have expanded southward and been seen in the hydrographic data, very close to the coast.

In contrast to the large coastwise extent of SST anomalies in the Pacific, anomalies in the eastern Atlantic are more local and do not have the large coastwise extent. The Atlantic anomalies generally were restricted to one of the three regions: Benguela Current, Gulf of Guinea, and Canary Current. Only the warm events in 1972-73 and mid-1981 in the Benguela and Gulf of Guinea regions spanned more than one region. This suggests that different oceanic or atmospheric processes affect the three regions. Also, SST anomalies in the Pacific tended to occur in northern winters, but Atlantic anomalies occurred throughout the year.

RELATION OF TROPICAL ATLANTIC AND PACIFIC ANOMALIES

Because there was an anomalous warm event in the tropical Atlantic in early 1984, one year after the major warm event in the Pacific in 1982-83, it was thought that similar Atlantic warm events might have occurred following earlier Pacific warm events. To examine this question, we made time series of monthly mean SST for the years 1946 to 1979 by 5° blocks for the eastern tropical Pacific and Atlantic from the

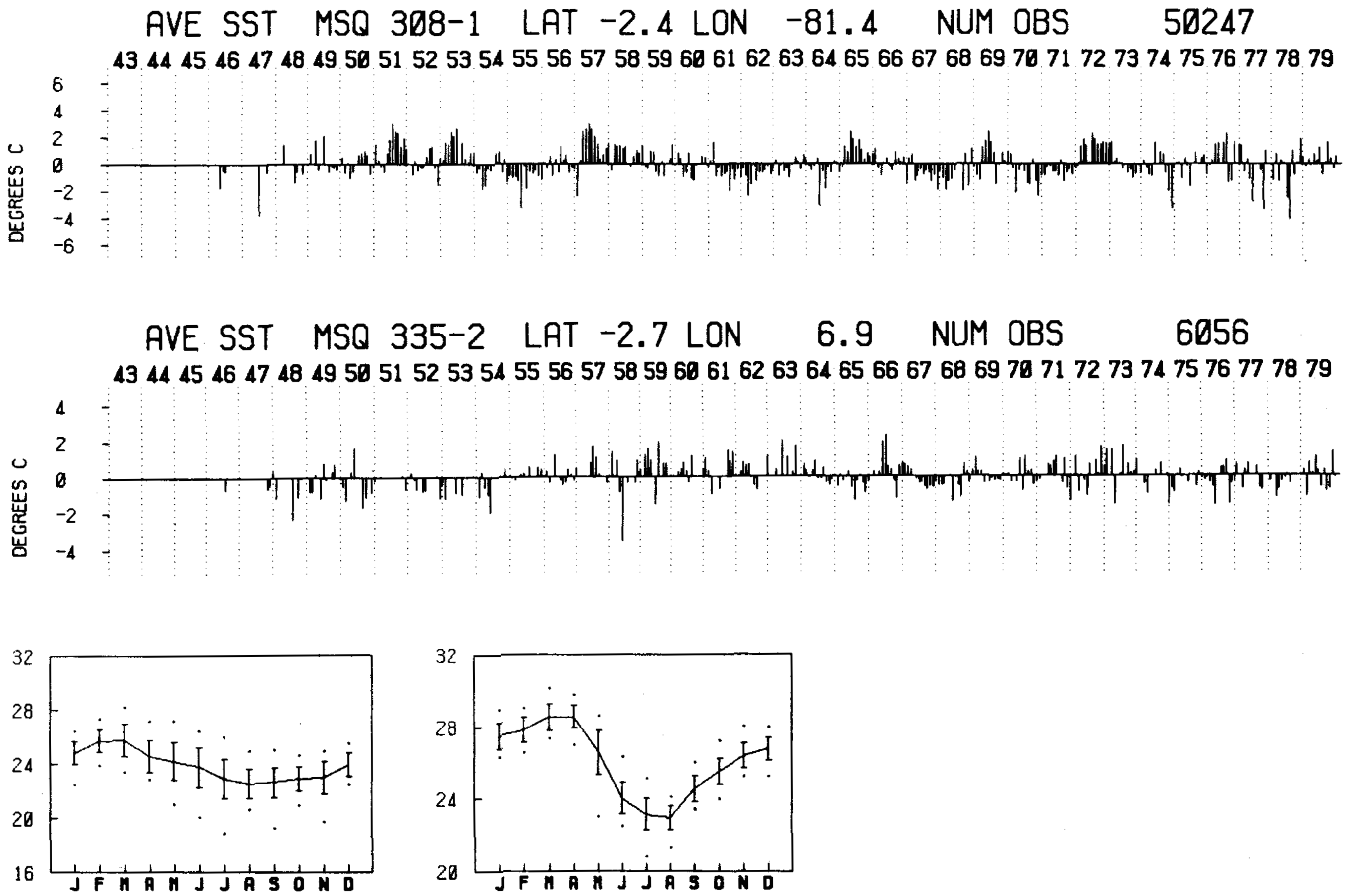

Figure 8. Time series of anomaly of SST in 5° blocks in eastern tropical Pacific (*upper*) and Atlantic (*lower*) oceans for the years 1943 to 1979. Mean annual cycle of SST and range and standard deviation of interyear variability are shown in small boxes (Pacific, *left*, Atlantic, *right*). Areas are Marsden 5° blocks 308-1 off Ecuador in the eastern tropical Pacific (0° to 5°S, 80° to 85°S) and 335-2 off Gabon in the eastern tropical Atlantic (0° to 5°S, 5° to 10°E).

Consolidated Data Set of Fleet Numerical Oceanography Center (FNOC). This data set comprises marine weather reports from two sources: (1) historical logbook reports in the TDF-11 data file from the National Climatic Data Center for the years 1946 to about 1976, and (2) the reports received in real time by FNOC for 1971 to 1979. Time series of SST anomalies (Figure 8) were made for an area off Ecuador (Marsden 5° block 308-1) and an area off Gabon in the tropical Atlantic (5° block 335-2). Although the Atlantic data are very sparse, there is no obvious lag relationship between the two series.

The most obvious difference between the Atlantic and Pacific SST time series is the generally greater persistence of anomalies in the tropical Pacific relative to the tropical Atlantic. We examined this in greater detail by computing autocorrelation functions for the two series (Figure 9). The autocorrelation function of the Atlantic series drops to less than 0.1 in 3 months, whereas it takes 8 months in the Pacific. The slower response time in the Pacific reflects the larger size of the Pacific and the greater energy required to displace the thermocline vertically.

CONCLUSIONS

Although sampling density was extremely nonhomogeneous, we computed monthly mean SSTs and anomalies from the long-term mean for series of 3° blocks along the coast in the eastern boundary current systems of the Pacific and Atlantic oceans. From these data, anomalous warm and cold events can be seen in all four major eastern boundary current systems. In the Pacific, coherent anomalies can extend over great stretches of coast from Chile to British Columbia, causing the California and Peru current systems to have similar SST anomalies simultaneously. Other local anomalies can occur in the California and Peru currents as well. There was less coastwise coherence of SST anomalies in the Atlantic than the Pacific, and thus the Canary and Benguela current systems do not generally have similar SST anomalies simultaneously.

Two major hypotheses for formation of anomalous

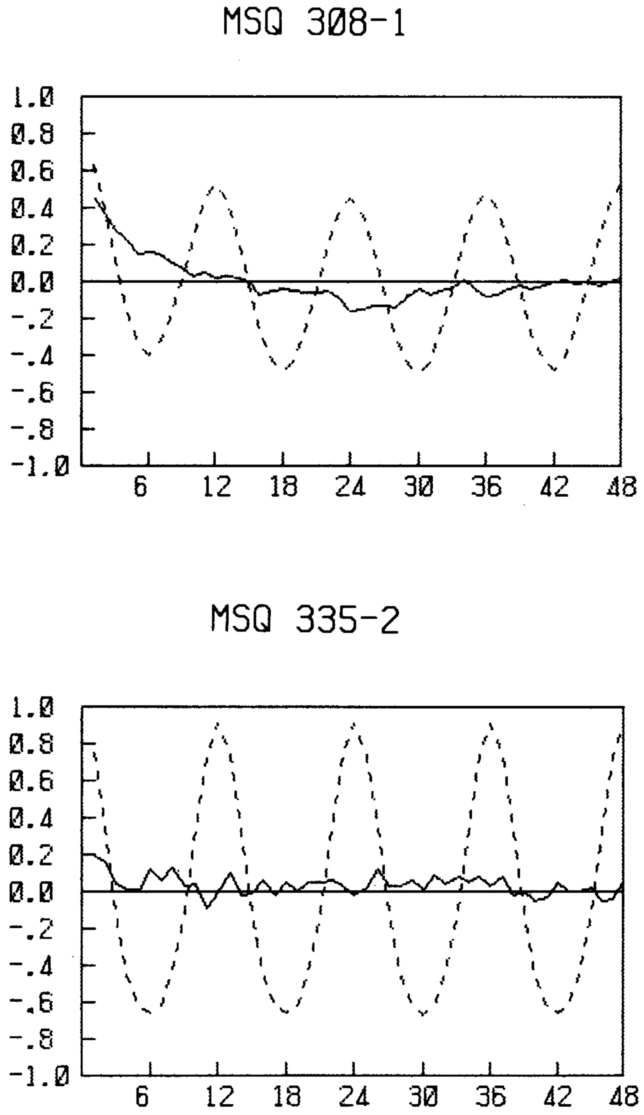

Figure 9. Autocorrelation function of monthly mean SST anomaly series for lags up to 48 months in 5° blocks in the eastern tropical Pacific (*upper*) and the eastern tropical Atlantic (*lower*). The dashed curves are the autocorrelation functions of the original SST time series, and the solid lines are the autocorrelation functions of the time series of SST anomalies.

warm events in the California Current have been suggested: (1) onshore transport of warm surface waters by strong southwesterly winds warms the surface water and depresses the thermal structure; (2) poleward-propagating coastally trapped waves from tropical El Niño events cause depressions of the thermocline to propagate poleward. Propagating coastally trapped waves narrow and lose energy with distance poleward from the tropics and do not explain the observed large coastwise anomalies. Onshore transport may occur in the same year as tropical warming events and cause local reinforcement of the effects of propagating coastally trapped waves in midlatitudes. Local heating by solar radiation is a third possible hypothesis for formation of anomalous warm events.

Two important effects of the anomalous warming events have biological significance: (1) geostrophic adjustments to the deepened thermal structure cause an intensification of normal seasonal poleward flow over the continental shelf. This intensification causes increased advection of warm water poleward and allows warm-water organisms to extend their ranges poleward. (2) A thickened surface layer reduces the ability of upwelling-favorable winds to upwell nutrients into the lighted surface waters, lowering the biological productivity.

An extremely anomalous warming event occurred in the California and Peru current systems during 1982-83. Off California exceptionally strong onshore transport of warm waters from offshore reinforced propagating coastally trapped waves from an exceptionally strong tropical El Niño. Anomalies were as large as +4°C at the surface and as large as +5° to +6°C at 100 m (Brainard and McLain in press), reflecting a deepening of the thermocline along the coast by 50 to 100 m. Off California the biological productivity of the surface waters was greatly reduced, and strong poleward flows advected many warm-water species northward.

SST anomalies in the Canary Current during 1971-84 have been relatively small but showed a general warming trend similar to that observed in the Pacific. Anomalies in the Benguela Current were extremely persistent and were positive during the years 1971-78 and cool during 1979-83. Anomalies then became strongly positive in early 1984, possibly because of an intrusion of equatorial water. There was no obvious lag relationship of SST anomalies in the Atlantic following similar warm events in the Pacific. SST anomalies are generally more persistent in the tropical Pacific than in the tropical Atlantic, but anomalous conditions in the Benguela Current can persist for five or more years.

The interannual variability of SST fluctuations in eastern boundary current systems is high near the frontal regions where the eastern boundary currents leave the coast. SST gradients are strong in these regions, and interannual variability of SST is locally high because of interannual variations in the seasonal migration of the fronts. Interannual variability of SST is higher in the Southern Hemisphere than in the Northern Hemisphere, but the anomalies in the Southern Hemisphere tend to be more persistent. Thus SSTs in the Northern Hemisphere tend to vary about a mean state, whereas Southern Hemisphere anomalies tend to switch between different regimes, lasting for a year or longer.

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ORIGIN OF PRODUCTIVITY ANOMALIES DURING THE 1982-83 EL NIÑO

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ABSTRACT

The biological changes of El Niño are clearly related to the sequence of physical changes in the marine environment. During years when there is no El Niño, a basinwide nutricline tilt set up by trade winds brings the nutricline to a favorable, shallow depth along the coast of Peru. During El Niño the nutricline is progressively depressed, so coastal upwelling transports reduced quantities of nutrients to the surface. Productivity of the coastal upwelling ecosystem during the 1982-83 El Niño was decreased fourfold to twentyfold by the reduced nutrient supply. The decrease of new primary production available to the food chain caused proportional reductions in the fish and seabirds.

RESUMEN

Los cambios biológicos vinculados con El Niño están claramente relacionados con la secuencia de cambios físicos en el ambiente marino. Durante años no-El Niño el declive de la nutriclina, a lo largo de la cuenca oceánica, condicionado por los vientos alisios, ubica a la nutriclina en una profundidad favorable, reducida, frente a las costas peruanas. Durante El Niño esta isolínea es progresivamente empujada hacia profundidades mayores, de manera tal que los afloramientos costeros aportan menos nutrientes a la superficie. La productividad de los ecosistemas de afloramientos costeros durante El Niño de 1982-83 se redujo en 4 a 20 veces debido al reducido aporte de nutrientes. La disminución de la producción primaria disponible para la cadena alimentaria provocó reducciones en los peces y en las aves marinas.

INTRODUCTION

The ocean off the west coast of South America is the most productive region of the world ocean; Buchanan (1886) reported, "No waters in the ocean so teem with life as those on the west coast of South America." Early in the twentieth century Coker (1918) associated cool ocean temperatures with the abundance of fish and seabirds (Coker 1908, 1919). Coker (1918) also correctly identified upwelling as the process responsible for persistent cool ocean temperatures in the tropical setting of the Peru coast, and he speculated that perhaps the greater solubility of gases in cooler seawater enabled the upwelled water to support more "growth of the minute plants that form the basis of the food supply of all the marine animals." Coker's speculation was surprisingly close to being correct; today we believe it is the abundance of available nitrogen and phosphorus in the cool, upwelled water that makes this region the world's richest (Ryther et al. 1971).

Accurate descriptions of El Niño and the changes in currents and rainfall that accompany it were published at the end of the nineteenth century by several Peruvian scholars such as Carranza (1892), Eguiguren (1894), and Pezet (1896). Murphy (1926) associated the decrease of plankton, collapse of local fisheries, and widespread death among seabirds in 1891 and 1925 with the sudden warming of the ocean off Peru. The common understanding was that upwelling failed during El Niño. To understand how El Niño affects the biota we must understand why the ocean off the west coast of South America is normally so fertile.

As Coker (1918) indicated, the process of coastal upwelling is responsible for the fertility of this region. Coastal upwelling is a circulation pattern that overrides both the nutrient limitation that characterizes permanently stratified waters, and the light limitation that characterizes deeply mixed waters. Coastal upwelling is set in motion by equatorward winds that transport water offshore, resulting in an equal volume of water flowing up close to the coast to replace the water moved offshore. The surface layer forced offshore by the equatorward winds is extremely shallow, on the order of ten to twenty meters deep. Subsurface water is brought to the surface and, once there, is transported horizontally away from the upwelling site in a coherent surface flow (Barber and Smith 1981). The waters of the ocean below the thermocline are rich in inorganic plant nutrients like nitrate, phosphate, and silicate; the subthermocline nutrient reservoir of the ocean is one of the major nutrient pools of the globe (Redfield 1958). Vertical transport of subsurface water injects new nutrients into the surface and forms a shallow, wind-driven, surface Ekman layer that is vertically stabilized by a density gradient, and provides optimal light conditions for plankton photosynthesis.

This sequence in upwelling of vertical transport followed by vertical stabilization is analogous to the seasonal mixing and stratification cycle occurring in

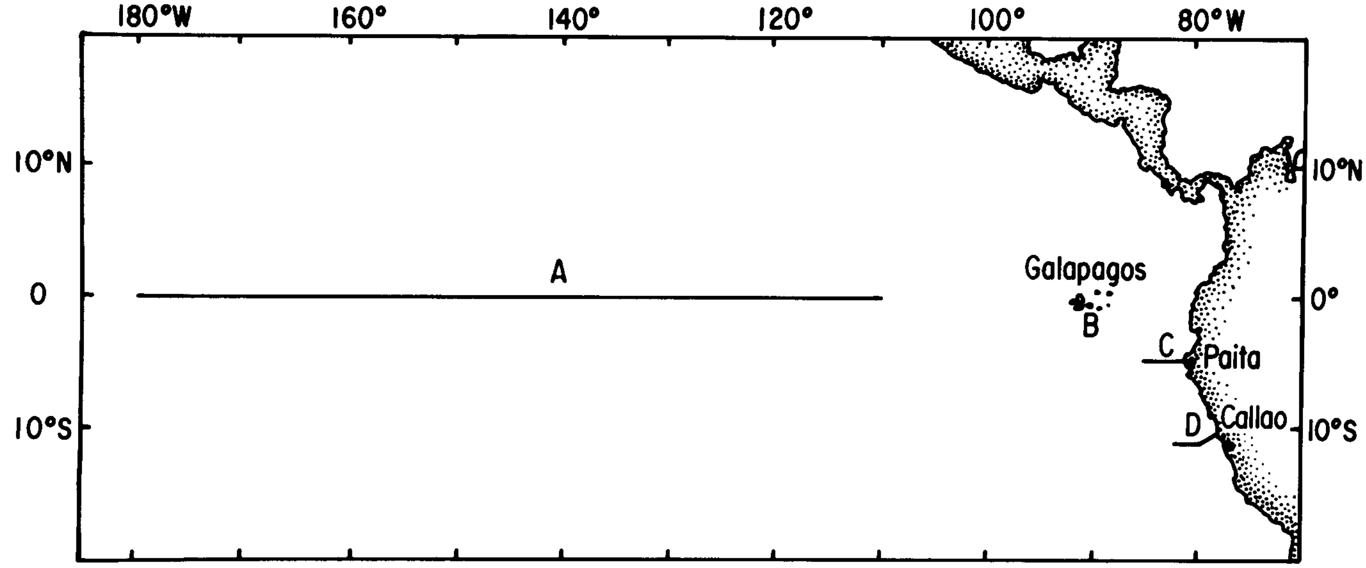

Figure 1. Chart of the central and eastern tropical Pacific showing the location of the transects and station described in this report: *A*, zonal section along the equator from 180°W to 110°W; *B*, Galápagos Islands time series station; *C*, Paita transect along 5°S from 85°W to the coast; *D*, 10°30′S transect from 82°W to the coast.

temperate and high-latitude waters. What is different about upwelling is that optimal juxtaposition of the two opposing processes continues as long as the equatorward winds blow, whereas in the "spring" bloom of temperate, high-latitude waters there are only a few episodes of optimal conditions each year. Time limits on productivity enhancement are removed by coastal upwelling as long as winds are favorable; thus the total annual supply of new organic material to the ecosystem is much greater, and food chain enhancement is greatly increased (Ryther 1969).

Coastal upwelling is a response of a particular area of the ocean to a large-scale wind pattern; implicit in the concept of a local response is the idea that the water upwelling to the surface layer is entrained from a relatively shallow depth of 40 to 80 meters. The gradient that separates the nutrient-rich subsurface waters from the nutrient-depleted surface waters is called the nutricline, just as the temperature gradient is called the thermocline. The thermocline and nutricline in the eastern portion of the Pacific (Figures 1 and 2) are much shallower than they are in midocean or in the west because of action of the large-scale winds on the ocean surface (Cane 1983; Rasmusson and Wallace 1983). Thus large-scale winds have two relatively separate connections to coastal upwelling: (1) they provide the local driving force for coastal upwelling, and (2) by setting up the large-scale thermocline and nutricline tilt, they determine the properties (temperature and nutrient content) of the water that can be entrained into the upwelling circulation when the local winds are favorable.

In describing the oceanographic processes involved in El Niño, Wooster and Guillen (1974) observed that warm water appeared and nutrients decreased during El Niño. Since cold water and high nutrients are signatures of coastal upwelling, it was widely assumed that upwelling weakened during El Niño. Analyses of coastal wind measurements in the last five years have indicated that in previous El Niño events (Enfield 1981) and in the 1982-83 El Niño (Smith 1983) the equatorward winds driving coastal upwelling did not weaken until late in the event's development. During the 1982-83 El Niño, observations indicated that upwelling continued as late as March 1983, but changes in temperature and nutrients between November 1982 and March 1983 showed that the water entrained by the upwelling circulation had an entirely different nutrient and temperature character. An explanation of this apparent contradiction is that as the thermocline and nutricline were progressively depressed below the depth where source water was entrained into the upwelling circulation (40 to 80 m), nutrient transport to the surface layer was reduced, and temperature increased.

The surprising conclusion we reach from these observations is that nutricline depression, not cessation of upwelling, was the process that decreased the nutrients and, in turn, caused primary production to decrease, eventually causing collapse of the upwelling food chain. A corollary of this conclusion is that it was collapse of the food chain, not direct thermal effects, that caused the biological anomalies during the 1982-83 El Niño.

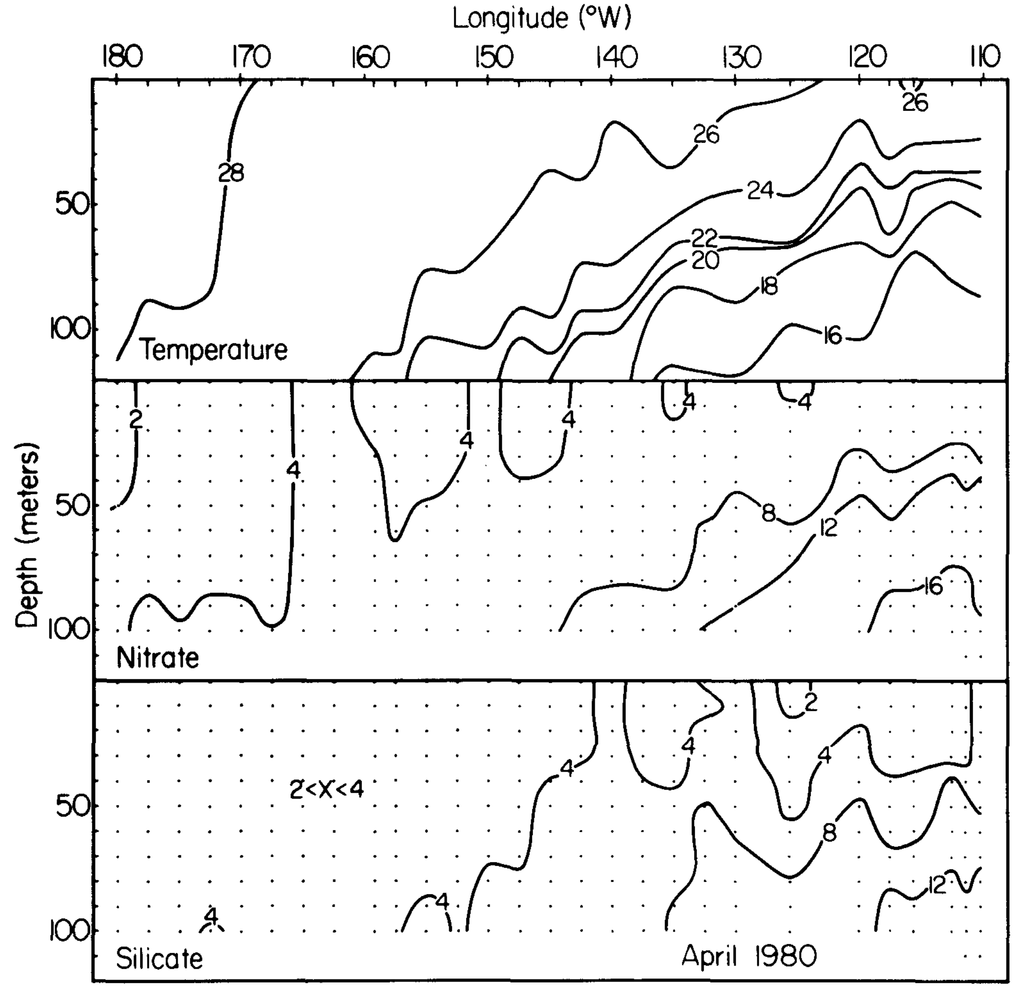

Figure 2. Zonal section along the equator from 110° to 180°W, showing temperature (°C), nitrate (μM), and silicate (μM) during April 1980. Temperature was measured as a continuous vertical record, and discrete nutrient measurements were made at the depths shown by the dots.

PROGRESSION OF THE 1982-83 EVENT

The 1982-83 El Niño began in August around the Galápagos Islands (Halpern et al. 1983), and in late September and October along the coast of Peru (Chavez et al. 1984). Figure 3 shows the change in surface and 60-m temperature at a shore station in the Galápagos Islands (Kogelschatz et al., in press). El Niño is well defined by both the surface and 60-m temperatures; in fact, the onset in September 1982 and recovery in June 1983 is more sharply delineated in the 60-m temperature signal. Another aspect of this time series is that an increase or decrease in surface temperature is always preceded by a change at 60 m; as has been noted previously (Enfield 1981; Barber and Chavez 1983), El Niño in the eastern Pacific is initially a subsurface (thermocline) anomaly that only secondarily reaches the surface.

The pattern of variation in nitrate (Figure 3) shows El Niño's large impact on nutrients in the eastern tropical Pacific. Surface-layer values at the beginning and end of the time series show that nitrate values of 2 to 6 μM are characteristic in this region. This is further supported by the large-scale zonal profile shown in Figure 2. The relationship between phytoplankton growth and ambient nutrient concentration is complex (Dugdale et al. 1981), but for a general understanding of El Niño's biological effects it is adequate to know that nitrate concentrations of 2 μM or higher constitute favorable nutrient conditions where the uptake-versus-concentration relationship is saturated. Figure 3 shows that, in the absence of El Niño, Galápagos waters are nutrient-rich; that is, there are saturating concentrations of nitrate in the surface layer most of the time.

The surface concentration of nitrate for six and one-half months during the 1982-83 El Niño, from December 1982 to mid-June 1983, was very low, often below the detection limit of 0.02 μM. Such concentrations are clearly nutrient-poor and will necessarily decrease the new production of organic matter by phytoplankton (Dugdale and Goering 1967). The silicate time series (not shown) indicates that this nutrient

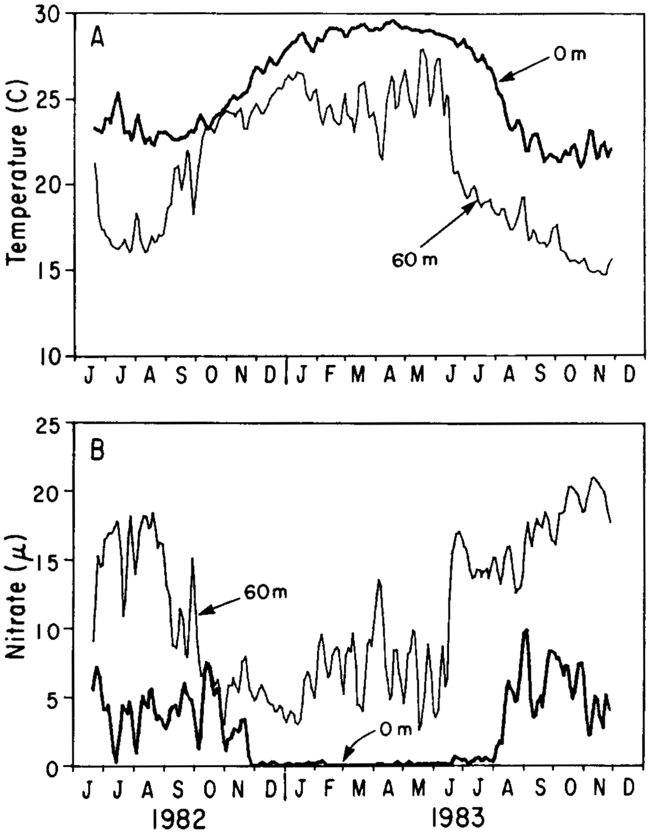

Figure 3. Time series plot of temperature and nitrate in Academy Bay, Galápagos Islands, at 0 m and 60 m during the 1982-83 El Niño.

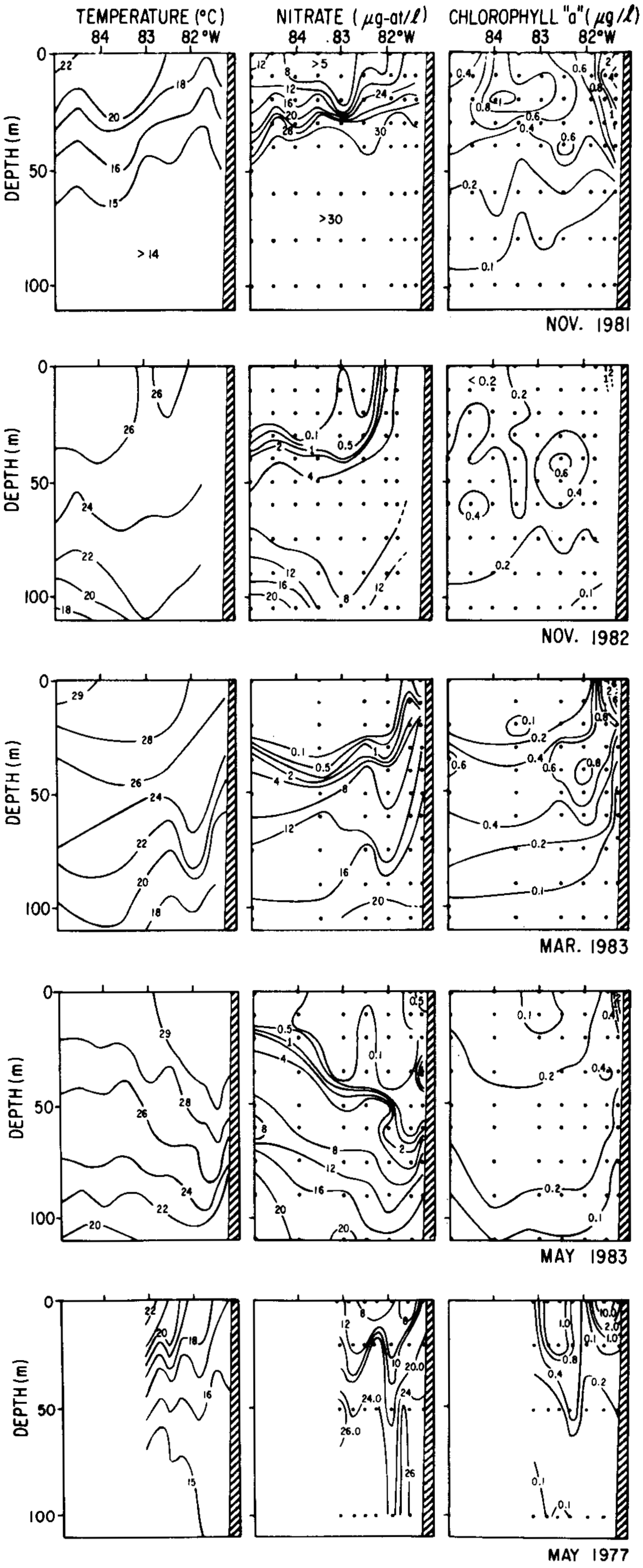

Figure 4. Cross-shelf profiles of temperature, nitrate, and chlorophyll *a* along a 5°S transect from 85°W to the coast. November 1981 shows normal conditions; November 1982 is during onset; March 1983 is during maturation; May 1983 is during the peak of the anomaly; May 1977 shows normal conditions.

covaried with nitrate at the surface and at 60 m, but unlike nitrate, it was never depleted in the surface layer. In the equatorial Pacific there is an atom ratio excess of silicate-silicon relative to nitrate-nitrogen; this is the reason we concentrate on nitrate in this description of nutrient conditions.

The two November 1982 sections at 5°S and 10°30′S off the coast of Peru (Figures 4 and 5) were during onset of El Niño, but the temperature anomaly had already reached 5°C. Evident in the November 1982 section is the characteristic thermocline and nutricline depression. The 20°C isotherm, which is the middle of the thermocline, is depressed over 100 meters close to the coast when compared to two sections made in November 1981 (Figures 4 and 5). Coastal upwelling driven by coastal winds continued in November 1982 to supply a band next to the coast with nutrients; this narrow zone of nutrient enrichment supported relatively high phytoplankton biomass.

Comparison of the SST along the 5°S transect during November 1982 and November 1983 (Figure 6) shows that the offshore-to-inshore temperature gradient is similar in magnitude even though the entire section is 5°C warmer during November 1982. The presence of the offshore-to-inshore gradient indicates

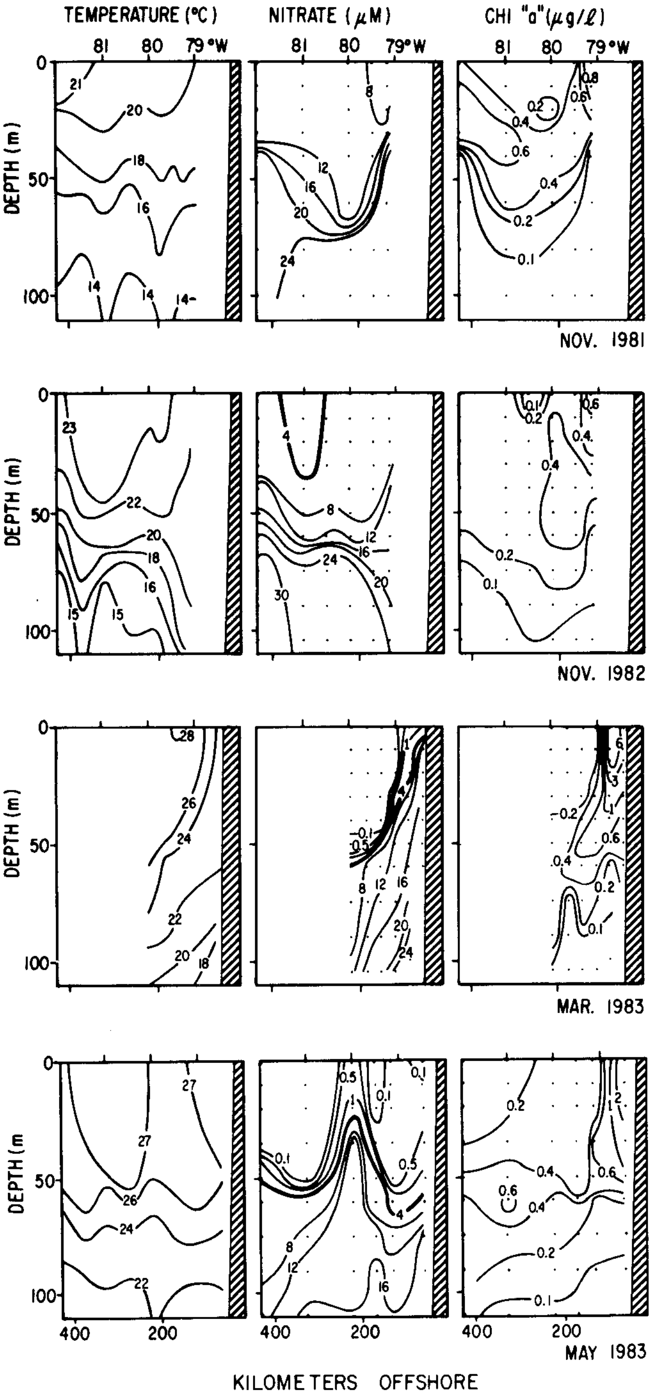

Figure 5. Cross-shelf profiles of temperature, nitrate, and chlorophyll *a* along 10°30′S from 82°W to the coast. November 1981 shows normal conditions; November 1982 is during onset; March 1983 is during maturation; May 1983 is during the peak of the anomaly.

that upwelling continued close to the coast despite the 5°C warm anomaly present throughout the water column. The concentrations of chlorophyll along the 5°S transect during November 1982 and November 1983 (Figure 6) show that during onset in 1982, the phytoplankton-rich band, as shown by the 1 mg/m^3 contour, extended only about 30 km out from the coast; after recovery in November 1983 it extended over 200 km from the coast. The primary productivity along the 5°S transect shows that an inshore productivity maximum was present in November 1982, but productivity integrated across the 5°S transect from the coast to 85°W was much reduced (Figure 6). The mean surface productivity along the transect during November 1982 was 51 mgC/m^3/day, whereas during November 1983 the average was 192 mgC/m^3/day, or 3.8 times higher.

Temperatures continued to increase as the 1982-83 event progressed into March 1983 (Figure 3); however, at the time of the March 1983 cruise the thermocline was slightly shallower along the 5°S and 10°30′S transects than it was during the onset phase (Figures 4 and 5). In March 1983, coastal upwelling continued, as shown by the upward tilt in the isotherms close to the coast and by the presence of the offshore-to-inshore temperature gradient of about 3°C (Figure 6). The narrow phytoplankton-rich band of water close to the coast is evident in the chlorophyll sections for March 1983, and the size of the area bounded by the 1 mg/m^3 concentration remained reduced. High chlorophyll concentrations were still restricted to a 30-km-wide zone next to the coast, whereas during April 1984 the zone of the phytoplankton-rich water extended 400 km from the coast. By March 1983 the mean surface primary productivity along the 5°S transect was reduced to 27 mgC/m^3/day, whereas during April 1984 the mean value was 245 mgC/m^3/day, or 9.2 times higher than the El Niño condition.

May 1983 conditions show the maximum expression of the biological and physical anomalies of the 1982-83 El Niño. The SST anomalies reached 10°C, and the middle of the thermocline was depressed below 100 m (Figures 4 and 5). Temperature profiles made during May 1983 and May 1977 provide an interesting contrast. During May 1983 there is no evidence of coastal upwelling; on the contrary, the isotherms tilt downward toward the coast. During May 1977, upward tilt typical of coastal upwelling is very evident. In May 1983 there is no longer an offshore-to-inshore SST gradient; on the contrary, the inshore waters are slightly warmer (Figure 6). The chlorophyll field for May 1983 shows that the normally rich coastal ocean has become relatively barren. However, the July 1983 results shown in Figure 6 show the rapid phytoplankton recovery that occurred in the nearshore zone all along the coast of Peru. After extremely low primary productivity in May 1983, phytoplankton production rapidly reestablished in mid-July 1983, and the coastal waters returned to their normally productive condition. During May 1983, the mean surface primary productivity along 5°S had

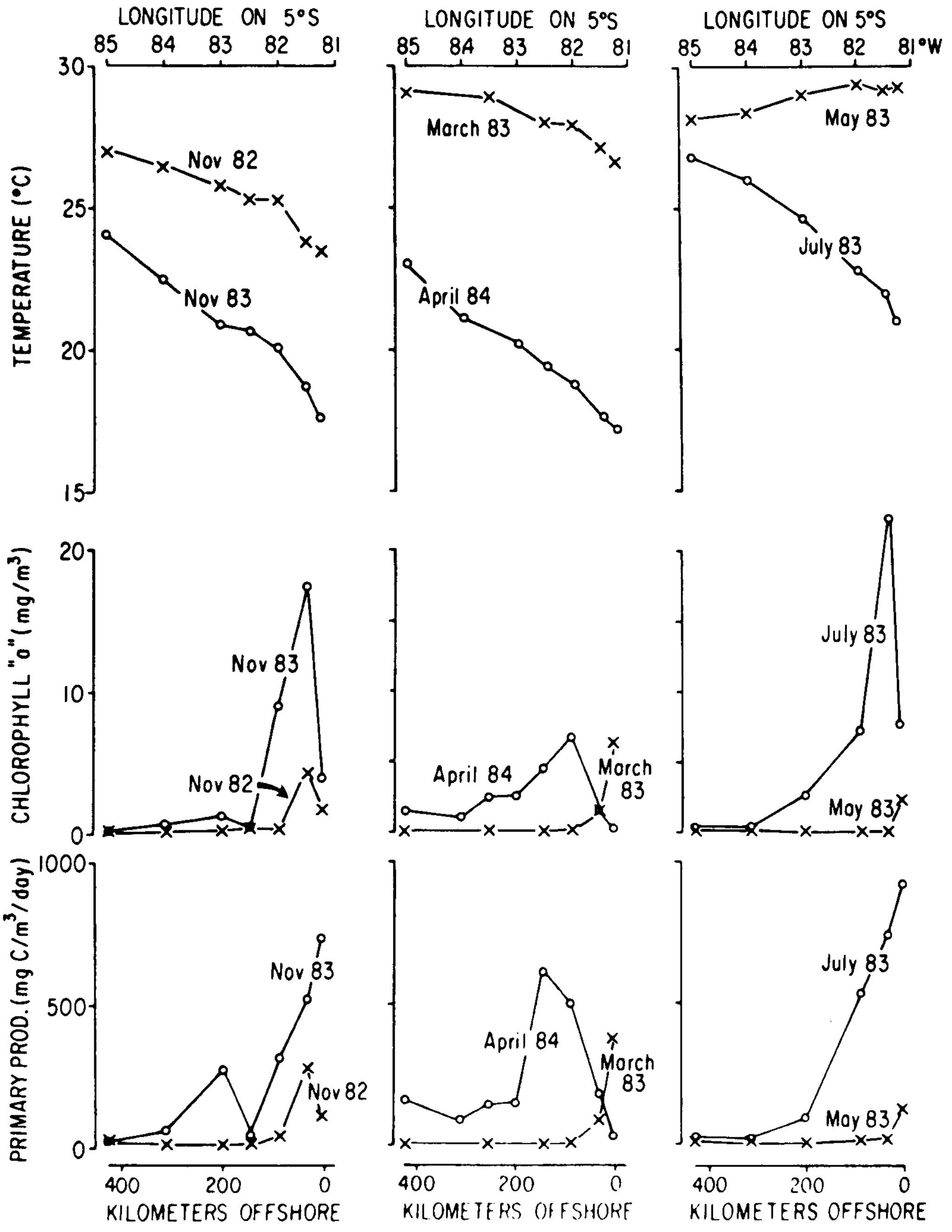

Figure 6. Comparison of surface temperature, chlorophyll *a*, and primary productivity along the Paita transect from 85°W to the coast.

dropped to its lowest value—10 mgC/m³/day—whereas during July 1983 it increased to 219 mgC/m³/day, a value 21.9 times higher than the El Niño condition. At the peak of the anomaly primary production was reduced to 5% of the normal quantity.

We believe this dramatic decrease in the supply of phytoplankton productivity was the primary cause of the widespread reproductive failures and adult mortalities (Barber and Chavez 1983) that were observed in fish, birds, and marine mammals during the 1982-83 El Niño.

ACKNOWLEDGMENTS

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THE INFLUENCE OF LARGE-SCALE ENVIRONMENTAL PROCESSES ON NERITIC FISH POPULATIONS IN THE BENGUELA CURRENT SYSTEM

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Cape Town, South Africa

ABSTRACT

Environmental variability in the Benguela eastern boundary current system appears to result from variability in mesoscale processes like upwelling, as well as from lower-frequency variability forced by periods of alternate stronger and weaker advection of warm tropical or subtropical water. Warm events can be more extensive in the northern region, where the seasonal advection occurs during an upwelling minimum. In the south the concurrent seasonal effect of warming and maximum upwelling may inhibit extensive warm events. The effects of SST anomalies on fish populations within the area indicate that moderate advection of warm water may be advantageous, whereas exceptionally strong warming may cause diminished reproductive success. High-frequency variability can be incorporated into fish population models as a stochastic term in order to evaluate the risk associated with alternative management strategies, but these models have no predictive value. Fish populations like the anchovy seem buffered against high-frequency variability. If environmental variability affecting recruitment is autocorrelated, it will modulate the central tendency of the recruitment, and the appearance of stock-recruit scatter will vary in a manner dependent on the fishes' generation time and the biomass growth pattern. A population like the anchovy will track the autocorrelated signal and be susceptible to depletion, particularly under a constant catch policy.

RESUMEN

La variabilidad ambiental en el sistema de la Corriente de margen oriental de Benguela parece ser el resultado de la variabilidad de procesos de mesoescala tales como afloramientos, así como de la variación de baja frecuencia causada por períodos alternos de fuerte y débil advección de aguas cálidas tropicales o subtropicales. Los eventos cálidos pueden ser de mayor envergadura en la región norte, donde la advección estacional ocurre durante los períodos de mínimo afloramiento. En el sur, el efecto estacional conjunto del calentamiento y el afloramiento máximo pueden inhibir eventos cálidos extensos. Los efectos de las anomalías térmicas superficiales sobre las poblaciones de peces locales indican que advecciones moderadas de aguas cálidas pueden ser beneficiosas, mientras que calentamientos muy pronunciados pueden provocar disminuciones en el éxito reproductivo. Las variaciones de alta frecuencia pueden ser incorporadas en los modelos poblacionales de peces en la forma de una variable estocástica con el fin de evaluar el riesgo asociado con estrategias de manejo alternativas, pero estos modelos carecen de valor predictivo. Las poblaciones de peces como la anchoveta (*Engraulis capensis*) parecen estar protegidas contra la variabilidad de alta frecuencia. Si la variabilidad ambiental que incide sobre el reclutamiento está autocorrelacionada, ello modelará la tendencia central del reclutamiento en función del tiempo de generación del pez y de las características del aumento de la biomasa. Una población como la anchoveta se guiará por la señal autocorrelacionada y será susceptible de agotamiento, especialmente en condiciones de una política constante de captura.

INTRODUCTION

The Benguela eastern boundary current region (Figure 1) has yielded large catches of pilchard (*Sardinops ocellata*), horse mackerel (*Trachurus trachurus*), mackerel (*Scomber japonicus*), hake (*Merluccius capensis/paradoxus*) and, more recently, anchovy (*Engraulis capensis*) (Butterworth 1983; Crawford et al. 1983). In most instances peak catches appear to have followed the entry of a number of good year classes into the fishery (Figure 2), and have not been maintained during subsequent population downswings. This pattern of recruitment variability may be related to the influence of large-scale climatic events rather than to mesoscale, intra-annual processes like upwelling.

The influence of large-scale, low-frequency climate variability on fish populations has been considered by a number of authors (Iles 1973; Soutar and Isaacs 1974; Cushing and Dickson 1976; Cushing 1978; Smith 1978; Lasker 1978; Caddy 1979; Bernal 1981; Chelton et al. 1982; Kawasaki 1983), and convincing supporting evidence has been presented. In turn, mesoscale (within season) variability in coastal dynamic processes has been successfully related, retrospectively, to fish population variability over short

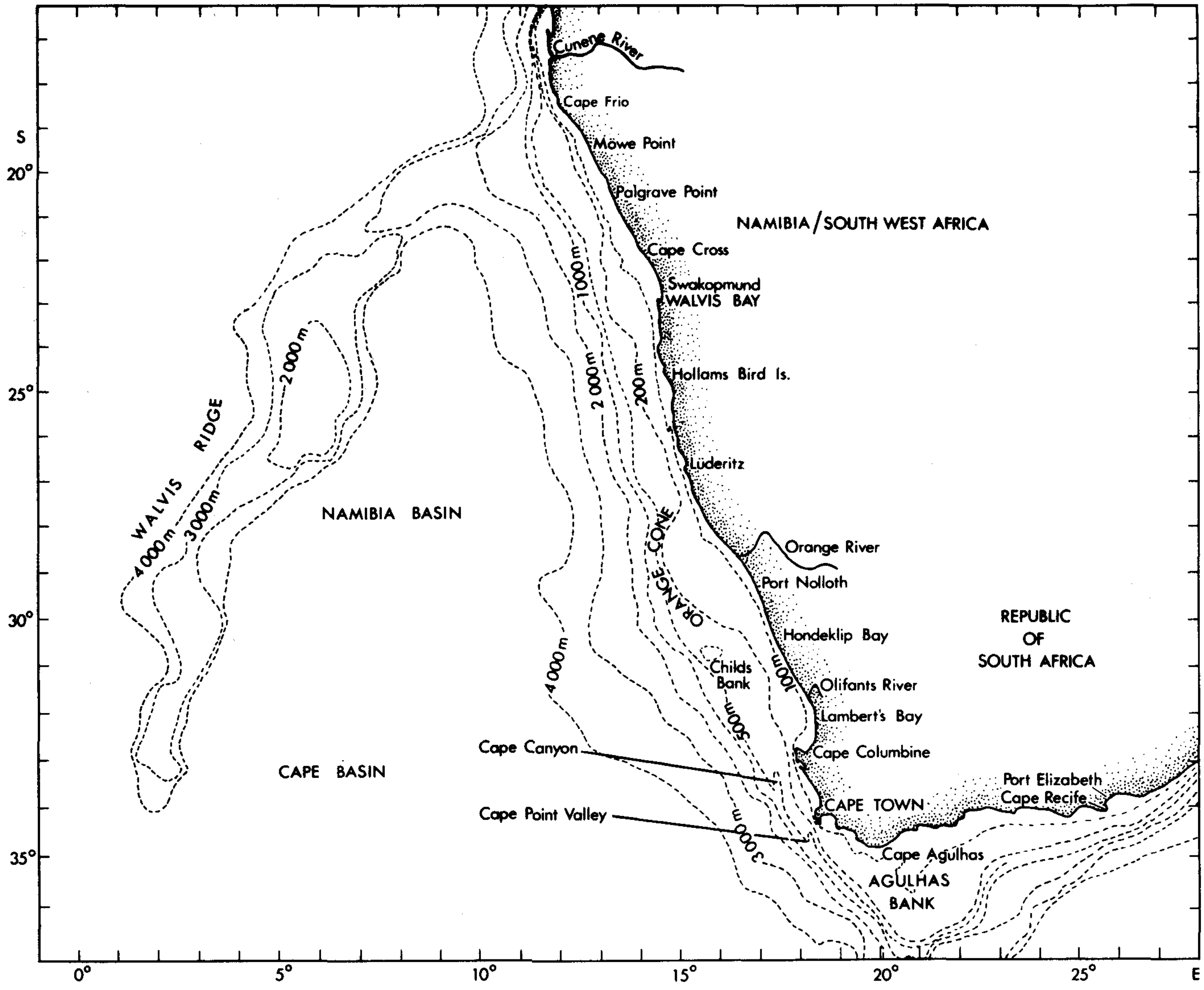

Figure 1. Bathymetry of the Benguela eastern boundary current region.

time periods for various fisheries (Parrish and MacCall 1978; Nelson et al. 1977; Schaaf 1979; Boyd 1979) although Hutchings and Nelson (in press) found no clear relationship between upwelling processes and pelagic fish population size variations in the southern Benguela region. There are few comparisons of the various scales of forcing on marine biota and even fewer occasions of successful forecasting.

Different scales of variability have important implications for fish population dynamics and consequently for management. It is relatively easy to incorporate a high-frequency component as stochastic recruitment variability into a model in which recruitment is functionally related to spawner stock size or egg production. This approach is valuable for demonstrating the dangers inherent in deterministic modeling and for comparing the risks associated with different harvesting strategies (Beddington and May 1977; Armstrong 1984), but it has no predictive value. In contrast, incorporating low-frequency variability into population models may allow some short-term prognosis based on the current position in the cycle, provided the underlying density-dependence of stock productivity has been elucidated.

In this paper, aspects of the average seasonal large-scale pattern of physical and biological processes in the Benguela region are described, and large-scale environmental anomalies are related to variability observed in neritic fish populations. The possible effect of an autocorrelated signal on the dynamics of fish populations is considered, by means of a theoretical model.

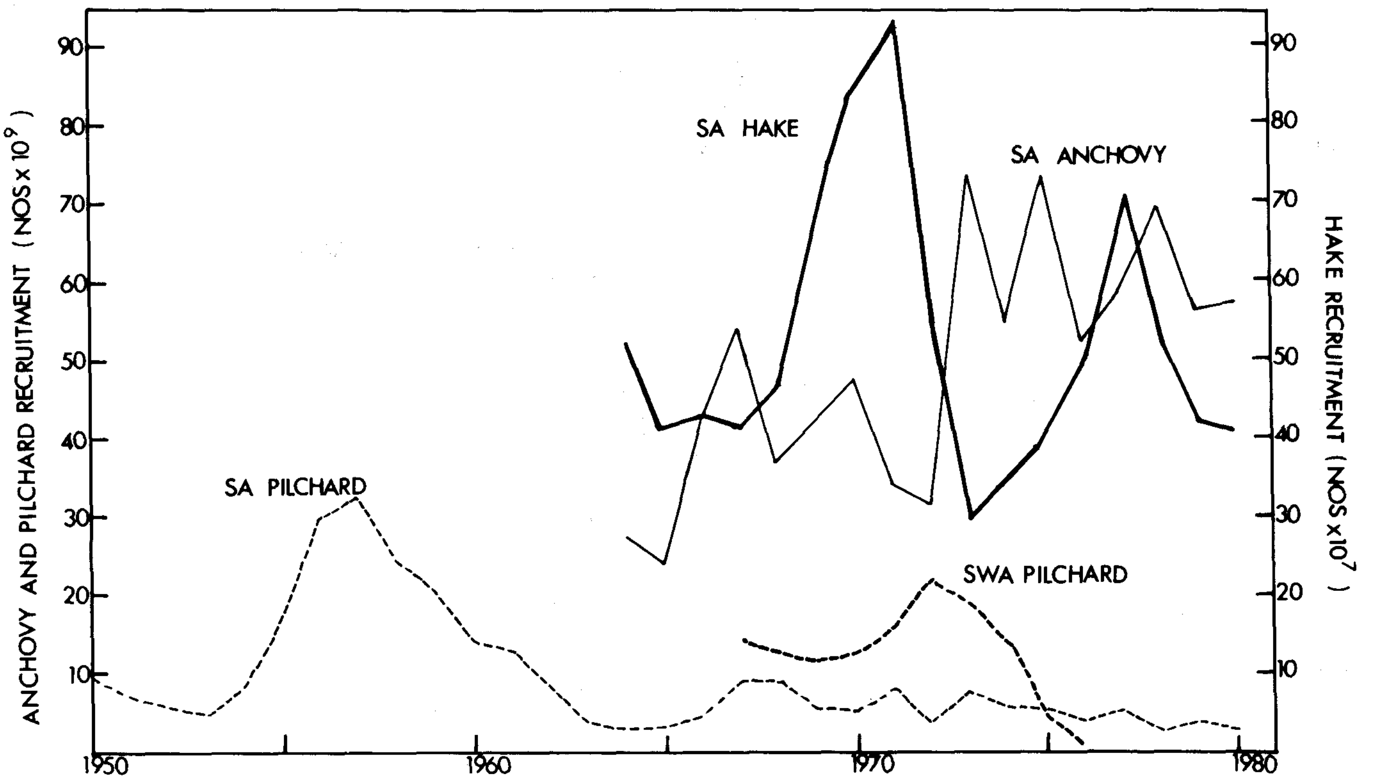

Figure 2. Recruitment calculated by cohort analysis for a number of neritic fish populations inhabiting the Benguela system.

SYSTEM DESCRIPTION

System Boundaries

In general terms, the Benguela is a cool, eastern boundary current, with equatorward flow at the surface, off the west coast of southern Africa. The longshore boundaries are formed by warm water of subtropical/tropical origin to the north *and* south, in contrast to other eastern boundary current regions, whereas the offshore boundary is formed by a circulation of warm subtropical water associated with the South Atlantic Gyre (Hart and Currie 1960; Shannon 1966). Bang (1971) adds the interesting but arguable caveat that the Benguela Current is the area east of the offshore divergence within which processes are dominated by short-term atmospheric interactions rather than longer-scale climatic influences.

The cool surface waters of the Benguela Current originate by upwelling of South Atlantic central water from depths generally between 100 and 300 m (Stander 1964; Shannon 1966). In contrast to the eastern boundary currents off the Americas (Chelton et al. 1982), these surface waters are not contributed to by surface advection of cool water from higher latitudes. The migratory nature of the offshore boundary is generally acknowledged (Shannon 1966; Bang 1971), and large, stationary eddies extending up to 500 km offshore are a feature of satellite imagery (Van Foreest et al. 1984).

Both the warm, western boundary Agulhas Current in the south and the warm Angolan water to the north form mixing areas of variable extent (O'Toole 1980; Nelson and Hutchings 1983) and are loci for the spawning of a number of neritic fish species. Pelagic eggs and larvae in the Benguela may drift substantial distances from the site of spawning as a result of mixing or transport (Shelton and Hutchings 1982). Stock separation in fish species may require distinct larval retention areas (Iles and Sinclair 1982); Badenhorst and Boyd (1980) and Boyd and Hewitson (1983) have presented evidence from anchovy larval distribution compatible with a southern retention area for anchovy extending as far north as Lüderitz. Catch-based information indicates anchovy recruitment epicenters in Walvis Bay and St. Helena Bay (Crawford et al. 1983; Crawford 1980). The Lüderitz region, a site of intense perennial coastal upwelling, lies between these two epicenters. Larvae must also be retained within the Agulhas Bank region in significant numbers, because juvenile anchovy and pilchard are eaten by inshore predators in the vicinity of Algoa Bay (Batchelor and Ross 1984); however, the relative strength of recruitment to the east of Cape Town has not been assessed.

Topography

The most striking difference between the Benguela region and other eastern boundary current regions is the termination of the land mass at a relatively low latitude, resulting in an overall convex shape in the south (Figure 1). These features allow easterly moving cyclones an unimpeded passage south of the continent (Nelson and Hutchings 1983), and the penetration of warm western boundary current Agulhas water onto the west coast under certain conditions, particularly in summer and early autumn (Shannon 1966). This latter feature is unique among eastern boundary current regions.

The bottom topography is characterized by a double shelf break over much of the coast, with strong gradients in the vicinity of the 100-m to 200-m and beyond the 500-m contours (Figure 1). The inner shelf is relatively wide in the vicinity of the Orange River (Orange River Cone), and to the southeast of Cape Town over the extensive Agulhas Bank; at these places the double break largely disappears. Off the Cape Peninsula (on which Cape Town is situated), Cape Columbine, Hondeklip Bay, Lüderitz, and Cape Frio, the 200-m contour lies particularly close to the coast, and a steep bottom slope occurs. Off Cape Columbine and the Cape Peninsula the outer break is contorted into the Cape Canyon and Cape Point Valley, respectively.

The general flow of the Benguela is considered to be topographically steered (Nelson and Hutchings 1983), with regions of enhanced flow resulting from baroclinic jet currents associated with regions where the shelf break is particularly steep (Bang and Andrews 1974). Shannon et al. (1981) have suggested that the Cape Point Valley may act as a conduit for cold water entering the system, and the Cape Canyon off Cape Columbine may have a similar role. The narrowing of the shelf at a number of localities along the coast coincides with areas of enhanced upwelling activity (Nelson and Hutchings 1983), particularly at Cape Frio, Lüderitz, Hondeklip Bay, Cape Columbine, and the Cape Peninsula.

Climatic Influences

The main climatic influences on the system are the South East Atlantic high-pressure anticyclone, which lies off the west coast of southern Africa causing perennial equatorward winds over the Benguela region north of 32°S, and the eastward-moving cyclones to the south of the continent. The possible influence of the Indian Ocean High on the Benguela system has not been investigated in any detail.

The South Atlantic High moves southeastward in spring to lie closer to the coast in summer (December to February) and retreats to the northwest in autumn to lie farther north and offshore in winter (June to August). The movement of the South Atlantic High is responsible for decreasing the equatorward wind stress over the region 25°-35°S in winter and increasing it in spring, summer, and, to a lesser extent, autumn. Therefore, the southern sector of the Benguela region, which includes the Lüderitz upwelling center at 27°S, has maximum upwelling in these seasons, in contrast to the northern Benguela region, which has a summer upwelling minimum (Stander 1963; Parrish et al. 1983).

The passage of easterly moving cyclones south of the continent (often accompanied by the rapid southward movement of a coastal low-pressure system formed in the Lüderitz vicinity) modulates the seasonal trends in upwelling winds on a time scale of 3 to 6 days in the southern Benguela region (Nelson and Hutchings 1983). A similar time scale of variation has been noted in the winds at Walvis Bay. Nelson and Hutchings (1983) describe in detail the sequence of events following the passage of a summer low-pressure center: the South Atlantic High elongates and ridges round the south of the continent, causing intense southeast wind stress in the southern Benguela region along both the south and west coasts. Schumann et al. (1982) showed that upwelling occurred at capes along the south coast as far east as Cape Recife under these conditions.

Large-Scale Circulation

Discussion of the water movement within the Benguela region by Nelson and Hutchings (1983) and Shannon (in press) underscores the complexity of the system. In this paper, a more generalized overview will be given.

Direct measurement of surface currents (in the upper 20 m) between 18° and 35°S by means of drift cards (Duncan and Nell 1969; Shelton and Kriel 1980) and drogues (Harris and Shannon 1979; Shelton and Hutchings 1982; Brown and Hutchings, in press; Boyd and Agenbag, in press) indicate that movement of the surface waters in the Benguela region is generally in the direction of the wind forcing and therefore equatorward. In the vicinity of a front between dense upwelled water and less dense oceanic water, this northward movement can take the form of a baroclinic jet current (Bang and Andrews 1974), which may persist for an entire season (Brundrit 1981). Inshore, a countercurrent has been observed to occur between 32° and 34°S, particularly in autumn and winter (Duncan and Nell 1969; Brown and Hutchings, in press).

Recently obtained current meter data indicate dominant southward flow over the shelf in the subsurface layer (deeper than 40 m) in the southern Benguela region between 32° and 34°S (Nelson and Hutchings 1983). In the northern Benguela the existence of a southward-flowing subsurface compensation current was proposed by Hart and Currie (1960). Although direct current measurements are sparse in this area, indirect evidence from analysis of low-oxygen water and dynamic topography convincingly supports the existence of such a countercurrent north of Walvis Bay and possibly as far south as Lüderitz (Stander 1964; Moroshkin et al. 1970; Nelson and Hutchings 1983). In the region between Walvis Bay and 32°S, De Decker (1970) showed that southward advection can also be detected by tracing low-oxygen water, but Bailey (1979) found the situation more variable in the Lüderitz region.

In the far north (15°-18°S) warm, high-salinity Angolan water regularly advances at the surface as far as Cape Frio in summer and early autumn (Stander 1964; O'Toole 1980; Badenhorst and Boyd 1980), but the presence of this water mass (with salinities > 35.5%; O'Toole 1980) is seldom recorded farther south, other than as a thin tongue or without substantial mixing having occurred. In 1984 Angolan water advanced much farther south than usual, with drastic effects on the biota (Boyd and Thomas 1984; Boyd et al., in press), and this event will be discussed later. In the south, Agulhas Current water and Agulhas Bank mixed water (a mixture of Agulhas Current water and South Atlantic surface water) frequently penetrate the west coast, particularly in summer and early autumn (Shannon 1966; Bang 1973; Bang and Andrews 1974).

The extensive western boundary between upwelled water and oceanic water has recently been shown by satellite imagery to contain dynamic features that have been largely overlooked in previous studies (Shannon et al. 1983; Van Foreest et al. 1984). The spatial scale suggests that this boundary may be important in the interannual variability of the productive zone's extent within the Benguela system. The offshore eddies described by Van Foreest et al. (1984) may be important leaks of productive eastern boundary current water off the shelf and may result in a loss of neritic larvae. However, these eddies may maintain zooplankton populations as food sources for large populations of mesopelagic fish, which are thought to exist offshore of the shelf break.

SEASONAL SIGNAL

Large-scale studies, which may be most relevant to the recruitment processes of neritic fish populations within the Benguela system, have been few (Wooster[1]; Parrish et al. 1983; Christensen 1980; Boyd and Agenbag, in press; McLain et al. 1985). However, these studies present a clear seasonal "average" sea-surface temperature pattern, which can be related to the observed pattern of fish distribution, spawning, and recruitment, and against which climatic perturbations can be measured.

Sea-Surface Temperature

Wooster[2] examined monthly averages of sea-surface temperature for one-degree squares (which often do not reveal coastal upwelling sites like those off the Cape Peninsula) for the entire west coast of southern Africa. The data (Figure 3) show two temperature minima, one centered between Cape Frio and Möwe Point, and the other off Lüderitz, from July through September. These minima correspond to the winter-spring upwelling centers of Cape Frio and the perennial upwelling center at Lüderitz. Water warmer than 18°C occurs north of Walvis Bay in summer (December-March) and in the Cape Town region in January and February. Between these two regions the perennially cold water centered at Lüderitz dominates the pattern.

In the most comprehensive analysis of its kind, Parrish et al. (1983) averaged one million sea-surface temperature measurements in the Benguela region to obtain bimonthly values for one-degree squares. They selected January and February to represent summer, and July and August to represent winter. Their data (Figure 4) support and extend the earlier perspective obtained by Wooster[3]. In particular, they show that in winter the area covered by water < 16°C is extensive both in the longshore and offshore directions, whereas in summer the 18°C isotherm encapsulates the Lüderitz to Cape Columbine area within a narrow segment close to the coast, with water warmer than 20°C forming a pincerlike pattern from the north and south. The isotherms from the north seem linked to subtropical Angolan water, whereas those from the south seem linked with the Agulhas Current.

Christensen's (1980) charts of monthly average sea-surface temperature, constructed from 10-day mean data spanning 1968-78, emphasize the apparent extension of warm water of Agulhas Current origin onto the west coast in summer (Figure 5). They also show the pronounced temperature front and the divergence of isotherms offshore in the vicinity of Cape Columbine. By comparison, in winter the front is weaker, and the cool coastal water extends farther offshore.

The data presented by Boyd and Agenbag (in press) extend Christensen's analysis and demonstrate that an

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[1] Wooster, W.S. 1973. Upwelling in the Eastern Atlantic. Abstracts of the South African National Symposium, Cape Town, 6-10 August 1973.

[2] Ibid.

[3] Ibid.

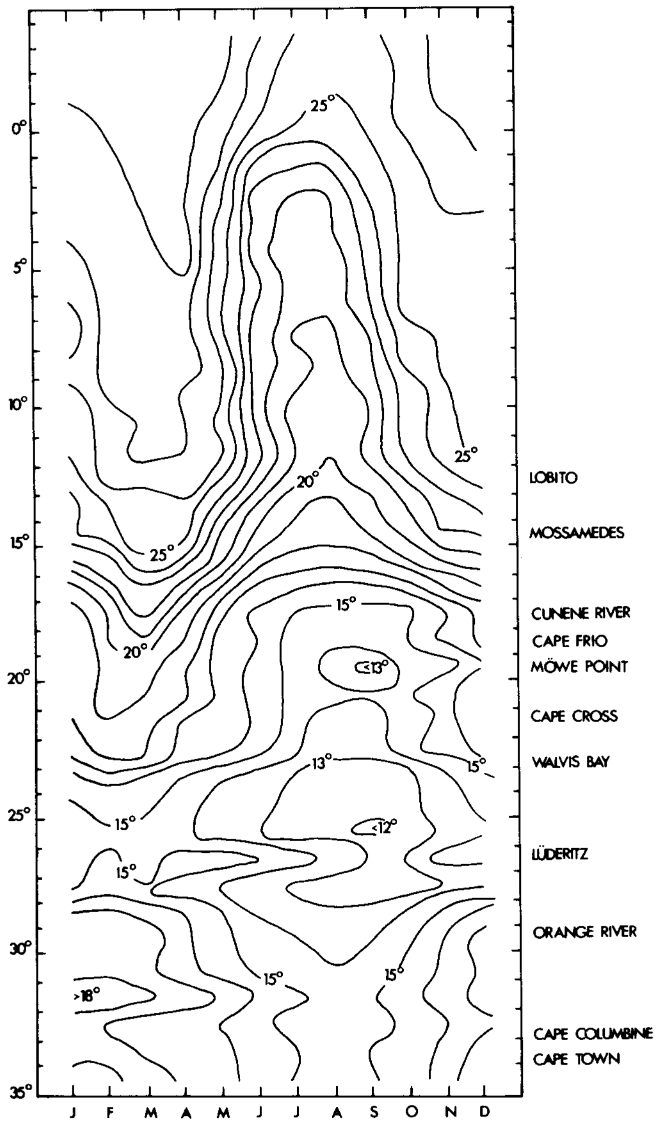


Figure 3. Monthly mean SST measurements for the coastal area of the Benguela system (from Wooster, W.S. 1973. Upwelling in the Eastern Atlantic. Abstracts of the South African National Symposium, Cape Town, 6-10 August 1973).

area of water cooler than 16°C extends along the entire coast between 18°S and 34°S up to 220 km offshore in winter (Figure 6). This cool area is considerably contracted in summer, with stronger offshore gradients set up by warmer water offshore.

Although the data from large-scale sea-surface temperature studies suggest that summer warming can be linked to the increased advection of water of subtropical and tropical origin onto the west coast, a component is due to solar heating of oceanic water. However, data from over 2,000 hydrocasts spanning 12 months taken in the southern Benguela region show that the warm water in summer can occur as a substantial layer of up to 60 m deep (e.g., Figure 7), indicating a strong advected component of Agulhas Current origin in the south. The observation that Agulhas Current water is advected considerable distances up the west coast can be substantiated from the distribution of certain Agulhas Current copepod species described by De Decker (1984).

Plankton Abundance and Distribution

As a result of having warm water close to the coast in summer and strong upwelling inshore, an exceptionally strong thermal gradient can be set up in the southern Benguela, particularly off the Cape Peninsula and off Cape Columbine. This feature takes the form of a front during upwelling (Figure 8a) and as a strong thermocline during lulls in upwelling (Figure 8b). Low levels of chlorophyll were found beyond the front in January 1978, but the chlorophyll concentration was high where upwelling displaced the nutricline toward the surface close to the coast (Figures 8a and 9a). During summer lulls in upwelling, the warm water advances as a substantial layer resulting in low chlorophyll levels with a weak subsurface maximum associated with the thermocline (Figures 8b and 9b).

The change in the distribution of high chlorophyll and plankton concentrations resulting from seasonal changes in temperature structure can be clearly seen in Figures 10 and 11. In winter, surface temperature is relatively isothermal, and chlorophyll is fairly widespread, but concentrations are low because of mixing and weak solar irradiation (Figure 10). Plankton concentrations in winter are most abundant north of the Cape Peninsula, particularly in the St. Helena Bay region (Figure 11a). As light levels and upwelling increase in spring, high concentrations of chlorophyll and plankton are encountered over a larger area. In summer, warm water close to the coast results in a strong thermal front and a severe reduction in the extent of the productive area. This area becomes limited to the vicinity of the upwelling centers off the Cape Peninsula and Cape Columbine, as well as St. Helena Bay—immediately downstream. Relaxation of the front in late autumn allows an expansion of the productive area and a return to winter conditions of relatively widespread concentrations of chlorophyll and plankton. As a result of this "bellows" effect, the distribution of plankton changes dramatically. Although the standing stock of plankton may increase in winter, the production may be less because of low light levels and reduced nutrient regeneration. Plankton standing stocks are consistently high in the inshore area north of the Cape Peninsula and particularly in St. Helena Bay (Figure 11b).

From the data presented by Kruger (1983) and Kruger and Boyd (1984), phytoplankton displaced volume

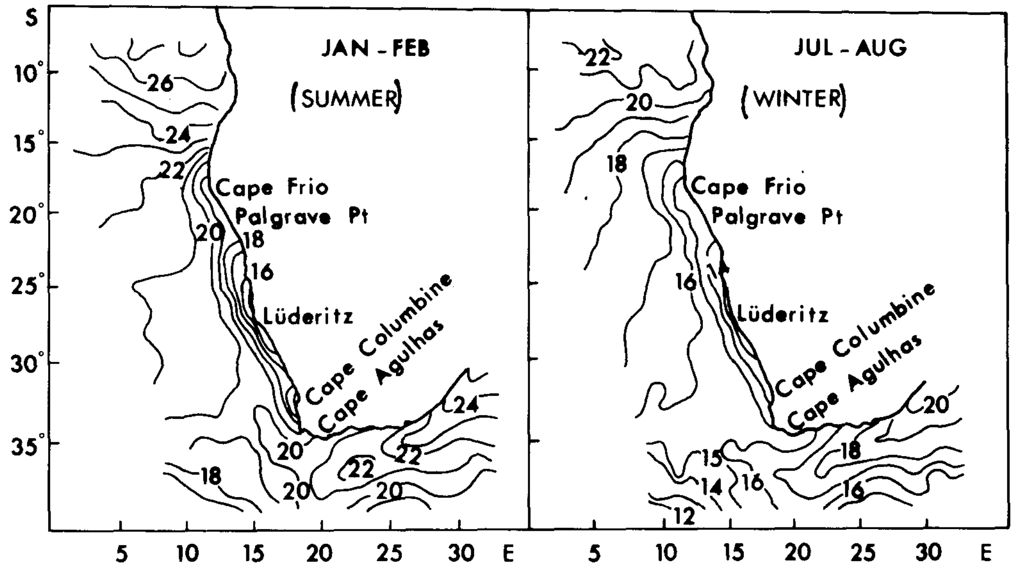


Figure 4. Summer and winter mean SST measurements for one-degree squares in the Benguela system (from Parrish et al. 1983).

in the northern Benguela region appears to be consistently high in the coastal area between Lüderitz and Walvis Bay, just north of the center of perennially strong upwelling. Zooplankton displaced volume is most often highest farther offshore and farther north between Walvis Bay and Cape Frio. During upwelling in the region north of Walvis Bay, the productive zone expands northwards (Figure 12a), whereas advection of warm surface water from the north and west results in generally lower productivity. (Figure 12b).

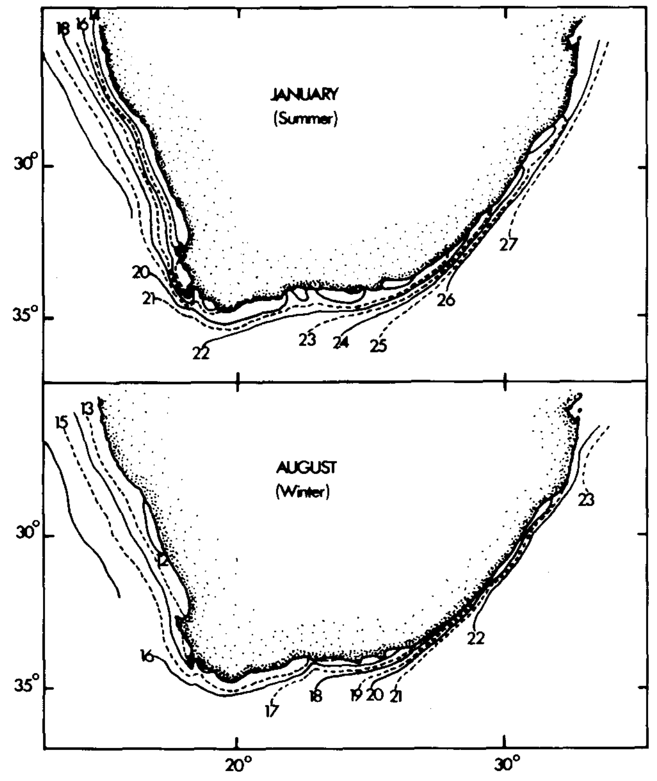


Figure 5. Summer and winter mean SST from an analysis of ten-day mean values from 1968 to 1978 for the coastal area off southern Africa (from Christensen 1980).

Fish Distribution, Spawning, and Recruitment

In both the northern and southern Benguela regions, spawning of a number of commercially important neritic species like pilchard, anchovy, and hake occurs mostly from spring to autumn, and is associated with the mixing areas between Benguela Current water and warm surface water advected into the system (O'Toole 1976, 1977; Crawford 1980; Crawford et al. 1983; Shelton and Hutchings 1982; Shelton 1984). Sites of strong offshore transport are avoided, even though productivity may be highest in these areas. Rapid egg development in the warmer water may result in increased early survival, and first-feeding larvae may benefit from food concentrated in strong fronts and thermoclines set up by the interplay between upwelling, advective processes and solar heating.

Dispersal after spawning is predominantly northwards in both regions, following the general equatorward flow of the Benguela Current at the surface. But accelerated transport of anchovy eggs and early-stage larvae has been recorded in a frontal jet off Cape Town (Shelton and Hutchings 1982) and may occur at other sites of strong horizontal temperature gradients, such as off Cape Columbine. In the southern region, recruitment of 0-year-old anchovy takes place along the west coast from midautumn onwards and is initially strongest to the north of St. Helena Bay (Crawford et al. 1983). Recruits may benefit from the consistently high plankton standing stock in the inshore region between Lamberts Bay and Cape Town (Figure 11b). In the northern region, anchovy and pilchard 0-year-

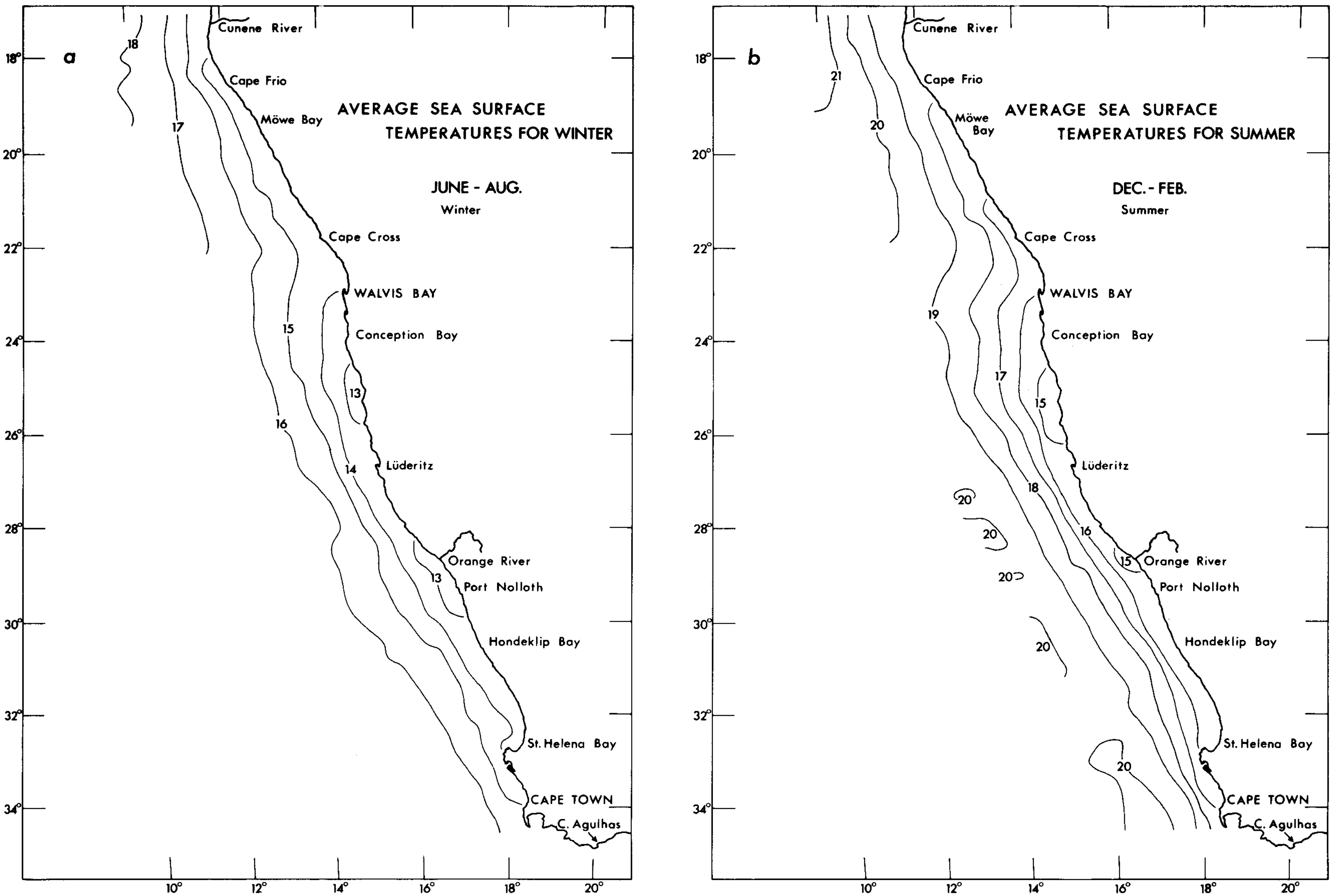


Figure 6. Winter and summer mean SST from an analysis of ten-day mean values for the Benguela system (from Boyd and Agenbag, in press).

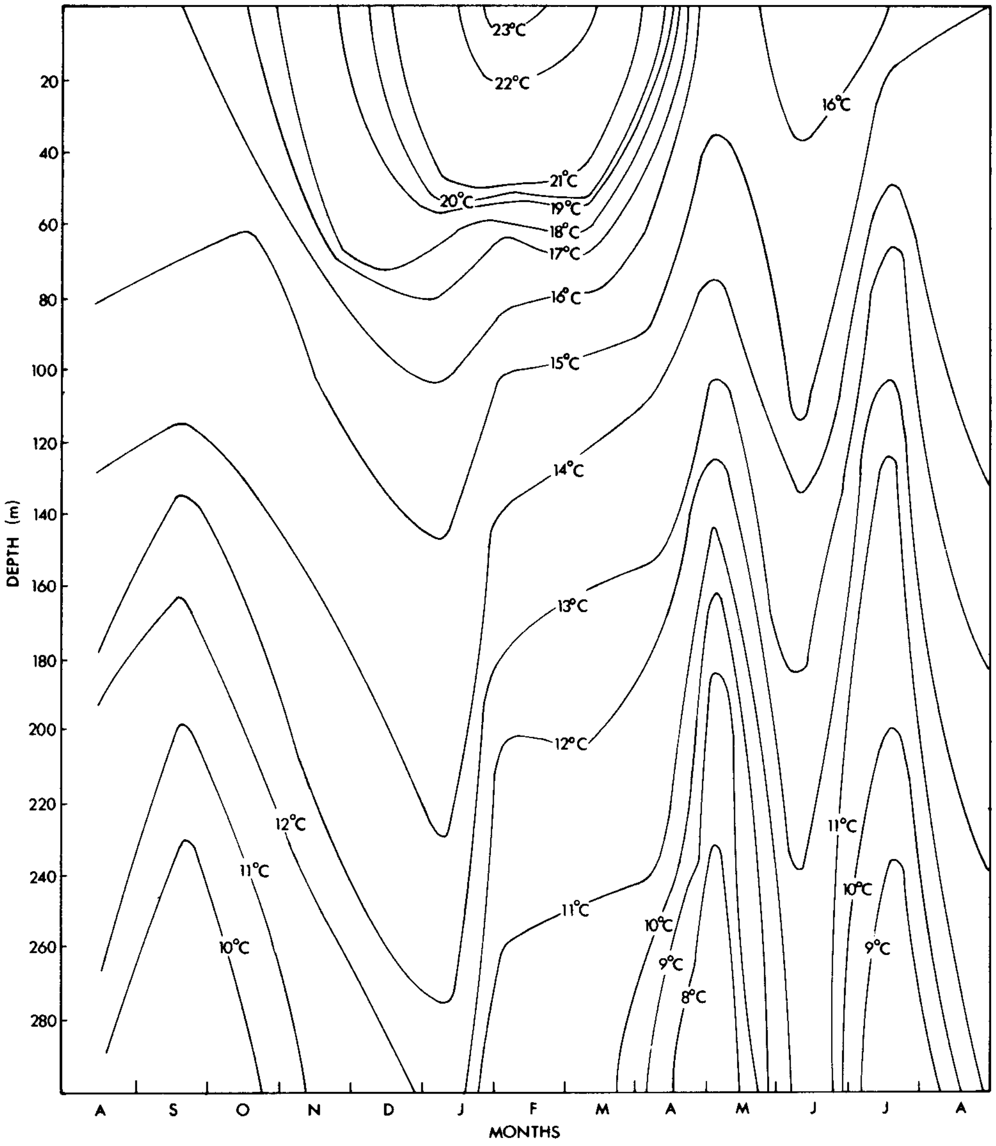


Figure 7. Temperature section from monthly measurements taken about 110 kilometers west of Cape Columbine between August 1977 and August 1978.

olds recruit into the fishery in the vicinity of Walvis Bay from May onwards (Crawford et al. 1983). Southward movement of shoals of 0-year-old fish detected by fishing boats at this time of year may be facilitated by inshore countercurrents in the two regions.

In the southern Benguela region, the southward migration is initially into the productive coastal zone, where the fish feed before moving offshore onto the Agulhas Bank to spawn. There, moderately warm 17°-18°C water is widespread in spring and early summer (Figure 10). Anchovy in the northern Benguela region recruit over several winter months off Walvis Bay before reappearing in the spawning ground farther north. This return migration may occur in northerly flowing water offshore of the main fishing ground, which is confined to the area close to the coast. Recruitment patterns are similar in both the northern and southern regions, but in the south anchovy larvae reach the recruitment ground by the northward-flowing Benguela Current and the spawning ground via a countercurrent; whereas in the northern Benguela region a countercurrent may assist the recruitment migration, and the main flow of the Benguela Current may aid the spawning migration.

The occurrence of water warmer than 20°C on the Agulhas Bank in late summer and early autumn (Figures 5 and 10) appears to reduce the area suitable for spawning and concentrate adult spawning fish closer inshore, since very few anchovy eggs are found in the warm water, and the catch rate of adult anchovy by the purse seine fleet operating inshore increases at this time. A rapid decline in the catch rate of adult

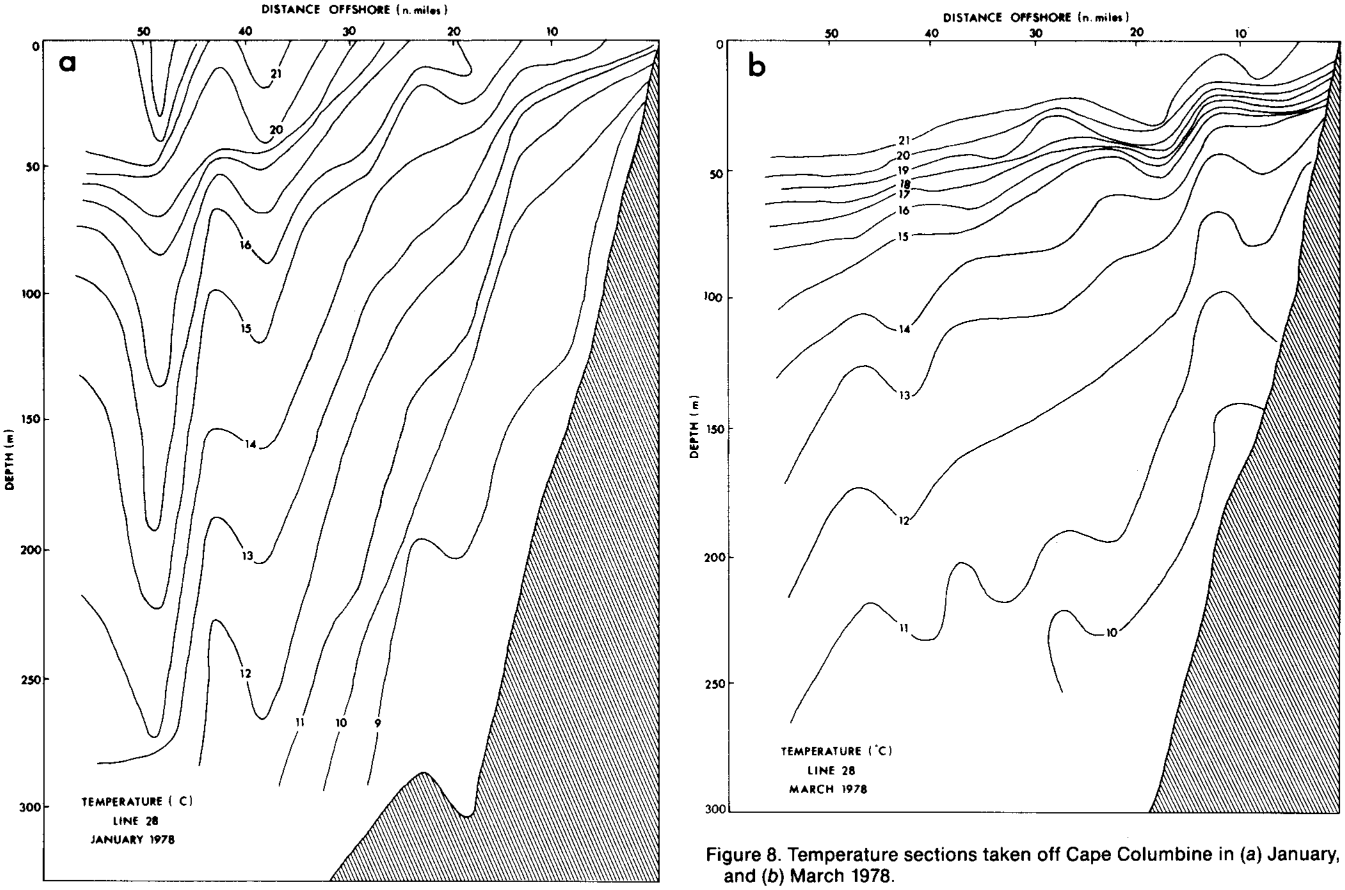


Figure 8. Temperature sections taken off Cape Columbine in (*a*) January, and (*b*) March 1978.

anchovy in late autumn is coincident with the seasonal cooling of surface waters on the Agulhas Bank. By winter the warm water is confined to the body of the Agulhas Current (Figure 5). There is a marked eastward movement of anchovy and pilchard up the coast in autumn (Crawford 1981a, b).

Neritic species inhabiting the Benguela system generally avoid winter spawning. This may be because in winter, onshore advection of warm water is at a minimum; temperature near the surface is cool and relatively isothermal; offshore transport is not constrained by strong fronts; and plankton is distributed over a large area rather than concentrated close to the coast. In the southern region, lantern fish, *Lampanyctodes hectoris*, and round herring, *Etrumeus teres*, are normally associated with the shelf edge and appear to spawn predominantly in winter (Figure 13), possibly in response to the more widespread distribution of plankton in this season.

INTERANNUAL SIGNAL

If the strong seasonality in plankton distribution as well as the distribution, spawning, and recruitment of pelagic fish in the Benguela system is linked to the seasonal influence of warm water, interannual variability in the strength and extent of warm conditions may have a major effect on year-class strength. Extensive occurrence of warm water could severely limit plankton production and concentrate fish in a restricted environment where density-dependent population responses may be intensified. Alternatively, during a cool period, spawning and dispersal of eggs and early-stage larvae, as well as food for first-feeding larvae may be adversely affected. The influence of within-season departures from the seasonal average of onshore, warm-water advection or upwelling may be difficult to detect in terms of year-class strength and may require intensive sampling of differential mortality within a cohort subsequent to spawning. However, prolonged periods of warming or cooling could be expected to have a more apparent influence on spawner biomass and recruitment strength.

Guano Record

A historic time series of the annual amount of guano collected on islands off Namibia and off South Africa (Figure 14) may reflect past fluctuations in the combined pilchard, anchovy, and horse mackerel biomass

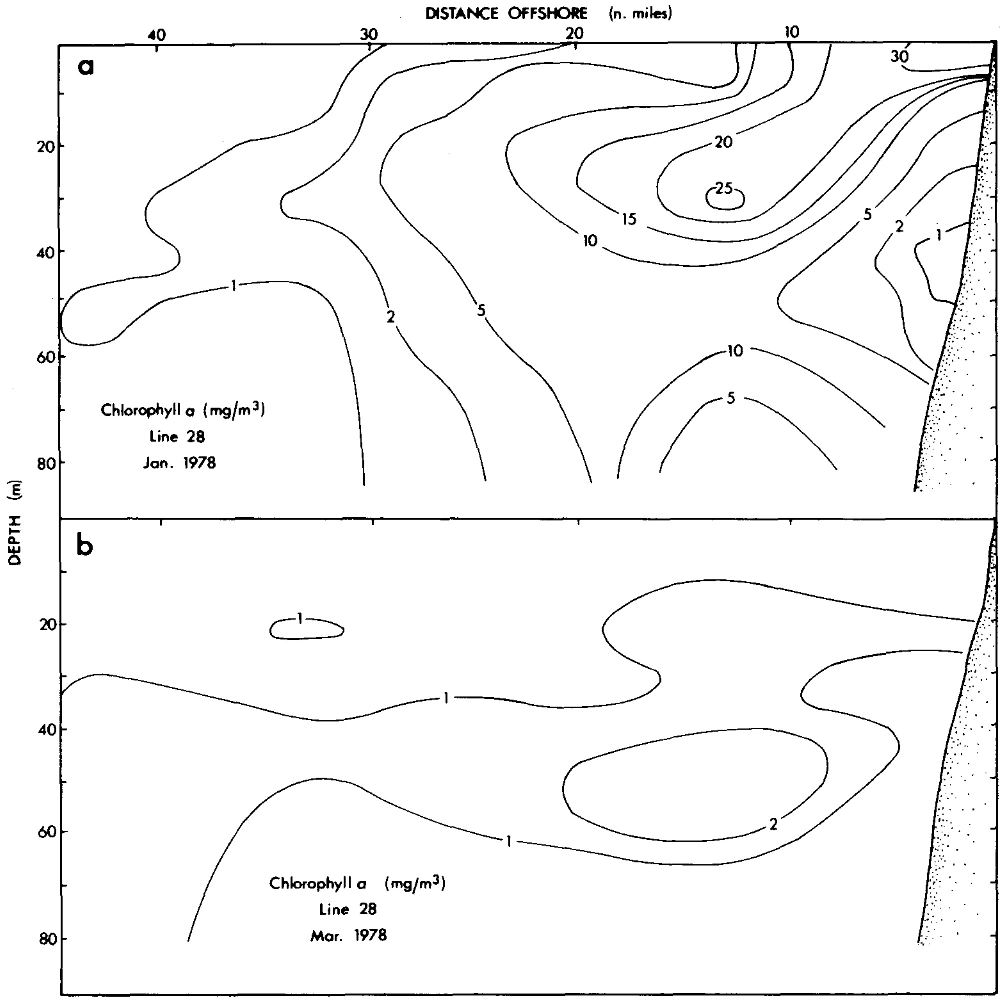


Figure 9. Chlorophyll *a* section off Cape Columbine in (*a*) January, and (*b*) March 1978.

(Crawford and Shelton 1978), in the absence of any more direct historic record. The Namibian and South African guano records are significantly positively correlated ($r = 0.37$, $n = 73$). This could be a result of similar trends in the abundance of pelagic prey species off both Namibia and South Africa, which in turn could have resulted from large-scale environmental phenomena that impacted the whole system over periods of decades.

The individual guano records for Namibia and South Africa show significant autocorrelation with time lags of up to five years (Figure 15). This could be attributed to similar autocorrelation in the prey biomass resulting from the smoothing of random environmental variability by the multiple age-group prey spawner populations, or by smoothing within the seabird populations themselves. Alternatively, autocorrelation in the guano records could be caused by low-frequency environmental effects directly on the seabird populations or on their prey. While no unequivocal interpretation of the guano record is possible, the argument that environmental autocorrelation in the Benguela system is an important signal is not invalidated.

Sea-Surface Temperature and Sea Level

In the southern Benguela region, advection of warm water outside the upwelling front is most marked during the seasons of strongest upwelling and is aided by the prevaling upwelling-favorable wind stress, whereas in the northern Benguela region the normal seasonal advance of Angolan water occurs during the upwelling minimum, tending to oppose the wind forcing. Hence the mechanisms for advection of warm water differ within these two regions in the Benguela Current system. In the south, advection of Agulhas Current and Agulhas Bank mixed water outside the coastal upwelling zone would tend to reinforce the frontal feature, whereas in the north, a southward intrusion tends to deepen the thermocline and suppress upwelling. The

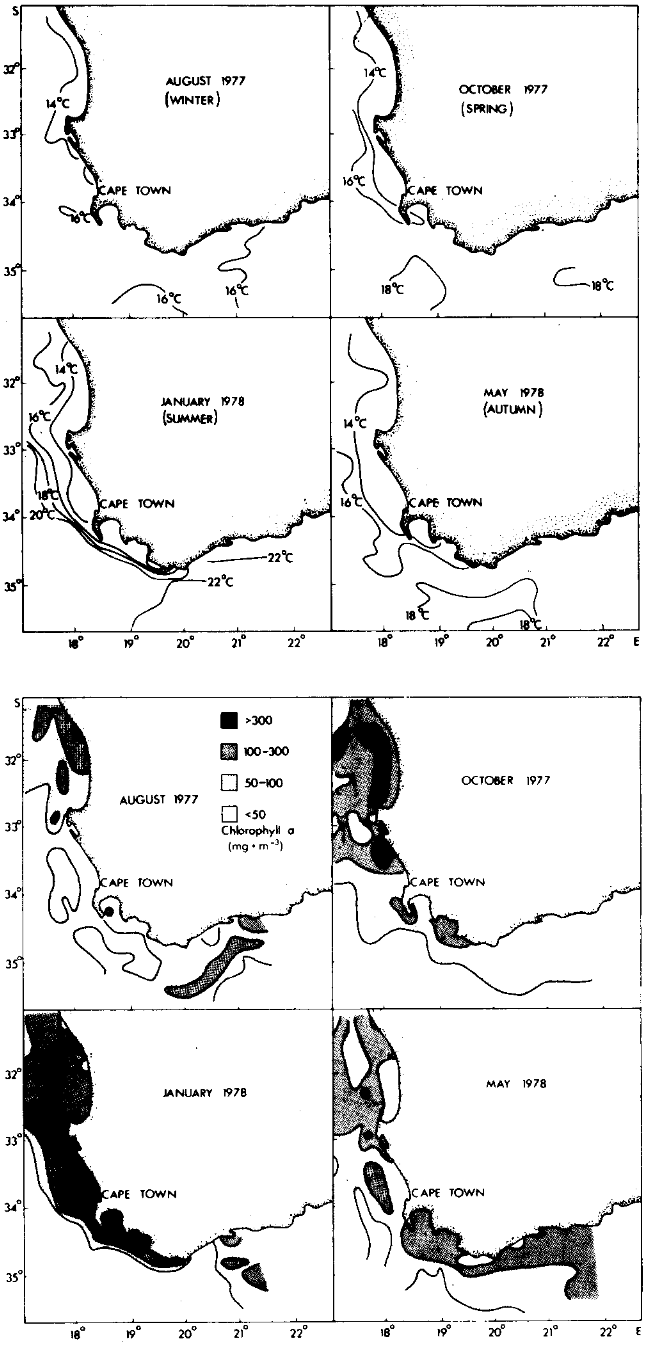


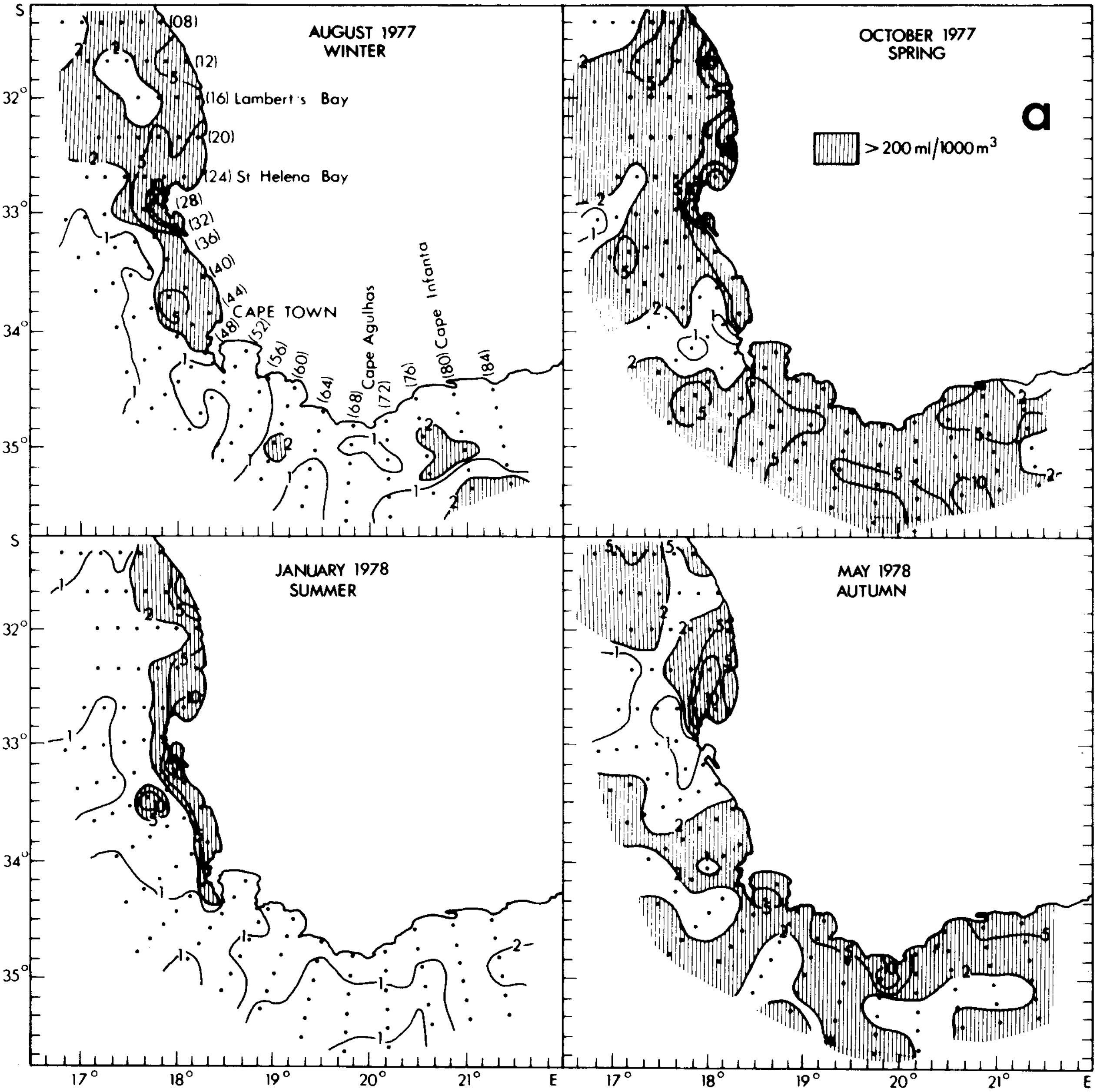
Figure 10. Seasonal pattern of surface temperature and chlorophyll a distribution in the southern Benguela region in 1977-78 (from Shannon et al. 1984).

northern Benguela region would therefore seem more susceptible than the south to a large-scale El Niño-type anomaly, although a high incidence of onshore (westerly) winds or periods of calm in the south during summer and early autumn could be expected to have a measurable effect in terms of SST anomaly in the coastal zone.

A major warm event was recorded in the northern Benguela region in 1963 and was well documented by Stander and De Decker (1969). Brundrit (1984) found that this coincided well with a mean sea-level peak that is clearly visible in the records from Walvis Bay and Lüderitz and detectable as far south as Cape Town. Annual mean SST measurements recorded in the vicinity of Walvis Bay from 1955-67 and from 1969-79 from two different sources (Figure 16) show that 1963 was the warmest year in a warm period that began in 1961. A similar but less intense warm period began in 1972 and peaked in 1974 (Figure 16) and is reflected by increased sea levels at Lüderitz (Figure 2 in Brundrit 1984). McLain et al. (1985) present mean SST data for three-degree squares for the entire west coast of southern Africa from 1971-84. Their data show that a large portion of the Benguela system was subject to a positive temperature anomaly between 1972 and 1977.

Boyd and Thomas (1984) and Boyd et al. (in press) report a further major warm event in 1984 when warm, saline Angolan water penetrated particularly far south, suppressing upwelling and leading to extremely low volumes of phytoplankton. In March and April 1984, water temperatures were 3° to 6°C warmer than average over large areas, but conditions appeared to return to normal in May. However, monthly monitoring cruises in the winter of 1984 showed warmer and more-saline-than-average water off Walvis Bay in June and August 1984, indicating a sustained warm period throughout the winter. The 1984 anomaly in the northern Benguela region is particularly clear in the data presented by McLain et al. (1985) as a southward projecting tongue of Angolan current water that raised temperatures by more than 2°C from the mean shown in the three-degree-square analysis.

Although SST anomalies as strong as those that occurred to the north of Lüderitz in 1963 and 1984 are not apparent in data records for the southern Benguela region, SST measurements made in Table Bay at Cape Town from 1956-80 (Figure 17) and mean annual SST values for three-degree squares for the period from 1971-84 (McLain et al. 1985) show that a generally warm period spanned the late 1950s and early 1960s, with a maximum SST anomaly in September and November 1963. A second warm period from 1972-77 is evident in the three-degree-square analysis as well as the Table Bay data. The three-degree-square analysis also shows that a substantial cool period extending over much of the Benguela system began in 1978 but may have terminated in 1984, coinciding with the warm event north of Lüderitz. The cooling in SST corresponds to decreased sea levels measured at Simons Bay near Cape Town (Figure 3 in Brundrit et al. 1984).



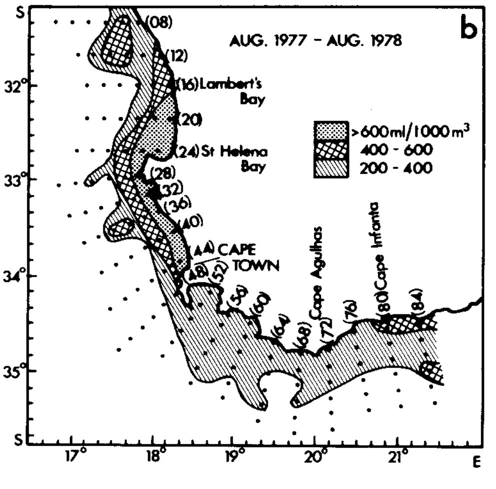


Figure 11. Southern Benguela region: (*a*) seasonal pattern of plankton standing stock from a double oblique tow with a bongo net fitted with 300-micron mesh, taken down to a maximum depth of 100 m; (*b*) mean distribution of plankton retained by the 300-micron mesh net from monthly surveys conducted between August 1977 and August 1978.

The mechanisms causing prolonged warm and cool periods in SST and changes in sea level in the Benguela system may be linked to changes in large-scale climatic processes, such as deviations in the seasonal change in the position of the South Atlantic high-pressure system, which may affect both upwelling and advection. The Pacific El Niño is known to be forced by the Southern Oscillation phenomenon (Philander 1983), and Walker et al. (1984) have quoted Van Loon

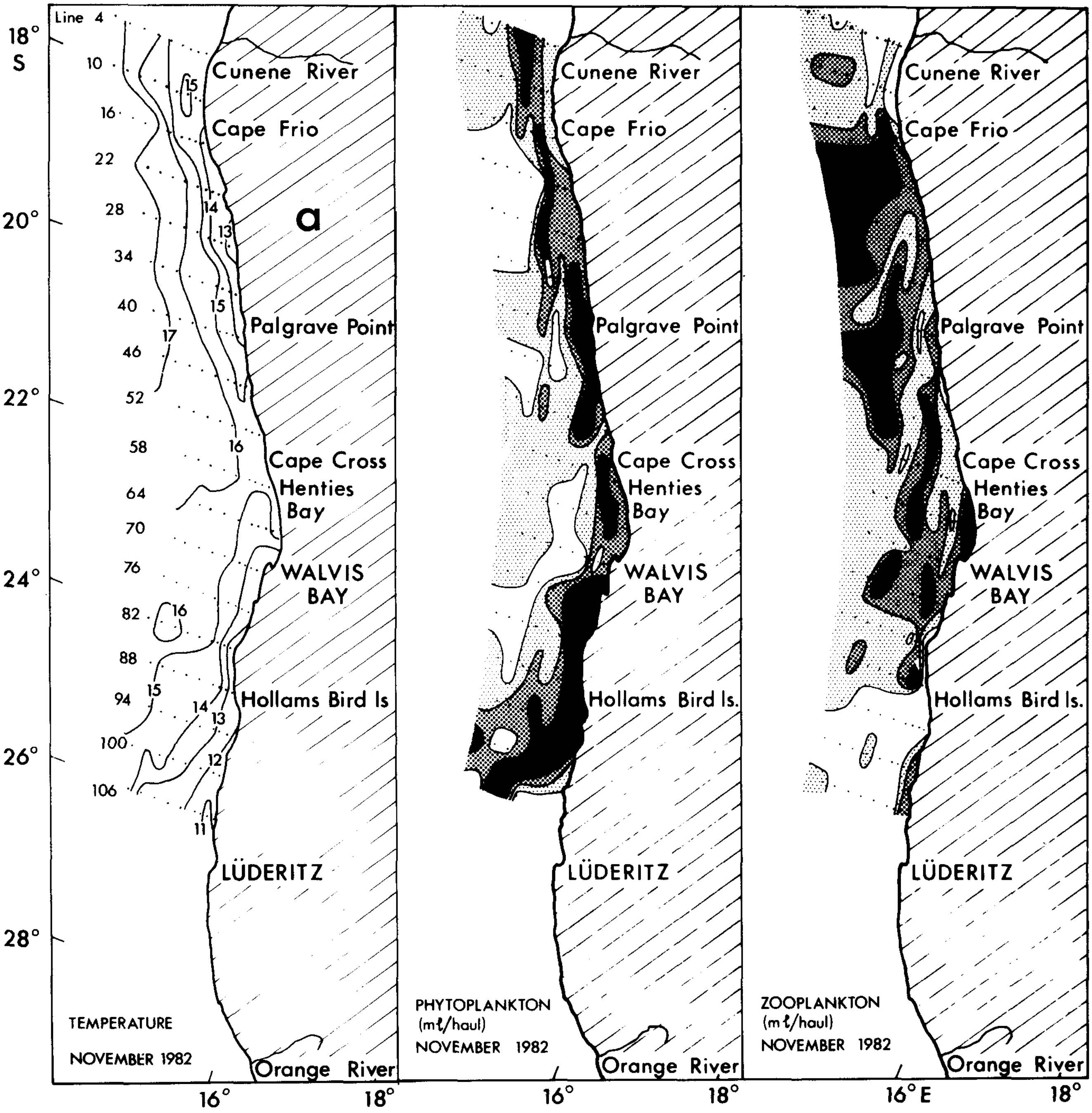


Figure 12a. Northern Benguela region surface temperature and plankton displaced volume from vertical tows from 50 m to the surface with a 50-cm-diameter net fitted with 80-micron mesh for November 1982 (from Kruger and Boyd 1984).

and Madden (1981) as demonstrating that during a Pacific warm event, negative atmospheric pressure anomalies arise over the central South Pacific Ocean in phase with negative anomalies over the South Atlantic Ocean, south of 35°S. Walker et al. (1984) also show a close relationship between annual (1976-83) SST measurements in the southern Benguela region and the southerly extent of the Subtropical Convergence. Northward displacement of the Subtropical Convergence was found by Gilooly and Walker (1984) to indicate increased frequency of cold fronts to the south of the continent and a northward shift in the mean position of the South Atlantic High. This represents an annual shift toward winter conditions.

Tyson (1981) has examined the occurrence of extended wet and dry spells over the southern African

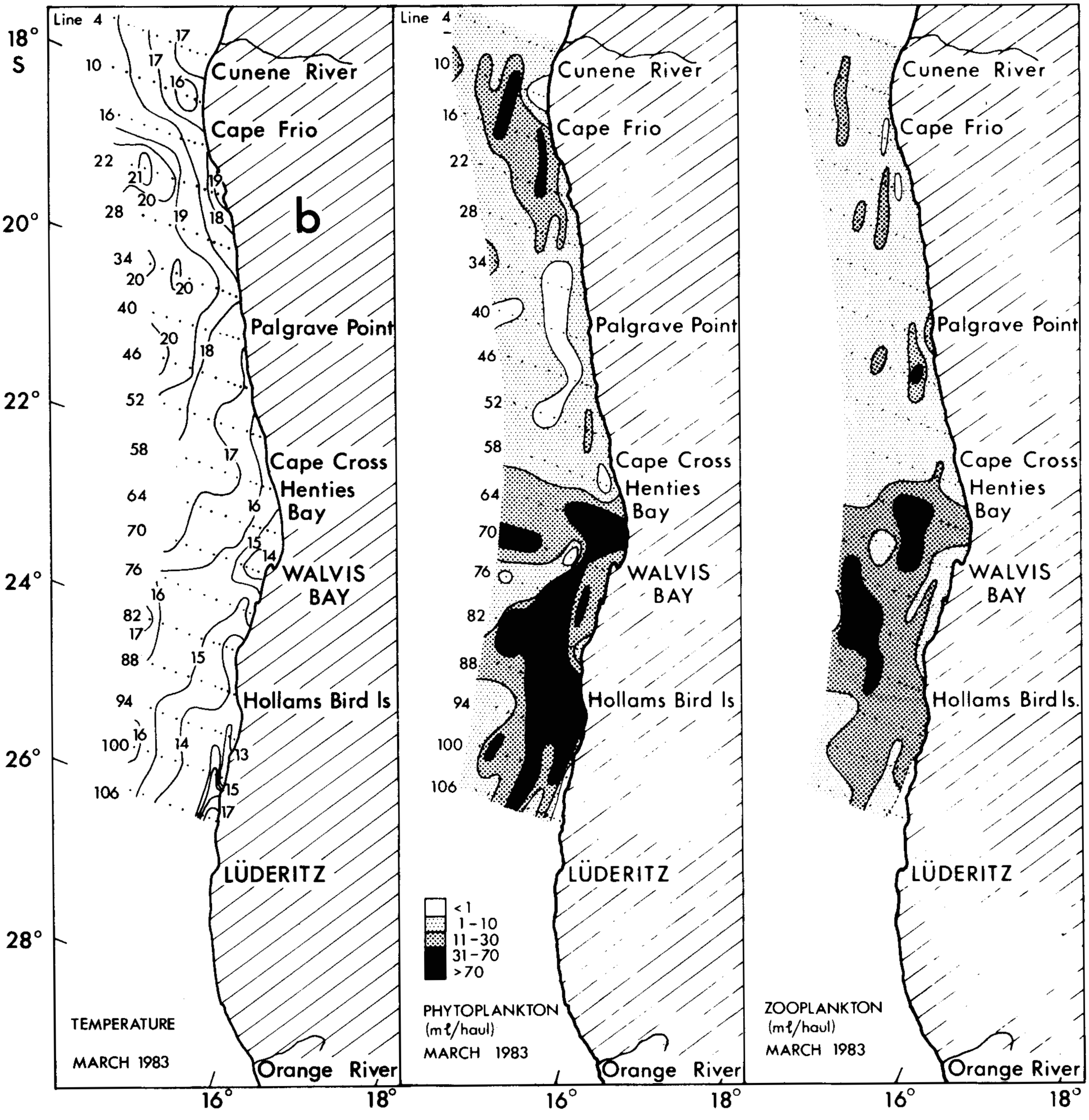


Figure 12b. Northern Benguela region surface temperature and plankton displaced volume from vertical tows from 50 m to the surface with a 50-cm-diameter net fitted with 80-micron mesh for March 1983 (from Kruger and Boyd 1984).

subcontinent, which is predominantly a summer rainfall area, and reports that 1963-72 was a dry spell and 1973-79 a wet spell. Since 1979, the southern African subcontinent has experienced severe drought conditions, which may have only recently been broken. The dry spells coincide with cold SST, and the wet spells with warm SST shown in both Figure 17 and in the analysis of McLain (1985).

Tyson (1981) showed that the subcontinental wet and dry spells have occurred in association with atmospheric circulation variations, which impart a quasi-18-year oscillation in rainfall. However, he also identified a 10-11-year rainfall oscillation for the winter rainfall area near Cape Town. A cycle fitted to the Cape rainfall data by Vines (1980), shown in Tyson (1981), is in phase with the variability shown in Figure

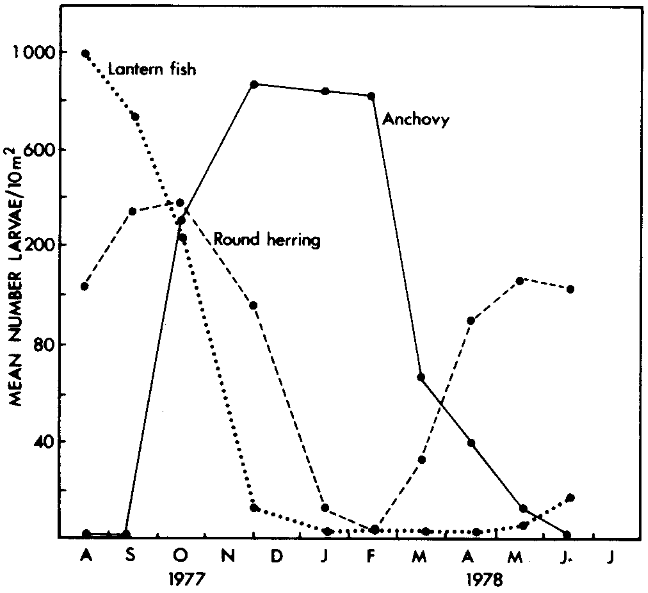


Figure 13. Mean number of anchovy, lantern fish, and round herring larvae from monthly bongo net tows in the southern Benguela region between August 1977 and June 1978.

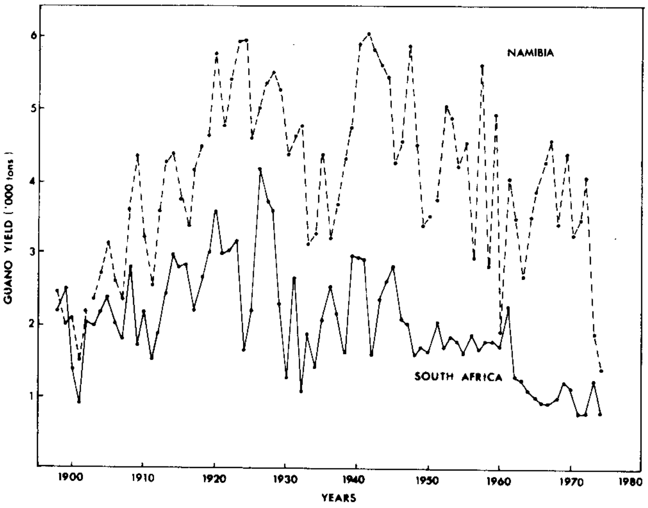


Figure 14. Guano yield from islands off South West Africa/Namibia and South Africa.

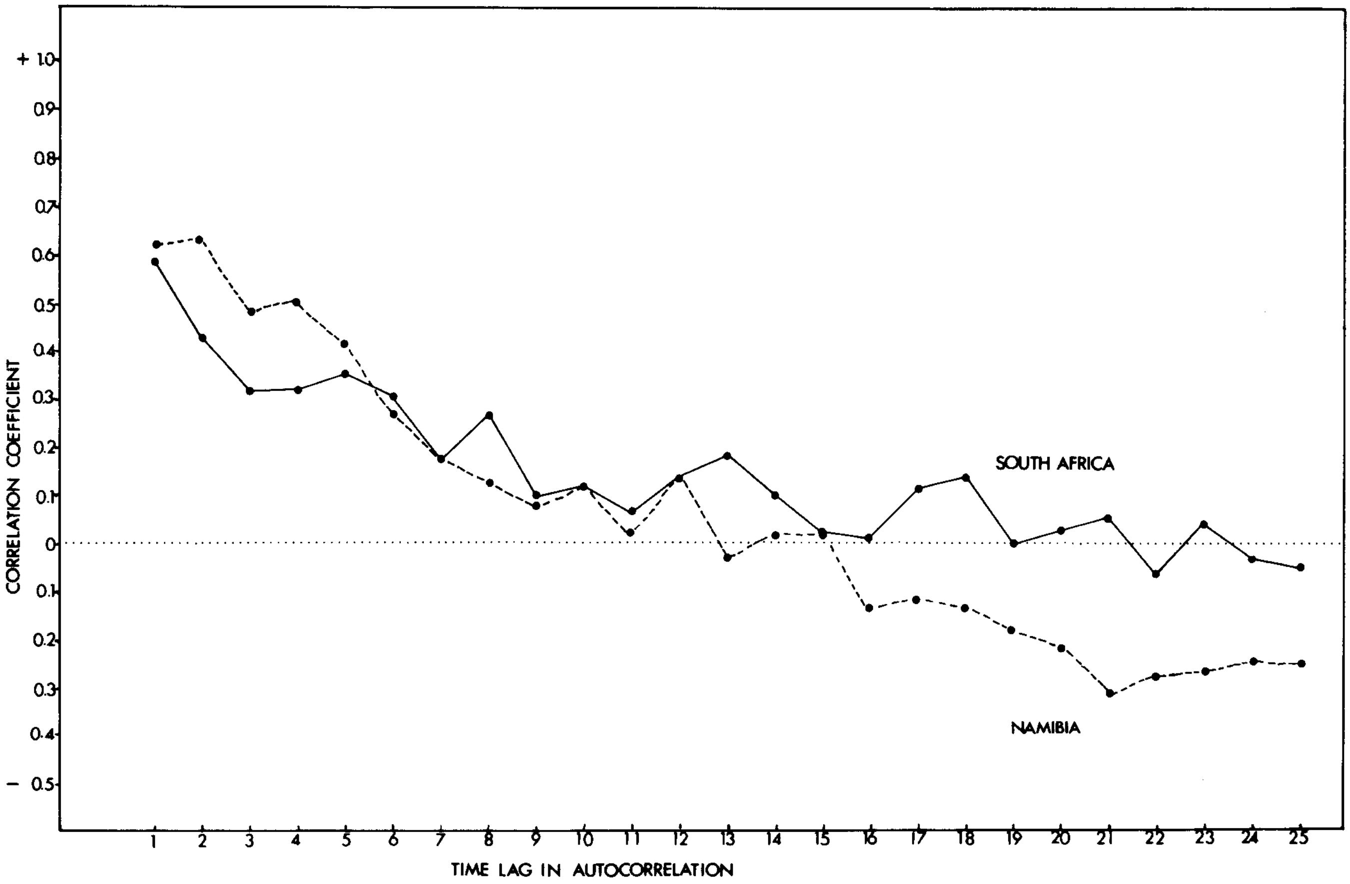


Figure 15. Time-lagged autocorrelation of guano yield data from islands off Namibia and South Africa.

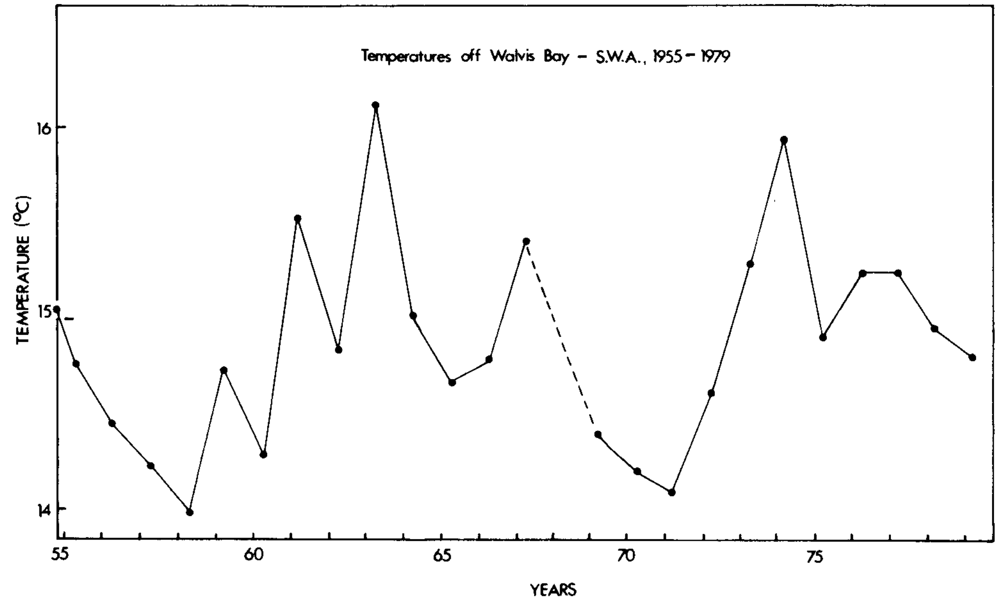


Figure 16. Mean annual SST measurements from a site near Walvis Bay for the period 1955-79. The temperatures for 1955-67 were from hydrological data, those from 1969-79 from general shipping. The latter data were adjusted to have the same mean as the former. Means were computed for each 12-month period beginning in September and extending through the following August; the resulting annual mean value was then plotted in the position corresponding to February on the time axis.

16 and links cool annual temperatures at Walvis Bay with increased rainfall in the Cape.

Effect on Fish Populations

The 1963 warm event in the northern Benguela region shifted shoals of pilchard southwards in the Walvis Bay region. These fish were in poor condition, gave low oil yields, and had reduced gonad development with consequently diminished egg production over the spawning grounds (Stander and De Decker 1969). The major warm event that occurred in the northern Benguela region in 1984 also caused pilchard to concentrate close to Walvis Bay, leading to high catch rates. There was a failure of anchovy recruitment caused apparently by reduced spawning activity accompanied by low survival of larvae in the excessively warm water of up to 26°C (Boyd and Thomas 1984).

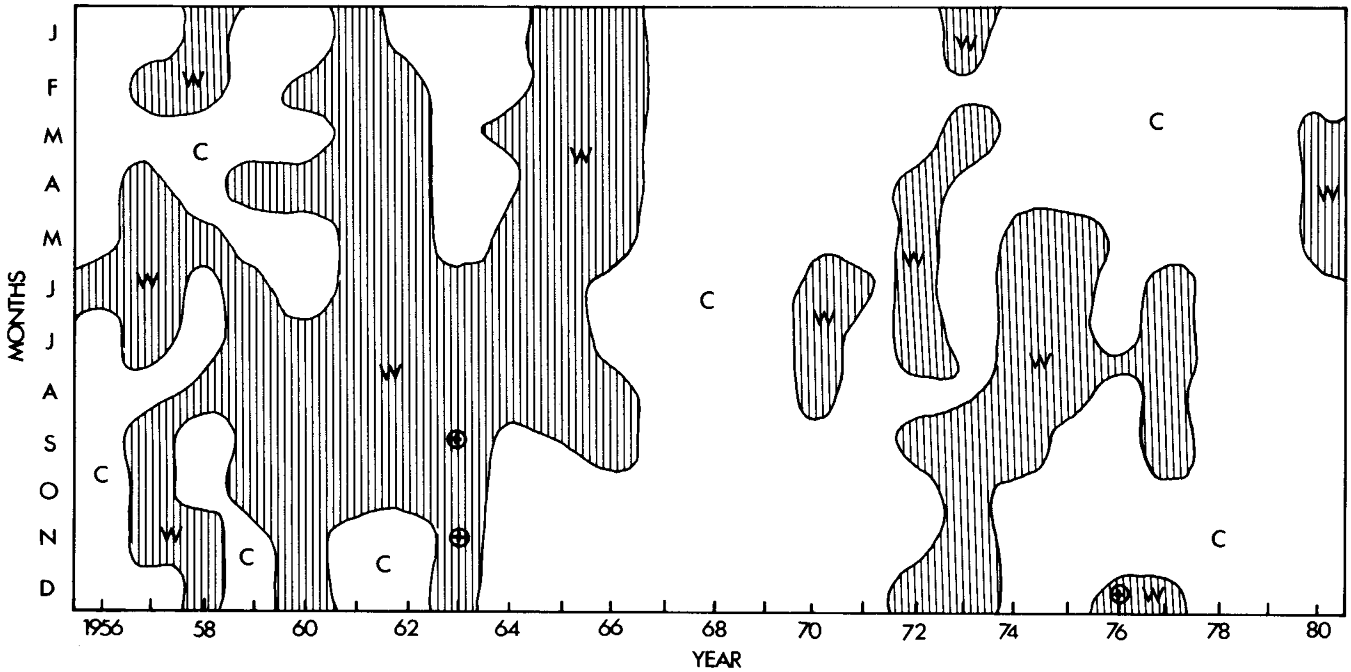


Figure 17. Mean monthly SST measurements from Table Bay near Cape Town for the period 1956-80, showing positive (hatched) and negative temperature anomalies. The (+) indicates a positive anomaly of more than 2°C (from M. Jury, Sea Fisheries Research Institute, Cape Town, unpublished data).

Boyd (1979) suggested that consistent and warm December-April temperatures from 1972-75 favored anchovy recruitment, whereas highly variable temperatures in 1976 and 1977 coincided with poor recruitment. Increased variability in SST has been observed to result from either intense upwelling events in summer (e.g., Stander 1963) or a major advection phenomenon (e.g., Stander and De Decker 1969; Boyd and Thomas 1984).

In the southern Benguela region the pilchard resource collapsed over the period 1960-67, with very low recruitment resulting from the spawning that took place in the summer of 1963-64 (Figure 2). This coincides with a maximum SST anomaly of more than 2°C in Table Bay in September and November 1963 (Figure 17). The warming that began in the southern Benguela region in 1972 corresponds to years of apparently good recruitment of anchovy (Figure 2).

However, an alternative interpretation of the anchovy response may be that availability of adult fish increased in the inshore fishing zone because of the increased influence of Agulhas Current water on the Agulhas Bank. The elevation of adult catchability under such conditions is not accounted for in the cohort analysis performed to estimate year-class strength and biomass. The period of cooling over the early 1980s coincided with a marked decline in the catch of adult anchovy in the southern Benguela. This has conventionally been attributed to poor recruitment, whereas a relaxation of advection may have reduced the incidence of adult anchovy close inshore.

Although the relationship between the Benguela system's neritic fish populations and periods of warming and cooling still must be rigorously examined, it can be inferred from this descriptive study that the populations do respond to low-frequency environmental forcing. Further, there is some evidence that periods of exceptionally strong SST anomaly adversely affect year-class strength, whereas moderate warming may be advantageous to some neritic fish.

Incorporation into Population Models

High-frequency and essentially unpredictable environmental variability can only be incorporated as a stochastic "noise" term in fish population models. These models have no predictive value, but can be used in Monte Carlo simulations to estimate the risk of collapse associated with alternative management strategies, provided the statistical description of the variability is adequately known. The central tendency of the variability can be expected to be strongly modulated if, in addition to random variability on a short time scale, autocorrelation over a longer period occurs. Swartzman et al. (1983) developed an approach for managing the Pacific whiting fishery in which separate stock-recruit curves could be used during periods of ocean warming or cooling, and risk of overfishing could be assessed according to stochastic recruitment variability around the appropriate curve.

The potential importance of autocorrelation of en-

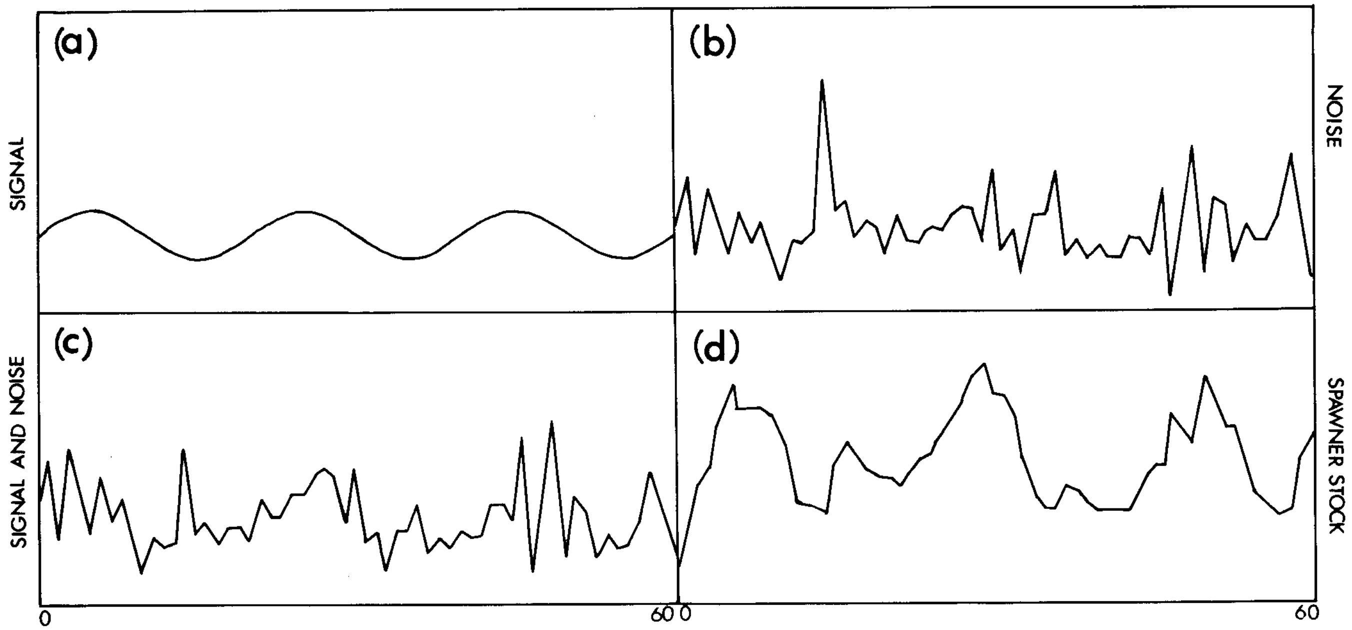


Figure 18. A sine wave with a wavelength of 20 years and an amplitude of 0.67 to 1.33 of the mean value (*a*), used multiplicatively to vary the central tendency of a log-normally distributed random number sequence with a range of 0.5 to 2.0 times the mean value (*b*). This resulted in the signal (*c*), which was used to modify recruitment generated in the model from which the spawner stock (*d*) was obtained.

vironmental variability that modifies recruitment success has been examined by means of a theoretical model of the anchovy population, which uses the same population parameters as those in Armstrong (1984):

$$R = (e^{\epsilon}\,\alpha)\,P\exp(-\beta P^{c})$$

where R is the number of anchovy recruits,

P is the parent biomass,

α is a parameter expressing density-independent prerecruit mortality and specific fecundity of spawners,

$\epsilon(0,\sigma)$ is a random number from a normal distribution with mean of zero and standard deviation σ,

β is a parameter expressing density-dependent prerecruit mortality, and

c is an exponent modifying the severity of density-dependence (MacCall 1980).

To simulate the response to an autocorrelated environmental variable, the density-independent term (α) of the stock-recruit function was made to follow a sine wave with a wavelength of 20 years and minimum and maximum values of 0.67 and 1.33 times the mean value (Figure 18a). To simulate the unpredictable component of environmental variability, this term was perturbed using a multiplicative log-normally distributed random number sequence with a mean of 0.0 and a standard deviation of 0.35, which resulted in a range of values of about 0.5 to 2.0 (Figure 18b). The resulting signal was used to modify recruitment generated by the model, which assumes an asymptotic stock-recruit curve, age at maturity of one year, and an instantaneous rate of natural mortality of 1.0. The spawner stock biomass sequence generated by the model shows that the population filters out the random variability and returns the autocorrelated signal (Figure 18d). This demonstrates that a population with parameters like those assumed in the model will be well buffered against random variability but strongly modulated by an autocorrelated signal.

The periodicity of any cyclical change will affect population growth according to the generation time of the fish and the biomass growth pattern of each year class. The spawner biomass of short-lived species will react quickly to changes in recruitment, whereas long-lived species may exhibit a considerable time lag between a period of enhanced or depressed reproductive success and its effect on subsequent spawner biomass levels.

Fish species with delays of several years between hatching and the maximum reproductive output of a year class may oscillate out of phase with an environmental cycle if the wavelength of the cycle is approximately double the average age of the spawning population. Reduced spawner biomasses following years of depressed year-class strength would coincide with a period of favorable environment for spawning and recruitment, giving the impression of high productivity at small spawner stock sizes (Figure 19b). This would result in an overestimate of the severity of density-dependence, and an overestimate of maximum average yield (MAY).

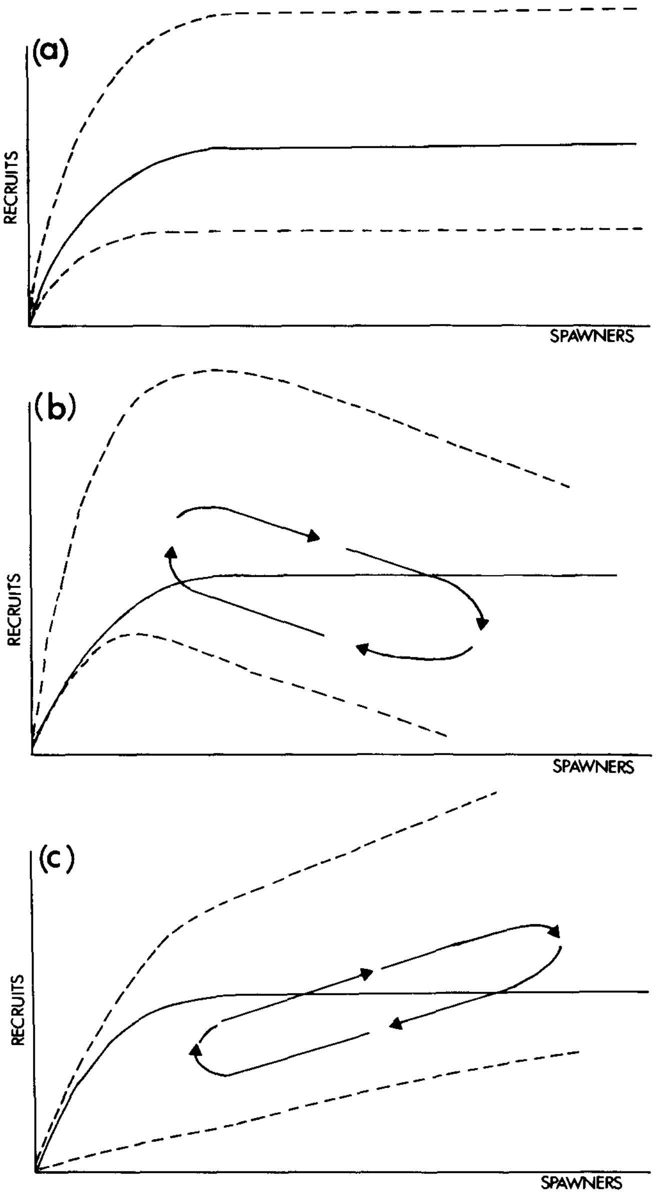


Figure 19: Theoretical stock-recruit functions for fish species, showing possible ranges of recruitment variability (broken lines): (*a*) with no autocorrelation in the environmental variable affecting recruitment, (*b*) with autocorrelation in environment exhibiting a periodicity of approximately double the average age of the spawner population, and (c) autocorrelation in environment exhibiting a periodicity of approximately eight times the average age of the spawning population. Arrows indicate temporal progression of stock-recruit values under the influence of the autocorrelated environmental signal without random variability.

If the environmental cycle is of long wavelength in relation to the average age of fish in the spawning population, the spawning biomass will tend to come into phase with the cycle, and the stock-recruit data will suggest low productivity at reduced biomass and high productivity at elevated biomass levels (Figure 19c). This will result in an underestimate of the degree of density-dependence and an underestimate of MAY. In either case, the influence of autocorrelation in year-class strength would increase the probability of severe stock depletions, particularly under constant catch policies.

The theoretical examination of the potential effect of autocorrelated environmental variability makes it seem important to improve the description of the larger-scale variability component in the Benguela system and in other eastern boundary current systems, and to develop appropriate harvesting strategies that are robust to runs of years in which environmental conditions adversely affect recruitment. If cycles in environmental conditions, similar to those found by Tyson (1981) for rainfall over the southern African continent, can be determined in the marine environment, and shown to consistently affect recruitment, then a measure of recruitment prediction may be feasible.

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THE EFFECTS OF VARYING NUTRIENT CONCENTRATION ON BIOLOGICAL PRODUCTION IN UPWELLING REGIONS

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ABSTRACT

The maximum steady state yield of a marine ecosystem is set by the input of primary nutrient, and the associated rate of production that is termed "new production." At the simplest conceptual level, new production can be related directly to, and estimated from, nitrate input or nitrate uptake. Using such a simple assumption, one can predict that, for a given vertical velocity during upwelling, the new production at 15°S, Peru, would be about twice that of the upwelling center at northwest Africa, as a consequence of the Atlantic's relative nutrient poverty. However, "regenerated" nitrogen production, based upon nitrogen recirculated through grazing pathways, also increases with increased new nitrogen production.

Additional complexities arise from the adaptive responses of phytoplankton to upwelling conditions. The maximum specific nitrate uptake rate is a function of the initial nitrate concentration, but the actual rate realized is often reduced below maximum by other environmental factors, e.g., deep mixing. This occurs in northwest Africa, where high upwelling rates induced by high wind stress do not compensate for low source-water nutrient concentrations caused by deep mixing of the phytoplankton.

There are other direct effects of nitrate concentration on phytoplankton physiology, including enhanced assimilation number. So the responses of phytoplankton to increased nitrate input and concentration should be nonlinear and will probably approximate an exponential relationship.

RESUMEN

La máxima productividad sostenida de un ecosistema marino estable está determinada por el aporte de nutrientes primarios y por el ritmo de producción correspondiente, denominado "nueva producción". Al más simple nivel conceptual, la nueva producción puede ser relacionada directamente a, y estimada directamente de la entrada o del consumo de nitrato. Usando un supuesto tan simple, se puede predecir que para una velocidad vertical de afloramiento dada, en Peru, a los 15°S, la nueva producción sería el doble que la del noroeste de Africa, como consecuencia de la pobreza relativa de nutrientes en el Atlántico. Sin embargo, la producción "regenerada" de nitrógeno, basada en el nitrógeno recirculado a través de los ciclos de pastoreo, también aumenta con el incremento en la producción de nitrógeno nuevo.

Complicaciones adicionales se generan por la respuesta adaptativa del fitoplancton a las condiciones de afloramiento. El máximo ritmo de incorporación específica de nitrato es una función de la concentración inicial de nitrato, pero el ritmo realmente alcanzado está a menudo por debajo del máximo debido a otros factores ambientales, e.g., mezcla a profundidad. Esto ocurre en el noroeste de Africa donde fuertes vientos inducen altos ritmos de afloramiento, pero no compensan el bajo contenido en nutrientes de las aguas de origen, provocado por la mezcla de fitoplancton hasta capas profundas.

Existen otros efectos directos de la concentración de nitrato sobre la fisiología del fitoplancton, incluyendo el aumento en el número de asimilación. En consecuencia, las respuestas del fitoplancton al aumento del aporte y concentración de nitratos deberían ser no-lineales y probablemente se aproximen a una relación exponencial.

INTRODUCTION

Recent investigations of major coastal upwelling systems of the world have indicated that there are consistent differences between areas in the magnitude and seasonal distribution of biological production (Codispoti et al. 1982). Although some of these differences are due to the persistence and intensity of upwelling, the depth of the mixed layer, and the presence of an undercurrent on the shelf, the primary variable is the vertical flux of inorganic nutrients (Barber and Smith 1981). In this paper I will discuss how nutrient flux and nutrient concentration, especially nitrate, affect the magnitude and patterns of biological production in coastal upwelling systems.

Source waters for upwelling, usually from depths of 200 m or less (Barber and Smith 1981), show differences in nutrient concentration as a result of oceanic circulation patterns. For example, the North Atlantic is notably poor in nutrients because there are more exports than imports across the equator (Redfield et al. 1963). These differences in source-water concentration are reflected in the reported values of the maximum surface nitrate concentration (Table 1). These

TABLE 1
High Nutrient Concentrations Observed at the Surface in Different Upwelling Regions*

Region	Reference	NO_3^- µg-at.l^{-1}	$PO_4^=$ µg-at.l^{-1}	Diss. Si µg-at.l^{-1}	
Aleutian Islands 53°N, 170°W	Hood and Kelley (1976)	30	2.5	70	
Coastal Peru 15°S	Hafferty et al. (1978)	27	2.2	22	Sta. 207
		21	2.2	31	Sta. 344
Somali coast north of 10°12′N	Smith and Codispoti (1979)	20	1.6	16	
N.W. Africa 22°N	Friebertshauser et al. (1975)	12	1.0	7	Sta. 14
		11	1.0	8	Sta. 161
Mediterranean Sea 43°N, 5°E	Minas (1968)	—	0.1	—	
Pt. Conception, Calif.	OP1, Hydro† (1981)	32	2.4	33	Sta. 123
Pt. Conception, Calif.	OP2, Hydro† (1983)	21	2.7	27	Sta. 78

*Modified from Codispoti (1984)
†Unpublished data reports

range from 32 µg-at.l^{-1} at Point Conception down to 11 at 22°N in northwest Africa (or even to 0 in the Mediterranean Sea). The range of dissolved silicon concentration maxima is even greater, from 70 µg-at.l^{-1} in the Aleutian upwelling to 7 in northwest Africa. The depth of upwelling source water varies with wind stress and other factors such as the depth of the pycnocline near the coast. The upper pycnocline is deficient in dissolved silicon relative to nitrate as a result of the slower regeneration of silicon (Dugdale 1972). During weak upwelling, when the source water comes from the upper part of the pycnocline (Dugdale 1983), dissolved silicon tends to be low relative to nitrate. Dissolved silicon is likely to play a major role in species concentration and diatom production in upwelling systems. However, the remainder of this paper will deal with the effects of nitrate.

EQUIVALENCE OF NITRATE FLUX AND NEW PRODUCTION

Although nitrogen may not always be the limiting primary nutrient for productivity of marine phytoplankton, ^{15}N can be used as a tracer to follow the partitioning of nitrogen during biological use and regeneration, and to evaluate the components of the phytoplankton production cycle.

Nitrate uptake is considered as a measure of "new production" (Dugdale and Goering 1967) or potential yield—the amount of production that can be removed from the system without causing its collapse—whereas uptake of ammonium and certain other organic-N compounds such as urea represent the "regenerated" or circulating nitrogen. Together these make up the "total" or primary production. Carbon fixation, the more common measure of primary production, is therefore based upon both new and regenerated nitrogen.

In an eastern boundary upwelling system, the vertical motion of the water near the coast feeds nitrate into the euphotic zone (Wooster and Reid 1963). The resulting rate of new production can be calculated with suitable assumptions from estimates of the vertical velocities and the nitrate concentration of the source water, as Andrews and Hutchings (1980) have done for the Cape Upwelling region of South Africa. In a similar way, it can be predicted, for a given vertical velocity during upwelling, that the new production at 15°S, Peru, would be about twice that of the upwelling center at northwest Africa, as a consequence of the low levels of nutrients of the North Atlantic (Table 1).

The resultant potential yield or new production enters the ecosystem, and a portion is regenerated through grazing and excretion of ammonium and organic nitrogen compounds (mainly urea; McCarthy 1972) by zooplankton and other heterotrophic members of the food web. This serves to support a higher rate of primary production than would nitrate alone. The regenerated production that occurs when these nitrogen compounds are taken up may constitute up to 50% of the total nitrogen production in upwelling regions (Table 2). Under these conditions, for each unit of nitrate upwelled, one unit of ammonium (plus some organic nitrogen) is maintained in the regeneration cycle between phytoplankton and grazers. This

TABLE 2
Mean Values of Nitrate and Ammonium Uptake Parameters for a Series of Cruises to Upwelling Regions

Region	Cruise	Nitrate product. (mgat/m²/d)	Ammonium product. (mgat/m²/d)	Total N product. (mgat/m²/d)	Nitrate product. (%)	$V_{max}NO_3^-$ (/h)	$V_{max}NH_4^+$ (/h)	Z_m mixed layer depth[a] (m)
Peru	Anton Bruun-15	—	—	—	—	0.0367	0.0167	12
	Pisco	30	10	40	75	0.0358	0.0172	13
Africa	JOINT-I	15.2	6.6	21.8	70	0.0192	0.0139	38
	CINECA-Charcot II	10.6	9.7	20.3	52	0.0221	0.0139	—

[a] Examples of the mixed-layer depths encountrered when the nitrogen uptake data were taken. They may differ from the depths that would be obtained from an examination of all the stations taken during each cruise.

Modified from Codispoti et al. (1982)

regenerated nitrogen thus amplifies the effect of nutrient concentration and results in a twofold increase in total nitrogen production and accompanying carbon production, but not overall yield.

The effect of increasing nutrient concentration of upwelled water on different components of the production cycle can be evaluated and then used to compare different areas. In northwest Africa, for each unit of nitrate upwelled and entering the euphotic zone there will be one unit supplying new production and one unit entering regenerated production, resulting in two units of total production. However, in Peru the nitrate concentration is doubled, and hence four units of total production result. Therefore, upwelling in the Pacific eastern boundary regions should show a total primary production two times greater than the same upwelling rate would give in North Atlantic eastern boundary situations, only because of the source water's larger nutrient concentrations. In the North Atlantic, the effect of low source-water concentration could be offset by a twofold relative increase in upwelling velocity. However, high wind stress that creates high upwelling rates also results in strong mixing. Consequently, the phytoplankton encounter decreased mean irradiance (Huntsman and Barber 1977), and productivity remains relatively low. Wind stress in northwest Africa during the JOINT I study was about three times higher than in Peru during JOINT II, 1977 (Smith 1981). The mean specific nitrate uptake rates (uptake per unit phytoplankton biomass) were lower in northwest Africa than in Peru (Table 2); a similar effect was observed by Huntsman and Barber (1977). Consequently, the integrated nitrate production for northwest Africa was half that of Peru (Table 2), despite the higher African upwelling rate, because of a combination of mixing and nitrate concentration of the source water.

EFFECT OF NITRATE CONCENTRATION ON PHYTOPLANKTON PHYSIOLOGY

Nitrate input and concentrations in the euphotic zone may also influence carbon processes more directly. When newly upwelled phytoplankton appear at the surface in an upwelling center, nitrate uptake per cell is initially low, but increases over a period of several days as adaptation to the high-irradiance, high-nutrient conditions takes place (MacIsaac et al. 1985). Carbon-related processes increase at a much slower rate during this initial period. The maximum rate of nitrate uptake achieved occurs just before nutrient limitation sets in. High nutrient concentrations postpone the onset of nutrient limitation. So high concentrations of nitrate in source water tend to lead to high maximal specific nitrate uptake rates. In Table 3, the maximum specific nitrate uptake rates for Peru can be seen to be about two times those for northwest Africa. Nutrient concentration, perhaps dissolved silicon (as in the 1977 JOINT II cruise), may affect the rate at which nitrate uptake increases, as well as the final rate achieved (MacIsaac et al. 1985). The effect of high nitrate concentrations on the maximum rate of uptake will certainly influence the length of the production cycle and consequently the spatial distribution of the phytoplankton produced from upwelled nitrate.

Nitrate concentration affects photosynthetic processes too, although the carbon-related changes from upwelling tend to occur later than the nitrogen processes (MacIsaac et al. 1985). Assimilation number, i.e., carbon fixed per unit chlorophyll at optimum irradiance, increases sharply when nitrate concentrations rise to about 10 μg-at.l^{-1} in eastern boundary upwelling (Minas et al. 1982); the data include measurements in northwest Africa and show that high assimilation numbers do not generally occur there, perhaps because of the generally low nutrient concentrations at

TABLE 3

Maximum and Minimum Values of V_{max} for Nutrient-Saturated Uptake of Nitrate and Ammonium in the Upper Euphotic Zone[a] from a Series of Cruises to Upwelling Regions

		V_{max} NO_3^- (/h)		V_{max} NH_4^+ (/h)	
Region	Cruise	min	max	min	max
Peru	Anton-Bruun	0.0170	0.0547	0.0129	0.0222
	Pisco	0.0089	0.0595	0.0268	0.0358
Northwest Africa	JOINT-1	0.0028	0.0329	0.0046	0.0261

[a] Defined here as the 100% to 30% light-penetration zone. Most values are from the 50% light depth.

Modified from Codispoti et al. (1982)

the surface during upwelling. Yet in South African coastal upwelling with higher nutrient concentrations characteristic of the south Atlantic subsurface waters, high assimilation numbers also occur (Andrews and Hutchings 1980). Results from the OPUS 1983 studies at Point Conception (unpublished) show a similar trend.

SUMMARY

A series of nonlinear positive relationships between nutrient (and especially nitrate) concentration and input and processes leading to phytoplankton production occur in upwelling regions. These relationships will lead to a more or less exponential rise in productivity as nitrate input and concentration rise. Eppley et al. (1979) found such a relationship between primary production and the proportion of nitrate uptake in southern California waters, and constructed a curve connecting Peru upwelling and the North Pacific Gyre that successfully spanned their data. Presumably, the factors discussed here are at least partially responsible for the nature of this relationship. Additional analysis of existing and future data sets from eastern boundary upwelling regions should help to refine these patterns and explain the key role of nutrients in limiting production processes in upwelling regions.

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ANCHOVY EGG DISPERSAL AND MORTALITY AS INFERRED FROM CLOSE-INTERVAL OBSERVATIONS

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> *Kiil.* Millions of tons of water come down that river. How do you know the day you made your tests there wasn't something unusual about the water?
>
> *Stockman.* No, I took too many samples.
>
> *Kiil.*How do you know? Why couldn't those little animals have clotted up only in the patch of water you souped out of the river? How do you know the rest of it wasn't pure?
>
> *Stockman.* It's not probable . . . .
>
> *An Enemy of the People*[1]

ABSTRACT

The oceanic boundary currents and continental borderlands that anchovy inhabit comprise diverse spatial and temporal scales of motion. Repetitive sampling at close intervals has been conducted to explore the sources and intensity of variance of observations and maximize the effectiveness of a management-oriented sampling program. The critical scale of repetitive sampling occurs when adjacent observations are so interdependent that they do not improve the precision of the abundance estimates. Sampling studies indicate that the scale of anchovy egg interdependence is on the order of several hundred meters for some days and somewhat less than this in the first few hours after spawning. Spatial correlation appears to diminish rapidly at scales larger than 2,000 m. The minimum distance between stations in the California egg production cruises is 7,500 m; in the Peru egg production survey it was 5,500 m.

In general, large structures in the ocean persist longer than small ones. One simple parameterization of this phenomenon is that a 600-m structure persists for 6 hours in the ocean and that structures of 2,800, 27,000, 147,000 m persist for a day, a week, and a month, respectively. From simple considerations, if the average value of food abundance is too low for larval fish to survive, the useful scale of oceanic feature that contains sufficient food is about 27 km if the food is required for a week, or 147 km if the food is required for a month. The critical scale of these features becomes smaller if production within the structure exceeds consumption and washout. The influence of persistence on survival may diminish as juveniles gain the ability to graze in schools and swim through larger intervening distances between favorable patches. We believe that experimental repetitive sampling supports the general scale for the passive dispersion of eggs: no obvious interrelations between interannual changes in these features and egg and larval survival were noted for the first 20 days of life. The consequences of a laterally incoherent and dissipated habitat may be delayed to the late larval and juvenile stages.

Will we be able to observe the later life stages with the same intensity and accuracy that we have observed the embryonic stages?

RESUMEN

Las corrientes oceánicas de margen y los aledaños continentales que habita la anchoveta sufren movimientos de diferentes escalas temporales y espaciales. Se condujeron muestreos replicados a intervalos reducidos con el fin de explorar las fuentes e intensidad de la varianza de las observaciones y maximizar la eficacia de un programa de muestreo orientado hacia el manejo del recurso. La escala crítica del muestreo repetitivo ocurre cuando las observaciones adyacentes son tan interdependientes que no aumentan la precisión de las estimaciones de abundancia. Muestreos experimentales indican que la escala de interdependencia para los huevos de la anchoveta es del orden de varios centenares de metros durante algunos días, y algo menor en las primeras horas después del desove. La correlación espacial parece disminuir rápidamente a escalas mayores de 2000 m. La distancia mínima entre estaciones en las campañas californianas de producción de huevos es de 7500 m; en los estudios peruanos de producción de huevos era de 5500 m. En general, las estructuras oceánicas mayores son más persistentes que las pequeñas. Una expresión cuantitativa sencilla de este fenómeno consiste en que estructuras de 600 m persisten en el océano durante 6 horas, mientras que aquéllas de 2,800, 27,000 y 147,000 m persisten durante un día, una semana, y un mes, respectivamente. Partiendo de consideraciones simples se deduce que si la abundancia promedio de alimento es demasiado baja para la supervivencia de las larvas

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[1] Henrik Ibsen. *An Enemy of the People.* An adaptation for the American stage by Arthur Miller. Dramatists Play Service, Inc., New York, 1951.

de peces, la escala útil de la estructura oceánica que contiene alimento suficiente es de, aproximadamente, 27 km, si el alimento es requerido para una semana, o 147 km si lo es para un mes. La escala crítica de estas características disminuye si la producción dentro de la estructura excede al consumo y la exportación. La influencia de esta persistencia en la supervivencia puede disminuir a medida que los juveniles van adquiriendo la capacidad de alimentarse en cardúmenes y de nadar distancias mayores entre lugares favorables. Creemos que el muestreo repetitivo experimental concuerda con la escala general de dispersión pasiva de los huevos: no se observaron interrelaciones obvias entre cambios interanuales en estas características y la supervivencia de huevos y larvas durante los primeros 20 días de vida. Las consecuencias de un hábitat lateralmente incoherente y disipado pueden ser pospuestas hasta los estados larvales avanzados y los juveniles.

¿Podremos observar los estados de desarrollo tardíos con al misma intensidad y precisión con que observamos los estados embrionarios?

INTRODUCTION

Demands on oceanic sampling have rapidly increased from the simple detection and description of resources (Ahlstrom 1968; Hempel 1973; Smith and Richardson 1977) to the testing of hypotheses on the causes of recruitment failure in dynamic coastal areas like the California Current (Lasker 1975; Vlymen 1977; Parrish and MacCall 1978; Lasker and Zweifel 1978; Parrish et al. 1981; Smith 1981; Hewitt 1981; Bakun and Parrish 1982). Smith (1981) described sampling strategies for testing several hypothesized sources of year-class failure; the sources include larval transport, critical period, predation including cannibalism, starvation, unfavorable distribution pattern, and parental deficiencies at the time of spawning. Success in the studies underway have encouraged international organizations (Bakun et al. 1982) to compare dynamic areas like the eastern boundaries of the oceans off South America and Africa with respect to the causes of massive fluctuations in fish reproductive success. These studies require additional work on efficient delineation of distribution and biomass estimation. Because of the nature of the survival mechanisms postulated, directed work on spatial pattern, turbulent diffusion, transport, and survival is also needed.

The spatial pattern of plankton may be considered from the aspects of interpreting existing samples and the strategy of future sampling (Silliman 1946; Sette and Ahlstrom 1948; Taft 1960; Zweifel and Smith 1981). Another aspect of spatial pattern of plankton is the interaction between predator and prey, in particular where food aggregations are necessary for sufficient feeding rates (Lasker 1975; Vlymen 1977; Lasker and Zweifel 1978; Hewitt 1981). Lastly, schooling coastal pelagic fishes proceed through a planktonic phase of weeks to months, and the eventual retention of viable concentrations of juveniles near the coast may be controlled by rates of turbulent diffusion and cross-shelf transport during the spawning season (Smith 1973; Smith and Lasker 1978; Parrish and MacCall 1978; Hewitt 1982; Bakun and Parrish 1982; Smith 1985).

The scale of spatial pattern contains additional information about the recent history and near future of the pelagic aggregation. For example, if individual (0.3 m) spawning pelagic fish like sardines are found in populations (1,000 km), school groups (10 km), schools (100 m), and spawning "cliques" (30 m), one can infer from the rate of dispersal by turbulent diffusion that the major sources of variance in samples are from individuals, cliques, and schools rather than from school groups and populations based on the length-scale assumptions (Smith 1973). Since this pattern of eggs imposed by the spawning and fertilization behavior of the adults persists several days into the larval stage, one may postulate that similar features like diatom patches or grazed gaps in diatom layers would persist equally long in the pelagic environment (Okubo 1971).

It is the purpose of this symposium to explore similarities among the eastern boundary areas of the world oceans, because these contain the potential of tens of millions of tons annual catch of schooling coastal pelagic engraulids, clupeids, scombrids, and carangids. These fisheries are generally not managed and are subject to large natural fluctuations, which seem to be augmented by present fishing practices (Murphy 1977; Smith 1981; Bakun and Parrish 1982; Lasker 1985; Smith 1985). Our objective in this paper is to present a small-scale empirical study of anchovy egg dispersal in a coastal site. The study may then be considered in the context of large-scale environmental features and biological surveys. We believe that existing techniques can be modified to measure offshore drift and dispersal within the coastal habitat and thus describe the habitat of schooling coastal pelagic fish in eastern boundary habitats.

METHODS

The methods used for close-interval sampling of the anchovy population off California are described in detail in Lasker (1984), Smith and Hewitt (1984), Smith, Flerx, and Hewitt (1984) and Moser and Ahlstrom (1984). We will only briefly describe the planning and conduct of the cruise, station activity, the

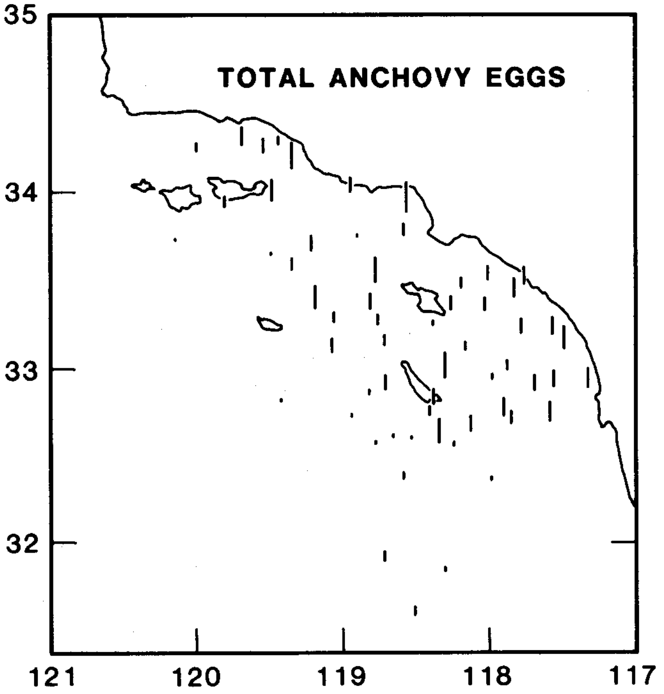

Figure 1. The survey area off southern California. Ordinate values are degrees north latitude, and the abscissa values are degrees west longitude. The lengths of the bars are proportional to the log of the number of anchovy eggs per 0.05 square meters as an average of eight replicates at each station. (See Table 5 for data.)

net, the procedures for sorting, staging and aging the eggs, and the data analysis.

Cruise

The cruise was planned to encompass the spawning habitat of the central population of the northern anchovy (*Engraulis mordax*) with groups of eight samples at stations 20 miles apart in the cross-shelf direction and 40 miles apart parallel to the general run of the coast. Unfortunately, the 25-m motor vessel (*Scorpius*) chartered for this cruise was not competent to occupy the preplanned stations in the weather of January 1979; therefore, stations in the general area of the spawning were occupied at haphazard positions that could be approached from safe harbors among the islands of the Southern California Bight. The stations that had at least one egg in eight tows are plotted in Figure 1 as "sticks" with height proportional to the log of the mean number of total anchovy eggs per observation.

On station we recorded position, cast a 10-m Nansen bottle with reversing thermometer to estimate the temperature, and made eight vertical plankton tows to a wire length of 70 m and back. The positions, date, and time of arrival at the station and the 10-m temperature are listed in Appendix Table 1. To maintain position on the station (relative to the water) as closely as possible, the officers of the vessel were instructed to keep the 45-kg weight on 10-m, 3/16" cable vertical between casts and tows for the entire duration of the station. The usual interval between vertical tows was 12 minutes, but occasionally repeat tows and delays between tows lengthened that period. The distribution of intervals between adjacent tows is depicted in a histogram in Appendix Table 2; this average interval will be used to interpret all tows.

The Tow

Of the 12 minutes between the initiation of tows, 3-5 minutes were involved with lowering and raising the net, another 5 minutes was required to wash the net and concentrate the sample in the cod end, and 4-5 minutes was needed to preserve the sample in Formalin and label the sample bottle. The winch on the charter vessel was incapable of obtaining the 70-m-per-minute towing rate specified for the project, and rates were commonly in the range of 25 to 40 m per minute.

The plankton net was based on the original design of anchovy egg net (Smith et al. 1968) and modified for vertical towing (Hewitt 1983; Smith et al. 1984). As the original net in the vertical tow series, it differed from the present design by being a single net, with mesh aperture area of 0.333-mm nylon mesh. The mesh-aperture-to-mouth-aperture ratio was 8.7:1, of which 35% was in the terminal conical portion of the net and 65% was in the cylindrical portion to reduce length and facilitate self-cleaning under tow. Nets were washed from the outside by a moderate rate of flow.

Laboratory Work

Anchovy eggs were sorted from samples with a dissecting microscope at a magnification of about 10 × (Kramer et al 1972; Smith and Richardson 1977). The sorted eggs were subsequently staged using criteria of Moser and Ahlstrom (1984). Ages were estimated from the temperature-specific stage development rate (Ahlstrom 1943; Zweifel and Lasker 1976; Lo 1984), the actual time of tow, and the 10-m temperature on the station.

Data Analysis

Descriptive statistics were performed on the UCSD-VAX using Minitab. A correlation matrix on all ages of egg for all 60 tows was performed, yielding 7 correlation coefficients for adjacent columns, 6 for tows 24 minutes apart, 5 for tows 36 minutes apart, etc. Negative binomial parameter estimates were accomplished using the iterative techniques described in Southwood (1978). The BASIC program implemented on the UCSD-VAX to estimate the negative binomial parameters is listed in the Appendix.

TABLE 1
Replicate Observations of Anchovy Eggs < One Day Old

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
1	1	2	4	9	23	3	15	64	15.125
2	0	0	1	0	0	0	1	0	0.250
3	0	0	0	0	0	2	3	17	2.750
4	4	5	0	8	7	8	10	12	6.750
5	0	0	0	0	0	0	0	0	0.000
6	4	2	7	0	0	0	0	0	1.625
7	0	0	0	0	0	0	0	0	0.000
8	1	0	0	0	0	0	0	0	0.125
9	0	0	0	0	0	0	0	0	0.000
10	0	0	0	0	0	0	0	0	0.000
11	1	0	0	0	1	0	1	0	0.375
12	0	0	0	0	1	3	0	5	1.125
13	0	0	0	0	0	0	0	0	0.000
14	0	0	0	0	0	0	0	0	0.000
15	30	39	51	0	0	0	0	0	15.000
16	0	0	0	0	0	0	0	0	0.000
17	0	0	0	0	0	0	0	1	0.125
18	0	0	0	0	0	0	0	0	0.000
19	13	6	20	6	4	6	0	0	6.875
20	0	0	0	0	0	0	0	0	0.000
21	0	0	0	0	0	0	0	0	0.000
22	0	0	0	0	0	0	0	0	0.000

RESULTS

We will consider three aspects of the data. The first will be the data set itself. Secondly, we will describe the data and a possible probability-generating distribution from which it may have been drawn. Thirdly, we will consider one interpretation of the change of the data with time.

The Data Set

The data set consists of four ages of egg, and the distribution of total eggs. The four ages of egg are those eggs less than 8 hours old, 1 day old, 2 days old, and 3 days old. These sets are from the same 8 replicates of 60 observations containing at least one anchovy egg per station.

Eggs produced in the first 8 hours after the onset of spawning are considered separately in the analysis of egg production because incidence and abundance are underestimated. (Smith and Hewitt 1984) In Table 1, it may be seen that of the 60 samples considered, only 22 were in the initial 8-hour period. In no case does a large sample observation continue across the entire set of eight observations on the station. For example, in row 1, replicates 5, 7, and 8 indicate that the ship drifted into a patch, whereas rows 15 and 19 indicate that the ship drifted out of a patch.

The chief difference for one-day-old eggs (Table 2) is that in most observations, the set of replicates is usually taken entirely within or outside of a patch. There are still instances, such as row 49, that indicate drifting out, but most show moderate changes within replicates on station. There are no visible differences in Tables 3 or 4 from Table 2 in terms of continuity of observations on station.

TABLE 2
Replicate Observations of Anchovy Eggs One Day Old

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
1	3	3	3	6	2	2	1	3	2.875
2	2	1	3	4	3	3	0	5	2.625
3	8	5	7	7	6	10	5	13	7.625
4	0	0	0	0	0	0	0	0	0.000
5	0	0	0	0	0	0	0	0	0.000
6	0	1	2	0	4	2	1	2	1.500
7	12	10	10	6	5	3	4	6	7.000
8	5	1	6	6	4	2	10	5	4.875
9	0	0	0	2	0	0	0	1	0.375
10	0	0	0	0	0	0	0	0	0.000
11	9	3	2	2	0	0	3	0	2.375
12	12	23	12	4	7	5	7	5	9.375
13	0	1	0	2	3	3	1	1	1.375
14	0	1	0	0	1	2	0	0	0.500
15	2	5	2	3	0	1	2	0	1.875
16	6	8	3	6	2	6	4	5	5.000
17	3	3	1	2	3	2	0	4	2.250
18	2	0	1	0	1	2	2	2	1.250
19	18	26	21	33	21	32	22	23	24.500
20	0	0	0	0	0	0	0	0	0.000
21	1	3	3	3	2	0	1	0	1.625
22	2	2	9	5	4	4	9	8	5.375
23	0	1	1	1	0	1	3	1	1.000
24	0	0	0	0	0	0	0	0	0.000
25	0	0	0	0	0	0	0	0	0.000
26	0	0	0	0	0	0	0	0	0.000
27	1	0	0	1	0	4	5	1	1.500
28	2	1	0	0	0	0	1	1	0.625
29	4	2	5	0	3	3	0	4	2.625
30	15	5	13	16	10	13	12	6	11.250
31	14	12	11	11	9	7	8	5	9.625
32	0	0	2	1	0	0	0	0	0.375
33	0	0	0	0	0	0	0	0	0.000
34	0	0	0	1	0	0	1	0	0.250
35	2	0	0	1	0	1	0	0	0.500
36	1	2	0	3	0	0	0	0	0.750
37	0	0	0	0	0	0	1	0	0.125
38	17	11	22	26	37	27	20	30	23.750
39	5	8	12	4	6	4	3	3	5.625
40	3	2	3	2	0	3	3	1	2.125
41	0	1	0	2	2	0	0	1	0.750

(continued)

TABLE 2 (continued)

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
42	0	0	0	0	0	0	0	0	0.000
43	0	1	0	0	0	0	0	1	0.250
44	1	4	0	3	5	3	4	3	2.875
45	7	4	4	1	3	2	2	3	3.250
46	0	0	0	0	0	0	0	1	0.125
47	1	1	2	1	1	3	1	5	1.875
48	0	0	0	0	0	0	0	0	0.000
49	3	22	3	0	0	0	0	0	3.500
50	0	0	0	0	0	0	0	0	0.000
51	0	0	1	0	0	0	0	0	0.125
52	0	0	0	0	0	0	0	0	0.000
53	0	0	0	0	0	0	0	0	0.000
54	5	4	3	0	3	2	2	3	2.750
55	0	0	1	0	2	0	0	0	0.375
56	1	2	3	2	4	3	3	4	2.750
57	64	65	64	63	48	82	54	48	61.000
58	1	0	0	2	1	1	5	3	1.625
59	11	20	5	20	20	12	22	18	16.000
60	5	10	8	5	5	7	4	7	6.375

TABLE 3
Replicate Observations of Anchovy Eggs Two Days Old

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
1	0	1	0	1	0	2	1	1	0.750
2	0	2	0	1	1	1	1	1	0.875
3	0	1	2	0	1	1	0	1	0.750
4	2	0	2	1	1	0	2	1	1.125
5	0	2	1	1	3	0	1	3	1.375
6	3	5	5	6	8	15	14	12	8.500
7	2	2	0	4	2	2	1	0	1.625
8	6	12	11	8	12	9	10	9	9.625
9	0	0	0	0	0	0	0	0	0.000
10	0	0	0	0	0	0	0	0	0.000
11	0	0	0	0	0	1	0	0	0.125
12	0	0	0	0	0	0	0	0	0.000
13	1	1	3	0	0	0	3	2	1.250
14	2	3	5	0	6	7	4	10	4.625
15	1	2	2	0	4	2	1	2	1.750
16	5	2	6	2	2	1	3	2	2.875
17	0	0	0	2	4	4	4	4	2.250
18	1	1	2	0	1	1	1	2	1.125
19	6	14	11	12	12	9	5	9	9.750
20	1	2	2	1	0	3	1	1	1.375
21	7	5	7	2	2	5	1	5	4.250
22	26	32	46	30	17	9	14	13	23.375
23	1	2	2	2	0	0	2	0	1.125
24	0	0	0	0	0	0	0	1	0.125
25	0	0	0	1	0	0	0	0	0.125
26	0	0	0	0	1	0	0	0	0.125
27	1	0	6	4	2	2	10	3	3.500
28	3	2	6	4	1	0	3	6	3.125
29	34	35	40	30	36	39	35	35	35.500
30	7	3	1	2	3	4	1	7	3.500
31	22	10	13	11	15	21	9	12	14.125
32	3	3	2	3	3	3	3	0	2.500
33	0	0	0	0	0	0	0	0	0.000
34	4	1	1	3	1	0	0	0	1.250
35	0	0	0	0	0	0	0	0	0.000
36	0	1	0	0	0	0	0	0	0.125
37	2	0	1	0	0	0	0	0	0.375
38	5	4	3	15	21	15	9	13	10.625
39	0	0	0	0	0	0	0	0	0.000
40	3	3	1	0	2	0	2	3	1.750
41	0	0	0	0	0	0	0	0	0.000
42	1	0	0	0	0	0	0	0	0.125
43	1	1	0	1	0	0	1	2	0.750
44	4	4	9	5	2	8	2	11	5.625
45	0	0	0	0	0	3	2	2	0.875
46	0	0	0	0	0	0	1	1	0.250
47	39	21	39	21	18	48	16	22	28.000
48	0	0	0	0	0	1	0	0	0.125
49	0	2	1	0	2	0	2	0	0.875
50	6	4	4	10	7	4	8	5	6.000
51	2	4	6	4	1	2	4	2	3.125
52	0	0	0	0	0	0	0	0	0.000
53	0	0	0	0	0	0	0	0	0.000
54	27	22	21	0	8	11	4	4	12.125
55	0	0	0	0	0	0	0	0	0.000
56	22	14	6	9	6	4	6	1	8.500
57	96	117	94	89	84	119	111	91	100.125
58	12	3	9	6	3	4	5	9	6.375
59	8	6	2	4	4	2	9	5	5.000
60	1	5	6	4	4	5	12	10	5.875

Table 5 contains the values for all ages of anchovy egg within each station set. At these temperatures, one may expect three ages of egg within close proximity. In this set, only rows 33, 52, and 53 had none of the three ages identified: row 10 had neither one- nor two-day-old eggs, row 35 had neither two- nor three-day-old eggs, and rows 24, 26, 42, and 50 had neither one- nor three-day-old eggs.

In summary, there is coherence among the replicate stations of anchovy eggs older than eight hours. This indicates that the scale of the pattern is large relative to the drift of the research vessel and the layers of water below over periods of one to two hours.

TABLE 4
Replicate Observations of Anchovy Eggs Three Days Old

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
1	0	0	0	0	0	0	0	0	0.000
2	0	0	0	0	0	0	0	0	0.000
3	3	4	4	2	1	3	0	2	2.375
4	1	0	4	3	3	1	0	2	1.750
5	3	4	5	4	4	4	1	11	4.500
6	3	0	2	1	2	2	2	2	1.750
7	2	6	9	4	3	3	3	2	4.000
8	1	1	5	2	3	5	5	5	3.375
9	0	0	0	0	0	0	0	0	0.000
10	0	0	0	0	0	0	0	1	0.125
11	5	4	0	3	1	1	4	9	3.375
12	9	11	8	5	8	1	5	5	6.500
13	1	2	2	1	1	3	3	2	1.875
14	2	4	5	3	2	7	2	4	3.625
15	1	0	1	0	0	0	0	1	0.375
16	8	5	3	5	10	6	8	3	6.000
17	9	3	3	0	1	0	1	1	2.250
18	1	0	3	0	1	0	3	0	1.000
19	17	16	15	20	10	10	11	5	13.000
20	4	5	8	4	3	7	5	2	4.750
21	13	7	6	4	9	7	7	3	7.000
22	24	16	16	10	8	9	4	6	11.625
23	1	3	1	2	0	4	1	2	1.750
24	0	0	0	0	0	0	0	0	0.000
25	0	3	0	0	0	0	0	0	0.375
26	0	0	0	0	0	0	0	0	0.000
27	5	0	9	6	6	5	11	10	6.500
28	1	1	0	1	1	0	1	0	0.625
29	21	17	15	23	14	11	14	17	16.500
30	20	6	18	22	9	11	3	9	12.250
31	6	4	5	4	5	2	7	1	4.250
32	1	0	0	1	0	1	1	0	0.500
33	0	0	0	0	0	0	0	0	0.000
34	0	0	1	0	0	1	0	0	0.250
35	0	0	0	0	0	0	0	0	0.000
36	0	0	0	0	0	0	0	0	0.000
37	0	1	1	1	1	0	0	0	0.500
38	3	4	5	4	3	2	4	5	3.750
39	0	0	0	0	0	0	0	0	0.000
40	0	0	0	1	0	0	1	1	0.375
41	0	0	0	0	0	0	0	0	0.000
42	0	0	0	0	0	0	0	0	0.000
43	4	8	4	7	8	5	3	11	6.250
44	2	5	5	2	5	5	6	12	5.250
45	0	1	0	0	1	0	2	2	0.750
46	0	0	0	0	2	1	2	0	0.625
47	25	29	32	43	41	53	52	45	40.000
48	1	2	4	1	0	1	1	0	1.250
49	1	1	0	0	0	0	0	0	0.250
50	0	0	0	0	0	0	0	0	0.000
51	61	69	75	84	76	62	61	68	69.500
52	0	0	0	0	0	0	0	0	0.000
53	0	0	0	0	0	0	0	0	0.000
54	10	10	12	0	5	8	2	5	6.500
55	120	86	119	107	136	114	104	102	111.000
56	0	0	0	0	0	0	0	0	0.000
57	22	26	16	34	16	28	42	26	26.250
58	1	2	2	6	1	5	3	3	2.875
59	3	8	5	2	6	3	3	3	4.125
60	7	12	12	14	9	12	15	17	12.250

TABLE 5
Replicate Observations of Anchovy Eggs All Ages Plus Disintegrated

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
1	4	6	7	16	25	7	17	68	18.750
2	2	3	3	5	4	4	1	6	3.500
3	14	11	13	10	8	14	5	16	11.375
4	4	0	8	5	4	1	4	3	3.625
5	3	6	6	6	7	4	2	14	6.000
6	6	6	9	7	14	19	17	16	11.750
7	16	18	19	14	10	10	11	25	15.375
8	17	19	22	24	26	24	35	31	24.750
9	0	0	0	2	0	0	0	1	0.375
10	0	0	0	0	0	1	0	2	0.375
11	15	7	2	5	1	2	7	10	6.125
12	21	34	21	9	16	5	12	10	16.000
13	2	4	7	4	4	11	8	8	6.000
14	4	8	10	3	9	16	6	14	8.750
15	4	7	5	4	4	3	3	3	4.125
16	19	15	12	13	14	13	15	10	13.875
17	19	9	13	7	15	7	5	11	10.750
18	9	9	18	12	8	13	10	7	10.750
19	56	74	63	74	53	64	48	44	59.500
20	6	7	12	6	3	11	7	3	6.875
21	22	15	16	9	13	12	9	8	13.000
22	57	58	76	50	32	27	30	30	45.000
23	2	6	7	5	0	10	7	4	5.125
24	0	0	0	0	0	0	0	1	0.125
25	1	3	0	2	0	0	0	0	0.750
26	0	0	0	0	1	0	0	0	0.125
27	8	14	15	11	9	11	27	14	13.625
28	9	6	6	5	3	0	6	7	5.250
29	59	54	60	54	53	54	50	58	55.250
30	42	15	32	37	22	28	20	22	27.250
31	42	26	29	26	30	33	24	23	29.125
32	4	3	5	6	4	4	4	5	4.375
33	3	0	0	2	1	0	1	0	0.875

(continued)

TABLE 5 (continued)

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
34	4	1	2	4	1	1	1	0	1.750
35	2	0	0	1	0	1	0	0	0.500
36	1	3	0	3	1	4	3	2	2.125
37	2	1	2	1	1	0	1	0	1.000
38	56	58	81	48	64	49	34	50	55.000
39	5	8	12	4	6	4	3	3	5.625
40	6	5	4	3	2	3	6	6	4.375
41	0	1	0	2	2	0	0	1	0.750
42	1	0	0	0	0	0	0	0	0.125
43	5	10	4	8	8	5	4	14	7.250
44	7	13	14	10	12	16	12	26	13.750
45	20	11	24	7	8	11	6	7	11.750
46	0	1	2	1	2	3	4	2	1.875
47	66	52	73	65	60	104	72	73	70.625
48	1	2	4	1	0	2	2	0	1.500
49	4	25	4	4	8	4	4	1	6.750
50	6	4	4	10	7	4	8	5	6.000
51	63	73	82	88	77	64	65	70	72.750
52	1	0	0	0	0	0	0	0	0.125
53	0	0	1	0	0	0	0	1	0.250
54	47	39	43	1	18	23	9	13	24.125
55	120	87	122	109	138	116	104	102	112.250
56	23	16	9	11	10	8	10	6	11.625
57	182	208	174	187	148	229	208	165	187.625
58	15	6	11	16	8	10	13	16	11.875
59	29	39	13	27	31	20	37	29	28.125
60	13	27	27	23	19	24	32	34	24.875

Data Summary

Owing to the wide range of numbers of eggs per sample, Tables 6, 7, and 8 are divided into classes whose boundaries encompass factors of four rather than unit frequencies. The general appearance of similarity among the replicate sets above is confirmed in the data summary table and the parameters calculated from them. The primary difference among the distributions of the eight replicates and the distribution of the mean of eight is the lower threshold (0.125 rather than 1 per .05 m^2) for the mean of eight samples on a station. Whereas one would expect the mean of the means to be the same as the mean of the replicates, one would expect the variance of the observations to be eight times the variance of the means of eight; instead, the variance of the means of eight is indistinguishable from the variances of the individual sets for one-, two- and three-day-old eggs.

The estimates of the negative binomial factor k are the same from replicate to replicate and between the means of eight and the eight replicates (Tables 6, 7, and 8).Thus the estimation of the negative binomial parameters, mean, and k from small sets of observations with high variance is relatively robust when small sample sizes are used. Furthermore, the negative binomial k is well estimated from the fraction of zero observations, and even the "moments" estimate (from the mean and variance) is reasonably close to the others and relatively stable under these conditions.

The distribution of the total eggs (Table 9) differs

TABLE 6
Anchovy Egg Sample Frequency Distribution
One-Day-Old Eggs

	Replicate Number								
Eggs/0.05 m2	1	2	3	4	5	6	7	8	Mean
0	26	24	27	25	29	27	27	25	13
0.0625 – 0.25	—	—	—	—	—	—	—	—	3
0.25 – 1	—	—	—	—	—	—	—	—	10
1 – 4	17	19	18	19	15	20	17	17	20
4 – 16	14	12	12	11	12	10	12	14	10
16 – 64	2	4	2	5	4	2	4	4	4
64 – 256	1	1	1	—	—	1	—	—	—
Mean	4.1	4.6	4.1	4.3	3.9	4.3	3.8	3.9	4.1
Variance	83.5	99.0	85.9	97.8	70.7	136.9	69.1	64.2	81.4
Neg. binomial									
$k(0)$	.321	.274	.277	.260	.283	.269	.327	.285	.312
$k(1)$	.158	.195	.163	.157	.118	.145	.155	.170	.202
$k(2)$	.264	.256	.254	.217	.234	.237	.252	.244	.296

$k(0)$ is the parameter of the negative binomial distribution as estimated from the proportion of '0' values.
$k(1)$ is the parameter of the negative binomial distribution as estimated from the sample mean and variance ('moments' estimate).
$k(2)$ is the maximum likelihood estimator (Southwood 1966).

TABLE 7
Anchovy Egg Sample Frequency Distribution
Two-Day-Old Eggs

	Replicate Number								
Eggs/0.05 m2	1	2	3	4	5	6	7	8	Mean
0	24	22	24	27	24	26	20	22	10
0.0625 – 0.25	—	—	—	—	—	—	—	—	7
0.25 – 1	—	—	—	—	—	—	—	—	8
1 – 4	18	21	16	14	19	15	21	18	17
4 – 16	11	12	15	15	12	15	16	17	14
16 – 64	6	4	4	3	4	3	2	2	3
64 – 256	1	1	1	1	1	1	1	1	1
Mean	6.1	5.9	6.3	5.0	5.0	6.1	5.4	5.4	5.7
Variance	213.2	265.7	222.0	163.8	148.8	292.4	225.0	163.8	198.8
Neg. binomial									
k(0)	.299	.347	.295	.268	.329	.262	.417	.363	.318
k(1)	.180	.134	.184	.157	.174	.130	.133	.184	.157
k(2)	.248	.276	.255	.241	.301	.227	.327	.316	.280

k(0) is the parameter of the negative binomial distribution as estimated from the proportion of '0' values.
k(1) is the parameter of the negative binomial distribution as estimated from the sample mean and variance ('moments' estimate).
k(2) is the maximum likelihood estimator (Southwood 1966).

from that of any of the individual nights' spawning. In the individual age groups the frequency of observations decreases from the "0" class to the "64-256" eggs per observation class. In the total eggs observations, the frequency increases from the "0" class to the "4-16" class and then descends. Even when each station has at least one egg in eight samples, the number of observations with "0" eggs in each of the replicates varied from 10% to 18%.

We concluded that nearly uniform results would have been obtained from any set of replicates. Also, the frequency distribution of the total is a composite of the day-class observations and may in fact exhibit a different type of distribution when three days' egg

TABLE 8
Anchovy Egg Sample Frequency Distribution
Three-Day-Old Eggs

	Replicate Number								
Eggs/0.05 m2	1	2	3	4	5	6	7	8	Mean
0	22	25	24	25	24	25	23	24	15
0.0625 – 0.25	—	—	—	—	—	—	—	—	1
0.25 – 1	—	—	—	—	—	—	—	—	10
1 – 4	19	11	10	15	17	14	19	17	13
4 – 16	11	17	20	13	15	17	14	13	16
16 – 64	7	5	4	5	2	3	3	4	3
64 – 256	1	2	2	2	2	1	1	2	2
Mean	7.0	6.4	7.3	7.3	6.9	6.7	6.7	6.8	6.9
Variance	316.8	216.1	334.9	346.0	412.1	316.8	295.8	278.9	302.8
Neg. binomial									
k(0)	.321	.274	.277	.260	.283	.269	.327	.285	.283
k(1)	.158	.195	.163	.157	.118	.145	.155	.170	.157
k(2)	.264	.256	.254	.217	.234	.237	.252	.244	.257

k(0) is the parameter of the negative binomial distribution as estimated from the proportion of '0' values.
k(1) is the parameter of the negative binomial distribution as estimated from the sample mean and variance ('moments' estimate).
k(2) is the maximum likelihood estimator (Southwood 1966).

TABLE 9
Anchovy Egg Sample Frequency Distribution
All Ages Plus Disintegrated

	Replicate Number								
Eggs/0.05 m2	1	2	3	4	5	6	7	8	Mean
0	7	10	11	6	10	11	10	9	—
0.0625 – 0.25	—	—	—	—	—	—	—	—	4
0.25 – 1	—	—	—	—	—	—	—	—	7
1 – 4	12	9	6	12	11	9	9	12	7
4 – 16	21	24	25	27	23	23	25	20	26
16 – 64	17	13	12	10	12	12	12	14	12
64 – 256	3	4	6	5	4	5	4	5	4
Mean	19.1	18.9	20.1	17.8	17.1	18.5	17.1	18.3	18.4
Variance	979.7	1049.8	1049.8	1004.9	852.6	1303.2	1024.0	829.4	961.0

production is present. This may be expected to differ for eggs that hatch in a day or persist for weeks.

Interpretation of Time Series

The correlation between recent observations of newly spawned eggs ends at intervals greater than 24 minutes, whereas one-day-old eggs have a persistent correlation over the entire 84-minute interval between the first and eighth tows (Figure 2). The coherence among tows increases gradually with the age of eggs. Coefficients of correlation over .24, or coefficients of determination over .06 are significant with 60 observations.

The time and space scales of controlled ship's drift in 1-2 hours are small in comparison with the change of distribution of a patch of eggs more than one day old. The scale of deposition of the eggs and their subsequent dispersal for a few hours is of significantly smaller scale. Lastly, since eggs are part of the totally passive plankton, these results suggest that other passive plankton patches, or gaps, would have been equally coherent and slowly changing with time, and that aggregating organisms would have had to expend relatively little energy in maintaining a patch under these conditions.

DISCUSSION

The unusual circumstances of this set of observations have led to a new appreciation for the origin of small-scale distribution of anchovy eggs and the three-day persistence of this distribution. The scale and intensity of this pattern may have important consequences, both for comparative sampling of the habitats of the eastern boundary currents, and for interpreting predation. Because this set of samples was taken for other purposes, we will discuss the relations between these observations and similar observations, the implications of the persistence of pattern, and what sampling design and effort are necessary to advance the pattern studies to an analytical level.

Sampling Consequences

The high variability of plankton samples has been attributed to variations in towing procedure (Windsor and Walford 1936); heterogeneous water masses (Windsor and Clarke 1940; Cassie 1959); and aggregations of organisms (Ricker 1937; Langford 1938; Barnes and Marshall 1951). In particular, sardine eggs, which last in the plankton only a few days, are known to be aggregated at spawning (Silliman 1946; Taft 1960) and diffuse away from school-sized (tens to hundreds of meters diameter) patches, which persist for several days (Smith 1973). Aggregations of organisms and heterogeneous water masses occur at several scales and may persist over various time periods (Haury et al. 1978), and our perception of the pattern is profoundly influenced by frequency and duration of cruises, the spacing between stations, and the width and trajectory of the sampling instruments as well as the length of tow (Weibe 1972).

Number of samples. The required number of observations can be determined for a first approximation from an existing set (Santander et al. 1982) or from a pilot cruise. In general, pattern is small-scale relative to the distribution of the species, so a pilot study of spawning pattern can be conducted in a small area (100 × 100 km). The results of this study indicate that one must be separated from an area by either space (km) or time (days) to gather a valid replicate versus a redundant sample. The same is true of the pilot study conducted on existing sample results.

If a study requires precise data on a single day's spawning, the variance of the total eggs will be an underestimate of the individual day's spawning by the ratio of the persistence of the egg and the sample variance of the total eggs: for an egg that persists 3

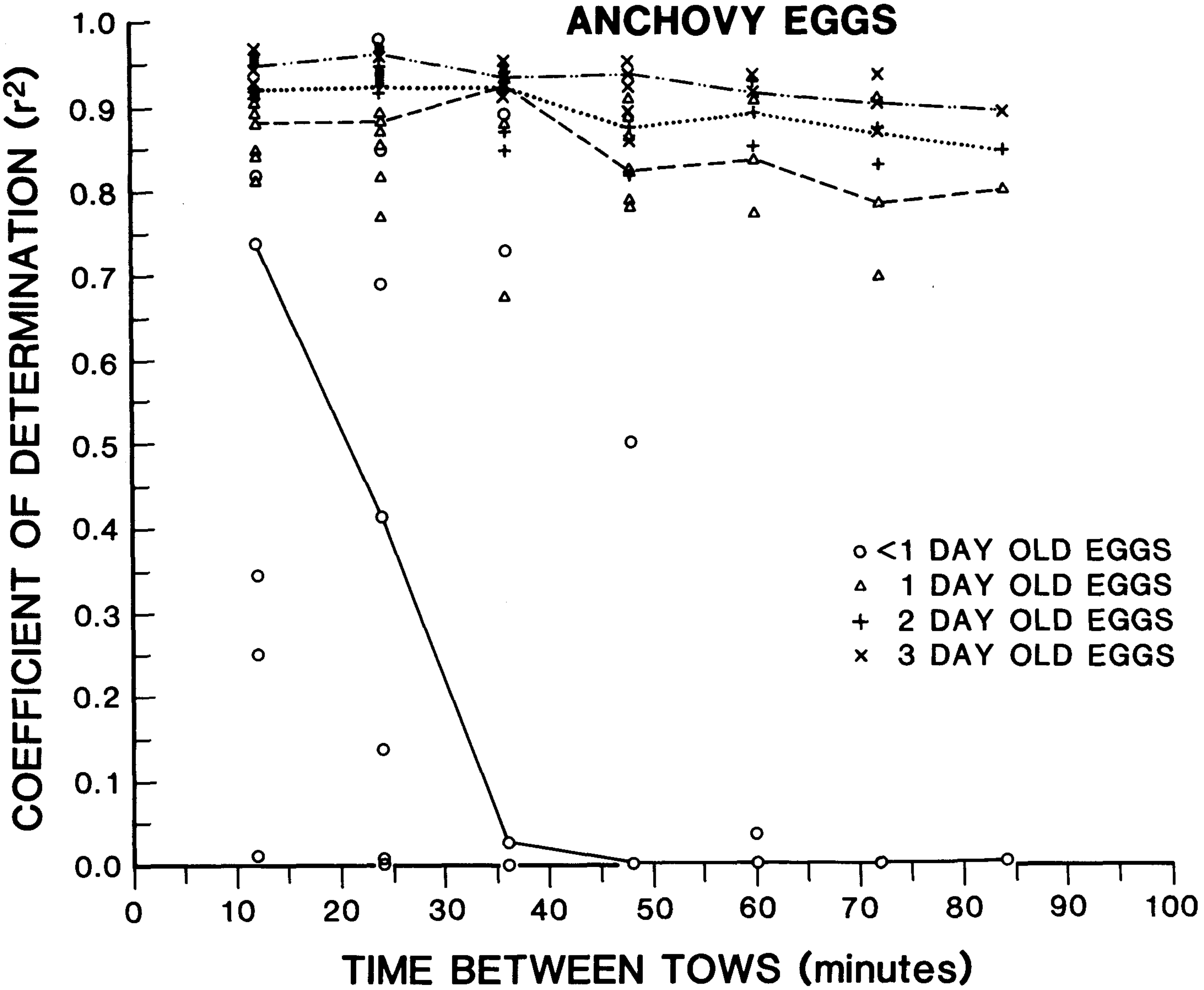

Figure 2. The persistence of correlation between tows as a function of time between tows. Points are from individual values of coefficient of determination for adjacent tows (7 sets), tows separated by 24 minutes (6 sets), tows separated by 36 minutes (5 sets), etc. The lines connect the medians of each interval. (For simplicity, only the nominal interval is graphed: the actual intervals varied from 6 to 36 minutes, with 92% of intervals between 9 and 17 minutes and 51% between 11 and 13 minutes. For complete distribution see Appendix Table 2.)

days, the variance of the total eggs can be multiplied by three to estimate the required number of samples for a given standard error. If the study requires 200 observations to suitably estimate the total number of eggs, it would require 346 samples to estimate the number of eggs spawned in a single day. To describe the onset of spawning between 1800 and 0200 hours with equal precision, it would take a similar number of samples each hour.

Geographic position of samples. Anchovy spawning habitats seem to vary considerably in different eastern boundary currents. The spawning habitat off North America comprises broad regions in relatively permanent gyrals. The spawning habitat off Peru is relatively narrow (Santander et al. 1982; Smith et al. 1983); the spawning habitat off South Africa appears to be a fast-moving coastal jet (Shelton and Hutchings 1982). The current practice is to make 1,000 observations per survey off California (Smith and Hewitt 1984). This may be the minimum required when one considers that the sample must encompass the spawning area, obtain a representative mean, and provide an estimate of egg mortality. Where the spawning habitat is too narrow to provide sufficiently independent adjacent samples, as in Peru, it may be necessary to occupy the habitat more than once. Where the habitat

TABLE 10
Ocean and Atmospheric Predictability Time for Different Scales of Motion

Scale	Predictability time	
	Atmosphere	Ocean
10 m	—	10 min.
100 m	3 min.	1.5 hr
1 km	13 min.	10 hr
10 km	1 hr	3 days
100 km	4 hr	3 weeks
1000 km	1 day	4 months
10000 km	5.5 days	x years

Modified from Platt et al. (1977)

is extremely dynamic, it may be necessary to expand the pattern with time to accommodate the rapidly moving jet and evaluate the survivors.

Consequences for the Study of Pattern

The egg distribution of schooled, coastal, pelagic spawning fish sufficiently resembles coastal plankton blooms like red tide (Kierstad and Slobodkin 1953; Wroblewski 1984) to allow evaluation of the influence of turbulent diffusion and transport at spawning time (Lasker 1975; Bakun and Parrish 1982). The 60 samples reported here (480 observations in samples of 8 per station) are not sufficiently numerous to describe even mortality, so we may expect the number of samples necessary to exceed 200 if interannual variations are relatively large. The assembly of 5 years of egg distribution observations (1,666 positive samples) was adequate to estimate mortality and dispersal (Smith and Hewitt 1984). There was no evidence of offshore transport in the 3-day period for which eggs persist: transport may be inferred from the distribution of older versus younger larvae (Smith 1972 [sardine, Fig. 6; anchovy, Fig. 7]; Hewitt and Methot 1982 [anchovy, Tab. 4, Fig. 15]). Because of this latter phenomenon, higher volumes will have to be filtered over longer distances than used for the vertical tows, to effectively describe transport. Also, the observations must be extended over time to describe transport in the mesoscale.

Predictability in the Eastern Boundary

A new process of modeling, empirical measurements specified by models, and modification of models based on new measurements is beginning (Bakun et al. 1982). For eastern boundary currents the models will have an atmospheric component, an oceanographic component, and a series of biological effects. We must remember that some causative factors in the air and ocean will remain unpredictable over certain space and time scales; thus biological responses will remain unpredictable. The nature of the problem of matching these time and space scales may be seen in Table 10. It seems reasonable to conclude from correlation of replicate samples for eggs less than 8 hours old that the pattern which yielded this result was on the order of hundreds of meters or the space scale of a fish school (perhaps in motion during spawning). Thus there is a new opportunity to design process-oriented cruises with the goal of determining the most important time and space scales of organisms of known age and distributional heterogeneity.

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APPENDIX

TABLE 1
Station Data for Replicate Series

CalCOFI line	CalCOFI station	Date	Time	10-meter temperature
90.0	28.0	790122	2043	14.8
82.0	47.0	790127	0810	13.1
83.0	42.0	790127	1254	13.6
83.0	40.6	790127	1832	13.5
87.0	35.0	790128	0645	13.7
89.6	34.6	790128	1419	14.1
93.0	30.0	790129	1855	13.8
93.0	35.0	790129	2313	14.1
93.0	40.0	790130	0337	14.4
93.0	45.0	790130	0757	13.2
89.5	41.0	790131	0959	13.2
88.4	40.6	790131	1413	13.5
89.2	32.9	790201	0813	13.6
90.1	32.0	790201	1150	13.7
90.8	35.1	790201	1549	14.0
91.7	39.8	790201	2057	13.9
90.6	42.8	790202	0127	14.0
88.9	45.3	790202	0632	12.9
87.6	44.7	790202	1031	13.2
86.3	44.8	790202	1905	13.0
86.1	42.6	790203	0010	13.1
84.3	43.4	790203	1108	13.0
83.8	47.2	790203	1444	13.1
83.9	52.3	790203	1839	13.1
89.4	51.2	790204	0947	13.4
91.9	44.2	790204	1855	13.3
92.9	38.1	790204	2346	13.6
91.9	32.8	790205	0423	13.6
92.2	27.7	790205	0817	13.5
93.5	27.4	790205	1142	14.0
93.8	31.8	790206	1945	14.3
91.9	40.6	790207	0728	13.8
90.8	46.5	790207	1222	13.2
90.5	44.2	790207	2127	13.8
92.2	42.9	790208	0845	14.1
93.1	45.2	790208	1717	13.8
91.8	45.8	790208	2104	13.9
92.7	40.9	790209	0126	13.9
94.9	50.2	790209	1802	13.7
96.7	50.2	790209	2213	14.3
96.0	45.9	790210	0319	14.2
94.4	38.6	790210	1106	13.9
93.3	34.7	790210	1526	14.4
92.8	31.6	790210	1859	13.9
91.2	30.2	790211	0040	12.4
91.9	34.3	790211	0540	14.1
91.2	37.8	790211	0939	14.7
89.7	36.5	790211	1400	14.7
88.9	40.7	790211	1739	13.8
88.2	43.9	790212	1519	14.0
87.8	39.1	790212	1907	13.3
86.4	38.5	790212	2300	13.7
85.6	45.8	790213	0749	13.2
82.5	43.3	790214	0640	13.4
83.8	40.6	790214	1050	13.8
85.2	37.2	790214	1452	13.9
86.5	33.9	790214	1920	13.8
89.4	30.6	790215	0320	13.8
90.2	29.3	790215	0655	14.0
91.7	28.0	790215	1050	14.9

TABLE 2
Distribution of Intervals between Tows

Interval between tows (min)	Proportion of observations	
6	.011	*
8	.017	**
10	.089	*******
12	.511	************************************
14	.260	*******************
16	.060	*****
18	.026	**
20	0	
22	.017	**
24	0	
26	.003	*
28	0	
30	0	
32	.003	*
34	0	
36	0	
38	.003	*

TABLE 3
Program to Estimate Parameters of a Negative Binomial Distribution

Original program by Hewitt Tektronix (1977)
Converted by Smith to TRS-80 (1980)
Converted by Smith to VAX (1982)

```
 10  rem uses three methods for estimating k of negative binomial”
 20  K=0
 30  K1=0
 40  K2=0
 50  PRINT“Enter total number of observations in sample, number of”
 60  PRINT“zero observations, mean and standard deviation of all”
 70  PRINT“observations.”
 80  INPUT N,Z,M,S
 85  V=S*S
 90  PRINT “trial k = ”;
100  INPUT K
110  X= -LOG(Z/N)/K-LOG(1+M/K)
120  PRINT“residual = ”;X
130  PRINT “press enter for another trial, otherwise any key”
140  INPUT Q$
150  IF Q$=“ ” GO TO 90
160  K1=(M*M)/(V-M)
170  PRINT“Enter the observation frequency table: first value”
180  PRINT“then frequency thus 15,6 - - enter 999,0 when finished”
190  DIM I1(1000),R(1000)
200  I=1
210  PRINT I; “value = ”;
220  INPUT I1(I)
230  IF I1(I)=999 THEN 290
240  PRINT “frequency = ”;
250  INPUT R(I)
260  A=I
270  I=I+1
280  GO TO 210
290  PRINT “trial K = ”;
300  INPUT K2
310  B=1
320  U=0
330  FOR J = 1 TO A
340  Q=0
350  FOR I = B TO A
360  Q=R(I)+Q
370  NEXT I
380  V=Q/(K2+J-1)
390  U = U + V
400  B=B+1
410  NEXT J
420  X=N*LOG(1+M/K2)-U
430  PRINT “residual = ”; X
440  PRINT “want another iteration?”
450  INPUT Q$
460  IF Q$=“ ” GO TO 290
470  PRINT “from the proportion of zeroes ............................................................ ”; K
480  PRINT “by the method of moments ................................................................ ”; K1
490  PRINT “by maximum likelihood ................................................................... ”; K2
500  END
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Part III

SCIENTIFIC CONTRIBUTIONS

GROWTH OF LARVAL SARDINES OFF PERU

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ABSTRACT

The growth rate of sardine larvae from Peru was determined from daily increments in the otoliths. Scanning electron microscopy was used to confirm the size of increments. The growth rate of sardine larvae is discussed in relationship to other clupeoid fishes, in particular the anchoveta and northern anchovy.

RESUMEN

Se determinó la tasa de crecimiento de las larvas de la sardina peruana sobre la base del incremento diario de los otolitos. Se utilizó microscopía electrónica de barrido para confirmar la magnitud de los incrementos. La tasa de crecimiento de las larvas de sardina es analizada en relación con otros clupéidos, en particular la anchoveta y la anchoveta del norte.

INTRODUCTION

Since El Niño of 1972 the population of Pacific sardine, *Sardinops sagax sagax*, in the Peruvian Current has increased greatly while the anchoveta, *Engraulis ringens*, has declined. The biomass of sardines was estimated at 3 million metric tons in 1978. The Pacific sardine is now the basis for the most important fishery off Peru, having replaced the formerly abundant anchoveta. The resurgence of the sardine population following the decline of the anchoveta raises many questions about the interactions between the two species.

Sardines and anchovies share many similarities in addition to their differences (Murphy 1966, 1967; Smith 1972). The sardine, anchoveta, and northern anchovy all spawn between sunset and midnight (Ahlstrom 1943; Hunter and Macewicz 1980; Ahlheit et al. 1984). The eggs of sardines and anchovies are quite different. The eggs of both the northern anchovy (*Engraulis mordax*) and the anchoveta (*Engraulis ringens*) are oblate spheroids about 1.34 mm long and 0.66 mm wide, with a narrow perivitelline space (Ahlstrom 1956; Fischer 1958; Einarsson and Rojas de Mendiola 1963). However, the sardine (*Sardinops sagax caeruleus*) egg is spherical with an average diameter of 1.70 mm (range 1.35-2.05 mm) (Ahlstrom 1943).

In spite of the differences in egg morphology, incubation times and larval morphology are quite similar. Sardine hatch in 2.8 days at 15°C (Lasker 1964); northern anchovy hatch in 2.9 days at 15°C (Zweifel and Lasker 1976); and anchoveta hatch in 2-2.5 days at 14-16°C (Ware et al 1981). The elongate larvae of sardines and anchovies are morphologically quite similar (Ahlstrom 1943, 1956; Smith 1972). Yolk-sac larvae begin feeding one to two days after hatching (Zwiefel and Lasker 1976). Feeding behavior of both sardines and anchovies is characterized by S-shaped feeding strikes.

Off California from 1951-60 anchovy larvae were taken at 71.3% of all stations where sardines occurred (Ahlstrom 1966). Sardine and anchovy larvae may interact through interspecific competition for food or through differential mortality. Copepod nauplii and copepodites are the dominant food items of sardine and northern anchovy larvae off California (Arthur 1976) and of anchoveta larvae off Peru (Rojas de Mendiola 1974; Ware et al. 1981). Interspecific competition for food implies that the abundance of one species affects the availability of food for the other species. However, even at the station where anchovy were most abundant, anchovy larvae constituted no more than 0.02% by volume of all organisms collected by .333-mm mesh plankton netting; many of these organisms consume the same food as the anchovy larvae (Bob Owen, pers. comm.). Thus intraspecific competition among anchovy larvae or interspecific competition for food between anchovy and sardine larvae seems unlikely. Differences in growth between species of larvae could lead to differential survival, since the smallest (youngest) stages are the most vulnerable to predation (Hunter 1984). High growth rates of sardine larvae during periods of warm water may be one mechanism whereby environmental variations may lead to large changes in abundance.

At present, however, little is known about the growth rates of sardine larvae in the sea, because the techniques for investigating such growth rates have only recently been developed (Brothers et al. 1976), and adequate samples were difficult to obtain when the populations were low. We investigated sardine growth as part of the continuing research at the Institu-

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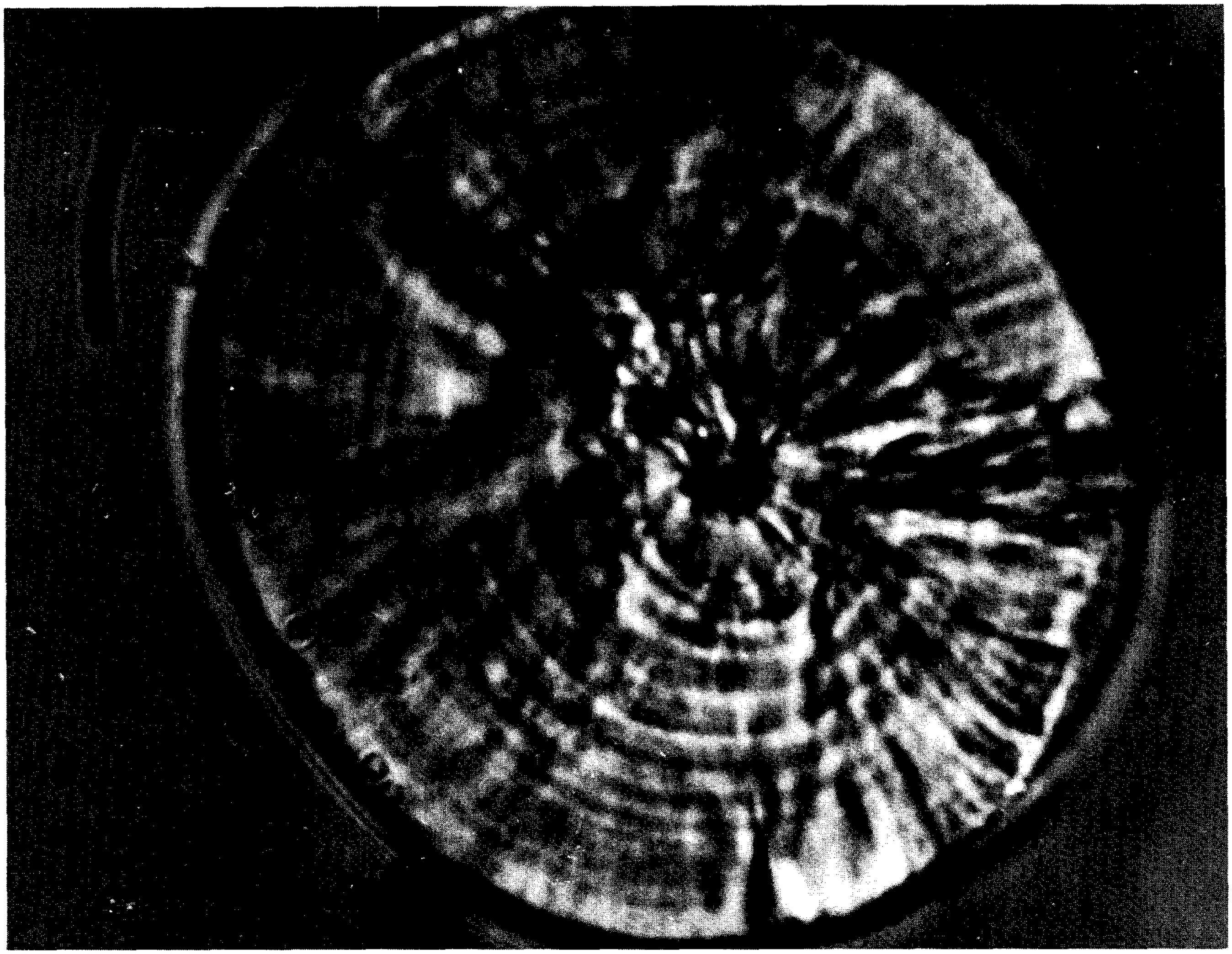

Figure 1. Photomicrograph of the otolith from a 13.8-mm sardine larvae (3400 ×). The increments are difficult to interpret in this specimen.

to del Mar del Peru on the pelagic resources of Peru and as a basis for estimating larval sardine mortality rates in the sea.

MATERIALS AND METHODS

Pacific sardine larvae (*Sardinops sagax sagax*) were collected with a 1-m ring net on August 27, 1983, at 09°39.8′S, 78°24.7′W off Chimbote, Peru. The sea-surface temperature at the time of capture was 18.6°C. Plankton samples were fixed in 80% ethanol at the time of collection and refixed with 80% alcohol one day after collection. Larvae were sorted from the preserved samples and stored in 80% ethanol.

Adult Pacific sardine (*Sardinops sagax caeruleus*) were spawned in the laboratory at the Southwest Fisheries Center on December 18, 1984. The eggs hatched two days later at 18.5°C. Ten to fifteen larvae were preserved in 80% ethanol. We used the laboratory-reared specimens to determine the length of the larvae and the size of the otolith at hatching. Daily increments in the otoliths (sagittae) were examined with light microscopy and electron microscopy. We dissected otoliths from larvae in water on a microscope slide, cleaned them of adhering tissue, and allowed them to dry before covering them with clear nylon nail hardener (Sally Hansen Hard as Nails with nylon) for examination under a compound microscope at 400 and 1000 magnification.

Otoliths examined with scanning electron microscopy (SEM) were transferred to a drop of nylon nail hardener on an aluminum SEM stub. We polished the otoliths with .3-micron lapping compound and etched them for one minute with 5% ethylenediaminetetraacetic acid (EDTA) buffered to pH 7.5. We then coated the specimens with gold before viewing them at 1790 × with scanning electron microscopy.

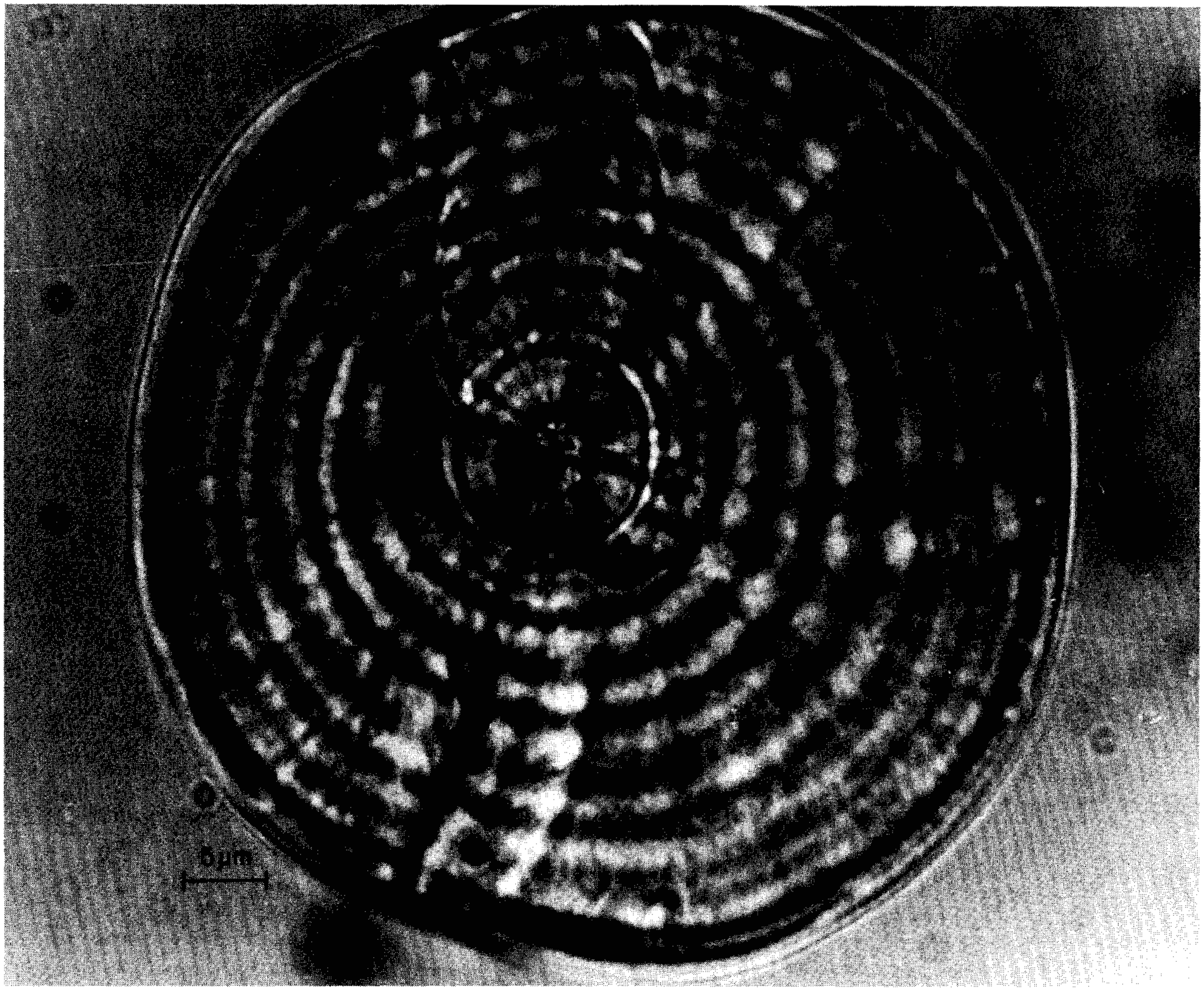

Figure 2. Photomicrograph of the otolith from a 14.5-mm sardine larva (3300 ×). The large dark lines correspond in size to the increments seen in scanning electron micrographs.

RESULTS

We examined the otoliths of sardine larvae hatched in the laboratory with light microscopy and with scanning electron microscopy. No increments were found in the otoliths from larvae sampled on the day of hatching (day 0) or the following day (day 1). Rearing conditions of the larvae were apparently suboptimal, because all larvae died within a few days. Otoliths from these larvae were ambiguous. Brothers et al. (1976) found that northern anchovy formed the first increment on day 5. Because of similarities in larval development (see Introduction), we assume that sardine larvae also form the first increment on the fifth day after spawning. This assumption is subject to verification.

The use of light microscopy (Figures 1 and 2) alone can lead to ambiguous interpretation of the number of increments in an otolith because small increments may not be resolved or because subdaily increments within large increments may be interpreted as daily increments. Thus we examined sardine otoliths using scanning electron microscopy. This technique confirmed the size of the increments (Figure 3) and a fast growth rate of sardine larvae (Figure 4). The laboratory-reared specimens indicated that sardine larvae do not form daily increments until about three days after hatching. Therefore the age of field-collected specimens was calculated by adding five days to the number of increments in the otolith (Figure 4). The length-at-age data were fitted to a Laird-Gompertz equation

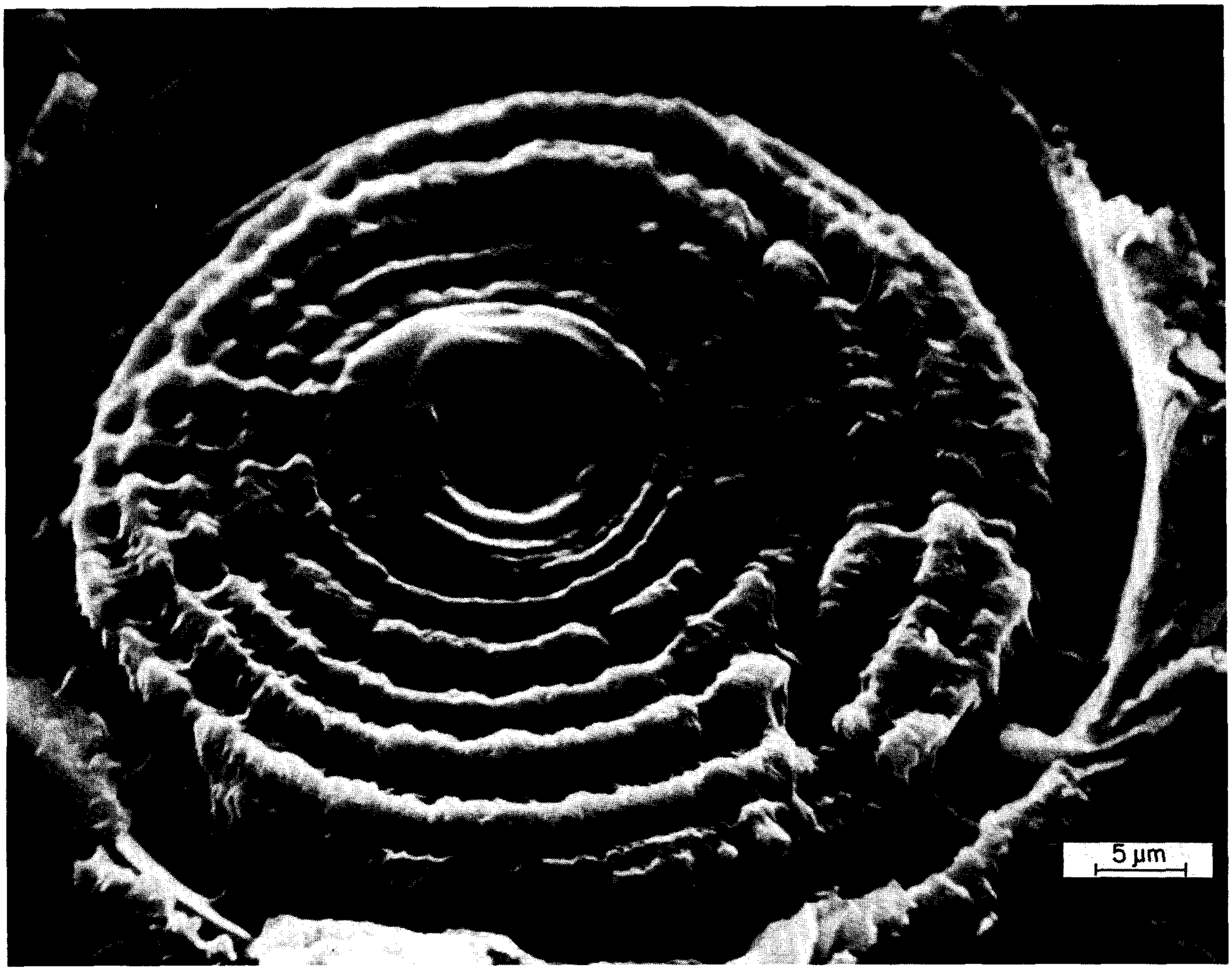

Figure 3. Scanning electron micrograph of a polished and etched otolith from a 14.8-mm sardine larva (3500×). The large pit in the center is the focus.

(Zwiefel and Lasker 1976) and to a logistic equation. The logistic equation gave a slightly better fit with more degrees of freedom, but neither curve adequately described the data.

DISCUSSION

According to the parameters from the logistic equation, sardine larvae grow at a rate of 0.8 mm per day at a size of 12.7 mm. This growth rate compares well with the average growth rate of 0.7 mm per day reported by Kimura and Sakagawa (1972) for laboratory-reared *Sardinops sagax caeruleus*, and the embryonic growth rate of 0.8 mm per day for *Sardinops sagax musica* at 18° (Garretón and Balbontín 1982). The growth rate of sardine larvae is among the highest reported for any clupeoid larva and greater than that of laboratory-reared anchovy larvae at the same temperature (Blaxter and Hunter 1982). It is also about twice the growth rate of the northern anchovy in the sea (Methot and Kramer 1979).

If early sardine larvae truly have a faster intrinsic growth than anchovy, then this may be a key to identifying a fundamental ecological difference between these superficially similar species. For example, faster growth probably implies higher ration and hence, at a given food density, larger search volumes and greater swimming speeds. Ahlstrom (1966) found that sardine larvae were most abundant where anchovy and sardine co-occurred. Faster growth may also imply lower predation risk to size-specific predators. Faster growth may also be a necessary feature of a seasonally later spawner. Sinclair and Tremblay (1984) have proposed that the timing of spawning of Atlantic herring populations is not coupled to spring phytoplankton blooms. Rather, it is associated with growth rates in larval retention areas that allow metamorphosis within a sea-

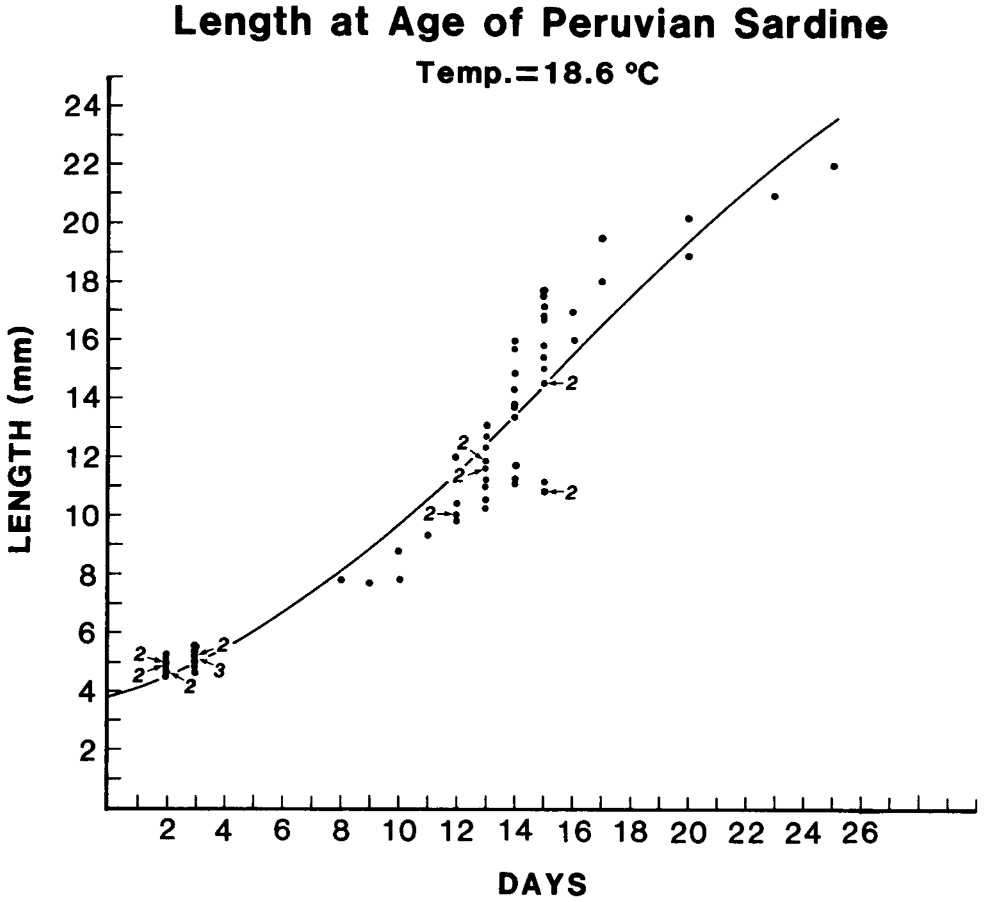

Figure 4. Length at age of Peruvian sardine larvae. The solid line is a logistic growth curve fit to the data points. Data points at 2 and 3 days are from laboratory-reared California sardines.

sonal window. Different stocks of herring exhibit different larval growth rates, but all reach metamorphosis at about the same time. It may be necessary for sardine larvae to grow faster than anchovy larvae in order to metamorphose and reach an optimal juvenile size before winter.

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RECENT INCREASED ABUNDANCE AND POTENTIAL PRODUCTIVITY OF PACIFIC MACKEREL (*SCOMBER JAPONICUS*)

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ABSTRACT

Cohort analysis (VPA) of recent Pacific mackerel catches off southern California and northern Baja California shows that total biomass (age 1+) increased sharply beginning in 1977. The increase followed a period of extreme depletion, and continued for several years, reaching a peak of 300,000 to 500,000 MT in 1982. Abundance decreased substantially in 1983 and 1984 because of very weak recruitment. The 1978 year class was considerably stronger than the previous largest year class. The recent pattern of reproductive success has been more variable than was seen historically, although the underlying cycle seems to continue.

We investigate potential productivity of the Pacific mackerel resource by simulating the fishery from 1929 to 1968. The model assumes a Ricker stock-recruitment relationship, and retains the historical pattern in anomalies in reproductive successes, logarithm of recruits per spawner. We examine sensitivity of the simulation results to several alternative models of stock-recruitment compensation; the results are most robust to these assumptions if exploitation rates (annual catch divided by total biomass) are near 0.2. A yield isopleth diagram summarizes average annual yields for linear harvest formulas of the type: harvest equals a *fraction* of the total biomass in excess of a *cutoff* level. The present California Pacific mackerel fishery regulations (*fraction* = 0.2, *cutoff* = 18,144 MT total biomass) should produce an average yield of 27,000 MT/yr with an annual standard deviation of about 15,000 MT. Average yield could be increased to about 29,000 MT/yr if the *fraction* is increased to 0.28, but the annual standard deviation would increase to about 19,000 MT, and the average total biomass would decrease by about 25 percent. Because present California fishery regulations do not include all catches of Pacific mackerel in the harvest formula, the present effective value of the *fraction* exceeds its nominal value of 0.2.

RESUMEN

Análisis de las cohortes en capturas recientes de la caballa del Pacífico a la altura del sur de California y norte de Baja California indican que la biomasa total (edad 1+) aumentó abruptamente desde 1977. El incremento sucedió a un período de gran pauperización y continuó durante varios años, alcanzando, en 1982, un máximo de 300,000 a 500,000 toneladas métricas (TM). En 1983 y 1984 la abundancia disminuyó considerablemente debido al escaso reclutamiento. La clase anual de 1978 fué considerablemente más robusta que la clase anual anterior de mayor magnitud. El reciente patrón de éxito reproductivo fué más variable de lo registrado históricamente, pero el ciclo subyacente parece continuar. Investigamos el potencial reproductivo del recurso de la caballa del Pacífico mediante la simulación de la pesquería desde 1929 hasta 1968. El modelo presupone una relación Ricker de stock-reclutamiento, y conserva el patrón histórico de anomalías en el éxito reproductivo, i.e., logaritmo de reclutas por desovante. Examinamos la sensibilidad de los resultados de la simulación con respecto a varios modelos alternativos de compensación stock-reclutamiento; los resultados mas coherentes frente a estos supuestos se obtienen si los ritmos de explotación (captura anual sobre biomasa total) se mantienen en alrededor de 0.2. Un diagrama de isolíneas de rendimiento resume los rendimientos anuales medios para fórmulas de cosechas lineales del siguiente tipo: la cosecha es igual a una fracción de la biomasa total la cual excede un valor límite dado. Las reglamentaciones californianas actuales sobre la pesca de la caballa del Pacífico (fracción = 0.2, valor límite = 18,144 TM de biomasa total) deberían producir un rendimiento promedio de 27,000 TM por año, con una desviación estándar anual de aproximadamente 15,000 TM. La captura promedio podría ser aumentada a alrededor de 29,000 TM por año si la fracción fuera incrementada a 0.28, pero esto llevaría a un aumento de la desviación estándar anual a unas 19,000 TM, y la biomasa media total disminuiría en un aproximadamente 25%. Dado que las actuales reglamenta-

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ciones pesqueras de California no incluyen todas las capturas de caballa del Pacífico en la fórmula del rendimiento, el valor actual efectivo de la fracción excede su valor nominal de 0.2.

INTRODUCTION

The Pacific mackerel (*Scomber japonicus*) resource off California is one of the most thoroughly studied in world fisheries. Its population dynamics, nonetheless, remain enigmatic in many respects. Fishery data have allowed cohort analyses to extend from the beginning of the fishery in 1929 to its collapse in the late 1960s, a period of about 40 years (Parrish and MacCall 1978). The California fishery was closed by legislation in 1970 and reopened in 1977, when abundance increased (Klingbeil 1983). Lack of fishery data during this closed period prevents detailed analysis of the collapsed population. However, the relatively large fishery since 1977 once again has supplied data sufficient for population estimates, the results of which are reported here.

In 1972 the California legislature enacted an innovative management law that established Pacific mackerel catch quotas according to a formula based on estimated resource abundance. The formula was changed in 1978 to its present wording, whereby seasonal harvest is to be no more than 20 percent of the excess over 20,000 short tons (18,144 MT). Klingbeil (1983) gives a detailed history of the fishery's management, including provisions for incidental catch allowances and size limits. Recent biological and economic conditions have caused both the southern and central California purse seine fleets to increase reliance on Pacific mackerel. The result has been that during recent seasons (1983-84 and 1984-85), quotas have been met much earlier than they otherwise would have been. Fishermen were then faced with several months of interseason restrictions on the catch of Pacific mackerel with virtually no alternative species available for redirected effort. Fishery managers have been faced with imposing short-term economic hardships on fishermen or else increasing quotas above the quantity dictated by the harvest formula and current abundance estimate.

Accordingly, some parts of industry and management have expressed interest in either modifying the harvest formula or replacing it with other management measures (e.g., constant quotas) in order to allow higher catch rates and/or lessen the need for in-season quota adjustments. Because the formula adopted in 1978 was not based on extensive fishery analysis, we have undertaken an evaluation of that formula in comparison with a range of alternative management measures. This analysis provides a guide for revising the management regime as well as an assessment of reasonable expectations for future catch levels and patterns.

ABUNDANCE ESTIMATES

Method

Because many segments of the Pacific mackerel fishery are highly seasonal, we have compiled catches on a quarterly basis beginning with the fourth quarter of 1976, when incidental catches rose to a level allowing monitoring (Table 1). Accuracy of abundance estimates by cohort analysis requires that all catches be accounted for, so we have included estimates of the northern Baja California commercial catch (provided by Biol. Walterio Garcia, Instituto Nacional de Pesca, Ensenada, B.C.N., Mexico), and the recreational catch on the Pacific coast of the United States. Some of these source data were aggregated by year, and others are not yet available; reasonable assumptions (documented in Table 1) were employed where necessary to complete the catch information base. Errors in cohort analysis that arise from converting annual

TABLE 1
Season (July-June) Catches (MT) for Commercial and Recreational Segments of the Pacific Mackerel Fishery

	California		Mexico [a]		Fraction sampled
Season	Comm.	Recr.[b]	Comm.	Total	(California comm./total)
1976-77	2603	190	1271	4064	0.64
1977-78	7787	872	5168	13827	0.56
1978-79	18249	1678	7376	27303	0.67
1979-80	27753	1648	5153	34554	0.80
1980-81	27910	1910	3368	33179	0.84
1981-82	37950	(1366) [c]	3045	42361	0.90
1982-83	30045	(1412)	(4518)	35975	0.84
1983-84	35908	(1412)	(4518)	41838	0.86

All fish for which ages were determined were sampled from the California commercial landings.

[a] Annual Mexican commercial catches and estimates of recent catches were supplied by Walterio Garcia (personal communication, Instituto Nacional de Pesca, Ensenada, Mexico). We calculated seasonal values by assuming 40% of the annual catch is taken in January-June.

[b] California partyboat catch is converted to total recreational catch based on the Marine Recreational Surveys of 1979 and 1980 (Holliday et al. 1984).

[c] Monthly partyboat catches are known through August 1981. Annual catch is known for 1981 and 1982. Annual catches for 1983 and 1984 are assumed to be the same as in 1982.

catches to nominal seasonal catches are not likely to be large (Sims 1982). Because age composition estimates are lacking for the Mexican and recreational fishery segments, their age compositions were assumed to be the same as that of the commercial fishery monitored at San Pedro, California. Although there are errors associated with these assumptions, much larger errors would necessarily result from omitting catch estimates for these incompletely reported segments.

The cohort analyses were conducted similarly to earlier estimates, except that the solution uses an accounting season beginning July 1 rather than May 1, as was used by Parrish and MacCall (1978). As before, fish 4 years old or older (age 4+) are assumed to be fully and equally available to the fishery; fishing mortality rates of age 4+ and age 5+ fish are equated in each season in order to "link" the solutions for adjacent cohorts. The instantaneous natural mortality rate (*M*) was assumed to be 0.5/yr (Parrish and MacCall 1978).

Current values of fishing mortality rates (*F*) need to be assumed in order to obtain *F* estimates for earlier time periods. The current values are imprecise, not being based on direct evidence; fortunately, estimates of fishing mortality rates for earlier periods become less arbitrary because of converging properties of cohort analysis (Parrish and MacCall 1978, 38-39). Lacking independent indices of mackerel abundance, we must base the estimate of current *F* (and hence the current biomass) on internal consistency and experience with fishery analysis; it would be misrepresentation to claim this to be more than an elaborate educated guess.

TABLE 2
Fishing Mortality Rate Estimates for Age 4+ Fish, for Various Initial Assumed Values

Season	Annual *F* estimate for age 4+		
1978-79	0.264	0.279	0.289
1979-80	0.417	0.450	0.473
1980-81	0.295	0.330	0.355
1981-82	0.292	0.341	0.378
1982-83	0.282	0.348	0.403
1983-84 (assumed)	0.3	0.4	0.5

Our rationale for postulating initial values of *F* is as follows:

Fully available ages (4+). Trial solutions using a variety of current (1983-84 season) *F* estimates (Table 2) showed that a value of 0.3/yr produced consistently similar values for the preceding three seasons, and would correspond to roughly constant fishing mortality rates generated by the fishery. However, since mid-1983 jack mackerel (*Trachurus symmetricus*, the main alternative species in the fishery) have been much less available than usual, suggesting that fishing has been directed more specifically toward Pacific mackerel than in previous periods. Also, the abundance of Pacific mackerel has declined in the 1982-83 and 1983-84 seasons for all trial solutions (Figure 1),

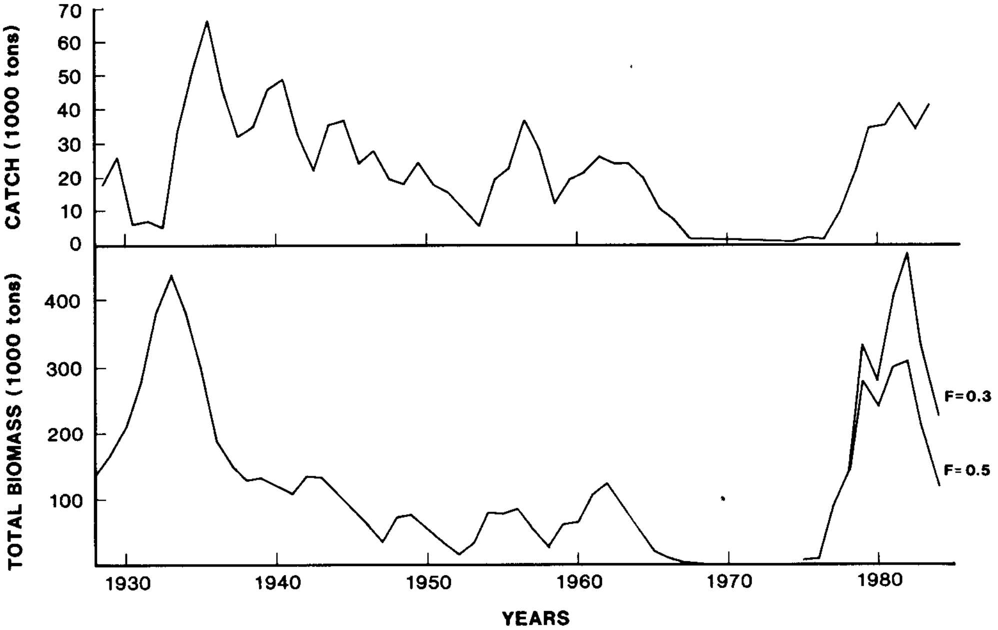

Figure 1. History of total harvest and total abundance (age 1+) of Pacific mackerel. Recent abundances reflect the range of assumed current fishing mortality rates (*F*) used in the analysis.

and *F* may have increased because of an abundance-dependent increase in the catchability coefficient, as is typical for coastal pelagic fisheries (cf MacCall 1976). Associated with this decline is a much older age composition, which in itself should result in higher average availability and consequently higher fishing mortality rates given similar levels of nominal fishing effort. Moreover, total catches during 1984 reached nearly 41,000 MT, one of the highest levels since the recovery began (Figure 1). On the other hand, the Pacific mackerel population extended northward much farther than normal in 1983 and 1984, probably in association with warm oceanic conditions. This would have reduced the available fraction of the stock, and would have reduced *F* accordingly. An *F* approaching 0.5/yr was generated on fully available fish in the 1979-80 season (Table 2), indicating that a value this high is clearly possible. We concluded that a range of current *F* from 0.3/yr to 0.5/yr is roughly consistent with these observations. These values provide nominal upper and lower abundance estimates, respectively (Figure 1). We feel that true abundance probably lies somewhere between these levels, but only future catch patterns can confirm these estimates.

Partially available ages (0,1,2,3). We obtained estimates of historical abundance of the 1980 and earlier year classes by assuming values of current *F* for fully available fish. We then evaluated availability of younger ages relative to age 4+ for the 1979-80 through 1982-83 seasons. Mean availabilities differed very little for the three solutions, and were 0.026, 0.153, 0.380, and 0.717 for ages 0 through 3 in the current $F = 0.4$/yr solution. Current *F* values for the partially available ages were obtained by multiplying estimated *F* for fully available ages by mean availability at age. These estimates become very imprecise for the younger age groups, but the effect on the 1984 abundance estimate is relatively small because the contribution from the 1982 and 1983 year classes is unusually small. Nominal estimates for age 0 fish are inaccurate because the fish appear in the catch only toward the end of the season.

Annual biomasses are calculated for July 1 of each year, using estimated abundances (Table 3) and observed mean weights at age for the third quarter of that year. We calculated spawning biomasses according to the spawning fractions at age given by Parrish and MacCall (1978, 26-27). Where comparisons with the historical fishery were desired, we projected numerical abundances back to May 1 by multiplying by EXP $[(F+M)/6]$, and calculated biomasses based on mean weights at age from the second quarter of the year.

Results

Pacific mackerel abundance from 1977 to 1984 was of a magnitude that has not been experienced for nearly 50 years in California (Figure 1). The high biomasses estimated by Parrish and MacCall for the 1930s were based on length-composition information that they considered unreliable. Thus the reality of those extremely high abundance estimates seemed questionable. However, the similar abundances estimated for the recent period confirm that the resource can attain such high levels. The contrast between recent abundances and those of the previous decade (1967-76) is even more remarkable. In view of this apparently unusual behavior of the resource, it is reasonable to inquire whether the recent patterns of Pacific mackerel population dynamics are similar to, or different from those of the preceding period.

The historical relationship between recruitment and spawning biomass has been nebulous, even when viewed on a log-log scale (Figure 2). Yet the recent estimates are variable even by historical standards: many of the new observations fall on the periphery or outside the "cloud" of points established during the previous 40 years of fishery analysis. The 1976 year class that initiated the fishery recovery was moderately strong, but was produced by a spawning biomass much smaller than any parental abundance previously

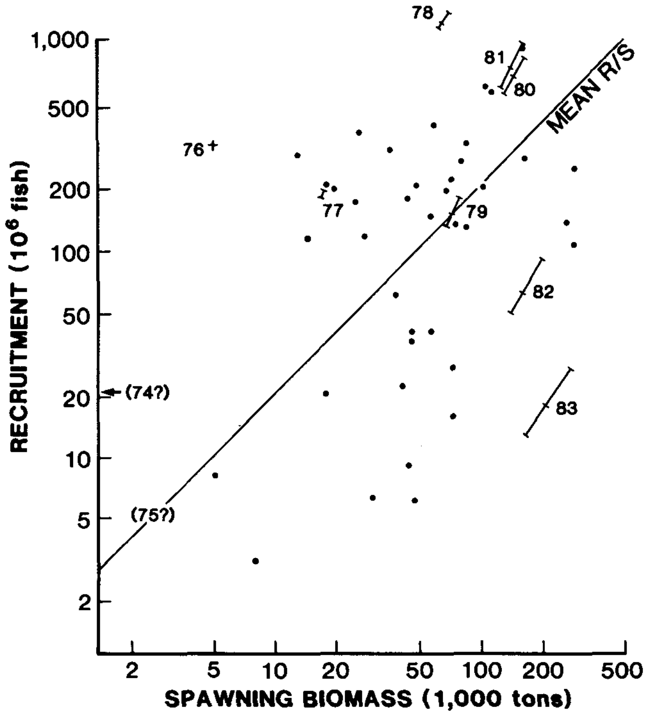

Figure 2. Relationship between Pacific mackerel recruitment and spawning biomass (log-log scale). Ranges of recent estimates reflect the range of assumed current fishing mortality rates (*F*) used in the analysis. Historical values (dots) are included for comparison.

TABLE 3
Annual Catches at Age (*C*, 10^6 Fish), Estimated Fishing Mortality Rates (*F*, Year^{-1}), and Initial Abundances at Age (*N*, 10^6 Fish on July 1) for the Current *F* = 0.4/yr Solution

	Age						
Season	0	1	2	3	4	4+	5+
1976-77							
C	15.5	0.05	1.3				
F	0.041	0.015	0.156				
N	—	5.0	11.7				
1977-78							
C	7.9	38.3	0.08	0.21			
F	0.034	0.172	0.036	0.045			
N	—	304.8	3.0	6.1			
1978-79							
C	64.2	20.9	30.8	0.85	0.68	0.68	
F	0.041	0.165	0.286	0.894	0.279	0.279	
N	—	173.7	155.6	1.8	3.5	3.5	
1979-80							
C	0.1	105.3	14.2	13.5	0.13	0.60	0.47
F	0.001	0.120	0.224	0.273	0.451	0.451	0.451
N	—	1181.8	89.4	70.9	0.4	2.1	1.6
1980-81							
C	16.2	1.4	77.7	7.6	7.3	7.5	0.18
F	0.019	0.012	0.167	0.249	0.330	0.330	0.330
N	—	141.6	636.1	43.3	32.7	33.5	0.8
1981-82							
C	6.1	33.8	5.8	66.6	4.7	8.1	3.4
F	0.007	0.069	0.090	0.296	0.341	0.341	0.341
N	—	641.7	84.8	326.3	20.5	35.1	14.6
1982-83							
C	0.6	19.9	23.7	7.4	34.5	38.1	3.6
F	0.008	0.037	0.086	0.221	0.348	0.348	0.348
N	—	693.9	363.2	47.0	147.2	162.4	15.2
1983-84							
C	0.2	2.8	45.3	40.2	6.0	—	18.4
F	0.010	0.061	0.152	0.287	0.400	—	0.400
N	—	59.9	405.6	202.1	22.9	—	69.6
July 1, 1984							
N	—	16.5	34.2	211.3	92.0	—	37.6

The 1974 year class (upper right diagonal) includes all older ages.

seen to have produced such a level of recruitment. The recruitment strength of the 1978 year class (1.21 to 1.44 billion fish on May 1) was 27% to 52% larger than the previous record 1932 year class (0.95 billion fish). Indeed, three of the four largest year classes on record (1978, 1980, and 1981) may have occurred since the recovery. In contrast, the 1982 and 1983 year classes appear to be unusually weak with respect to the large spawning biomasses that produced them. This belies the previous impression (Parrish and MacCall 1978, 42) that recruitment strength is much less variable when spawning biomass exceeds 100,000 MT, and that this abundance provides insurance against recruitment failure.

The temporal pattern of reproductive success, measured as the logarithm of recruits per spawning biomass, historically followed a roughly cyclic pattern (Figure 3). As expected from Figure 2, the amplitude of recent fluctuations is larger than was seen in the historical pattern. The decline in reproductive success

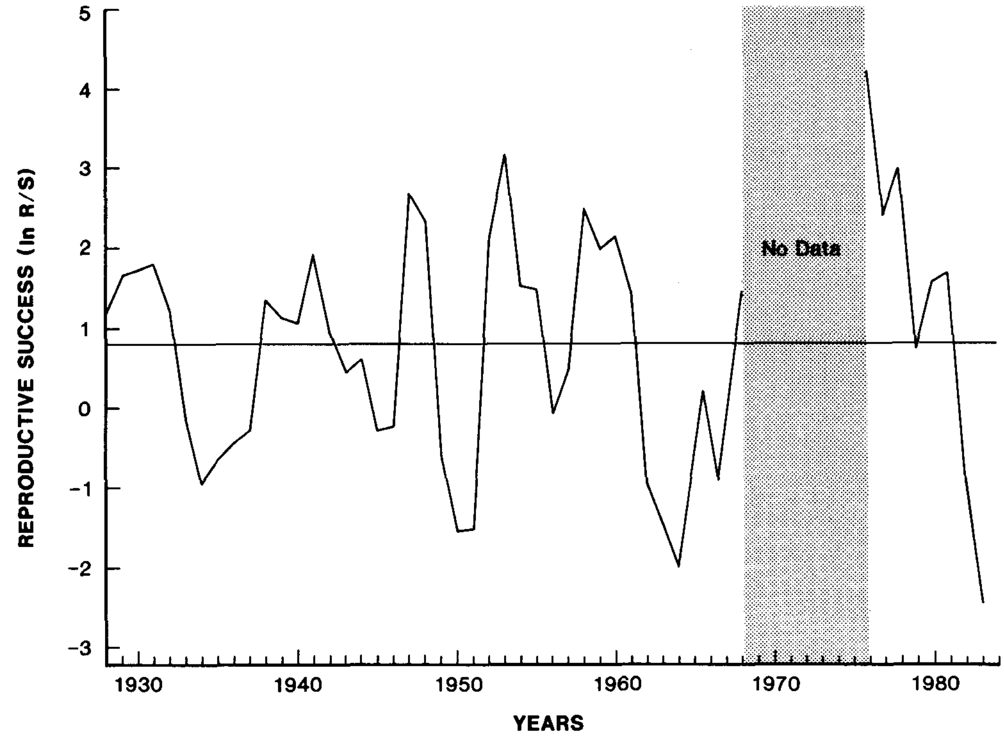

Figure 3. Time series of Pacific mackerel reproductive successes, based on an assumed current F of 0.4/yr. R is recruitment in numbers of fish; S is spawning biomass in kg.

from 1976 to 1983 shows a multiyear decline similar to previous declines, but with short-term reversals that have not been common previously. The presumptive cycle is not yet complete; early catches of the 1984 year class indicate that it is stronger than the two preceding year classes. Of course, a prolonged series of poor reproductive success is possible, especially in view of the historical pattern of poor recruitments from 1933 to 1938, immediately following the very high abundances of the early 1930s. The recent decline from the top (1976) to the bottom (1983?) of the present cycle in reproductive success has taken at least eight years, which is one year longer than the previous longest decline (from 1957 to 1964). The reproductive success at the top of the recent cycle was approximately 750 times that at the presumptive bottom of the cycle, making Pacific mackerel off California one of the more variable cases known to fishery science. The temporal pattern of reproductive success since the recovery is roughly congruent with the previous historical pattern, but the scale appears to be different. The unreliability of the values estimated by Parrish and MacCall for the 1930s limits our ability to draw definitive comparisons.

POTENTIAL PRODUCTIVITY

Method

The Pacific mackerel resource is by nature highly variable. Standard fishery models, most of which are based on equilibrium assumptions, are inappropriate for addressing this variability and its consequences. Here we assess potential productivity by means of computer simulations. We re-create the fishery from 1929 to 1968 under various harvesting policies, basing the simulated resource response on the observed history of reproductive successes, and thus preserving the important temporal pattern of the fluctuations (cf Figure 3). The calculations use Pope's (1972) approximation to the catch equation, whereby annual catches are removed from the simulated stock instantaneously at midseason. Weights at age are taken from Parrish and MacCall (1978, Table 7), and availabilities at age are based on the average F relative to that of age 4+ for the 1945-46 to 1964-65 seasons, during which period the resource was fully exploited. The natural mortality rate (M) was assumed to be 0.5, and ages 4 and older are combined into a single age group. Table 4 gives age-specific parameter values used in the simulations.

Treatment of the stock-recruitment relationship (SRR) has a strong influence on estimates of productivity, and deserves extensive discussion. Because the simulated spawning biomass is usually different from the historical spawning biomass for a particular year, the simulated recruitment should be correspondingly different from the historical recruitment. The nature and extent of that difference is given by the SRR. Unfortunately, the historical reproductive successes do not show a clear functional SRR (Figures 2,4).

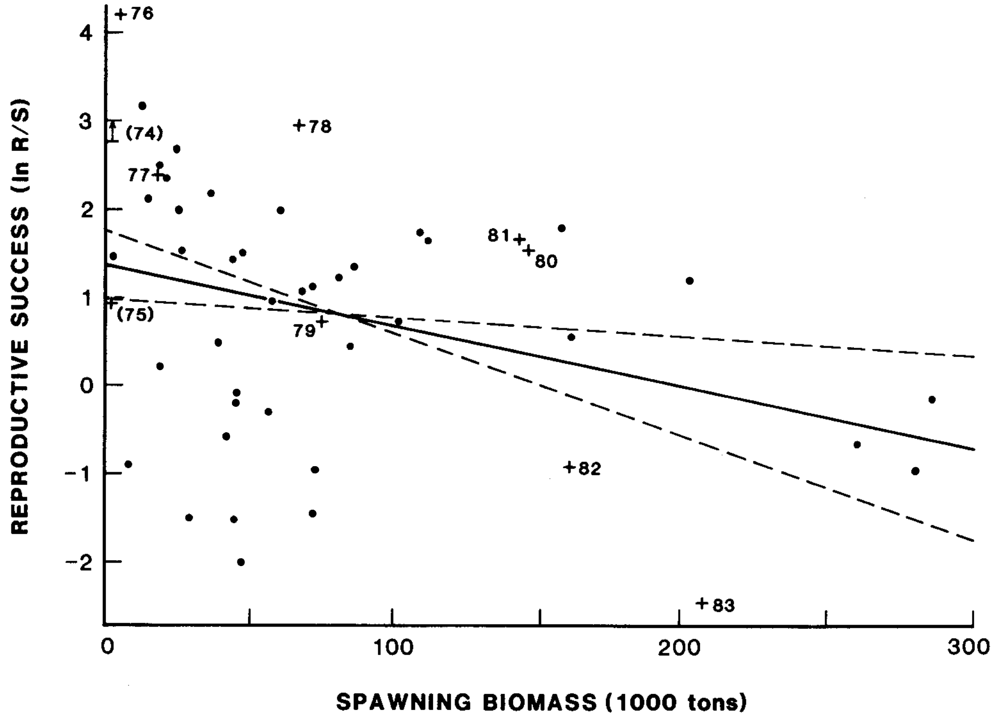

Figure 4. Relationship between Pacific mackerel reproductive success and spawning biomass, showing the linear regression estimates. Dashed lines show a nominal 90 percent confidence interval for the slope, *b*.

Therefore we consider two null models: first, that of "constant reproductive success" (CR/S), where historical reproductive successes are used without compensatory modification, and at the other extreme, "constant recruitment" (CR), where the historical recruitments themselves are used without modification, i.e., complete compensation. The true response must lie between the two extremes given by these null models, so they provide reasonable bounds on the estimated productivity of the resource. An intermediate level of compensation is represented by the Ricker SRR, which can be defined by a linear regression of ln(R/S) on spawning biomass (S). Some degree of compensation seems necessary because the abundance trajectory of the 40-year simulation reaches unreasonably high levels in the absence of harvest, whereas use of the Ricker SRR produces an abundance trajectory with upper bounds similar to the abundance levels observed in the 1930s and 1980s (Figure 5). It is important that we have no objective evidence that a Ricker SRR is appropriate. However, the model agrees with the trend in the data (Figure 4), and is mathematically convenient.

TABLE 4
Age-Specific Parameters Used in the Pacific Mackerel Fishery Simulations

	Age 1	2	3	4	5+
Availability	0.366	0.494	0.711	1.000	1.000
Weight (kg)	0.192	0.317	0.448	0.574	0.725
Fraction spawning	*	0.77	0.88	1.00	1.00
Initial abundance (10^6fish)	229.6	207.0	33.2	24.4	0.0

*Fraction age 1 is 0.54/EXP(15.8*B*), where *B* is total biomass (age 1+) in 10^6MT (Parrish and MacCall 1978).

The Ricker SRR used in the simulations retains the observed time series of anomalies in historical reproductive success,

$$\ln(R/S)_i = a - bS_i + e_i$$

where R_i is recruitment (in numbers) from the spawning in year i,
S_i is spawning biomass (kg),
a and b are parameters estimated from the historical data from 1929 to 1983,
and e_i is the anomaly in year i.

Although this regression estimate of parameters may be assumed to provide the best estimates of resource productivity from the simulations, the extreme variability of reproductive success (Figure 4) makes sensitivity analysis appropriate. In addition to the best-fitting Ricker SRR ($a = 1.242$, $b = 6.788/10^6$MT, $SE_b = 2.818/10^6$MT, 46*df*), we examined cases corresponding to the upper and lower 90% con-

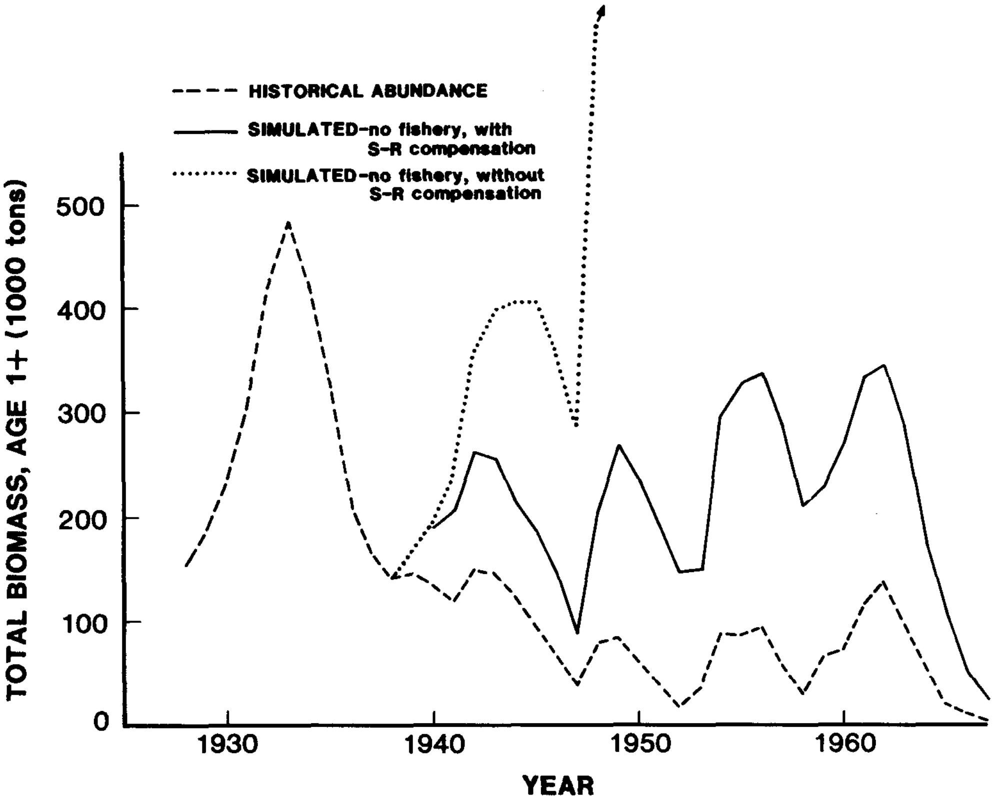

Figure 5. Time trajectories of simulated total biomass of Pacific mackerel. Solid line is based on the best-fitting Ricker SRR; dashed line is based on the CR/S model.

fidence limits of the slope parameter from the regression ($b_{\text{upper}} = 11.521/10^6\text{MT}$, $b_{\text{lower}} = 2.055/10^6\text{MT}$). Besides imprecision arising from natural variability, estimates of b are also influenced by systematic biases resulting from violations of simplifying assumptions. For example, Ludwig and Walters (1981) showed that random error in measurement of spawner abundance (S_i) tends to produce underestimates of b. In contrast, Walters (1985) showed that the time-series dynamics of propagation of environmental perturbations (e_i) tend to lead to overestimation of b. The extent of, and interaction among, these systematic biases is unknown.

Results

Although a wide variety of management policies could be evaluated by our simulation procedure, we present results for only one type of policy—that corresponding to the linear harvest formula of the present California management law. This type of policy can be written as

$$H = p(B\text{-}B_{\min}) \qquad \text{if } B>B_{\min}$$
$$H = O \text{ otherwise.}$$

Thus, the harvest (H) is specified by two parameters, and is given by the fraction (p, the *fraction*) of the excess of the total biomass (B) over a minimum total biomass ($B_{\min}$, the *cutoff*). Note that if the formula implies a negative harvest, no harvest is allowed. A *cutoff* of zero abundance is analogous to a constant effort policy. *Cutoff* values greater than zero approach a constant escapement policy, whereas *cutoff* values less than zero approach a constant harvest policy.

For the purpose of sensitivity analysis, we compare yields averaged over the 40-year simulation, given the five different stock-recruitment compensation models discussed above (Figure 6). This comparison examines the set of harvest formulas consisting of various *fractions*, given a *cutoff* of 18,144 MT (20,000 short tons) total biomass. The average annual yields are very consistent for *fractions* from 0.2 to 0.25; simulated spawning biomasses are most near their historical values (average is 80,573 MT); spawning successes are most near their historical values; and the influence of different assumed models of compensation is minimal. Accordingly, we should be able to place our greatest confidence in this region of the yield curves. Unlike the other models, the CR model produces an asymptotic yield curve because the model lacks feedback of harvests on subsequent recruitments. The CR/S model behaves badly at low fishing intensities, because it allows the simulated abundance to become unreasonably large, as was mentioned previously. As might be expected, the yield curve corre-

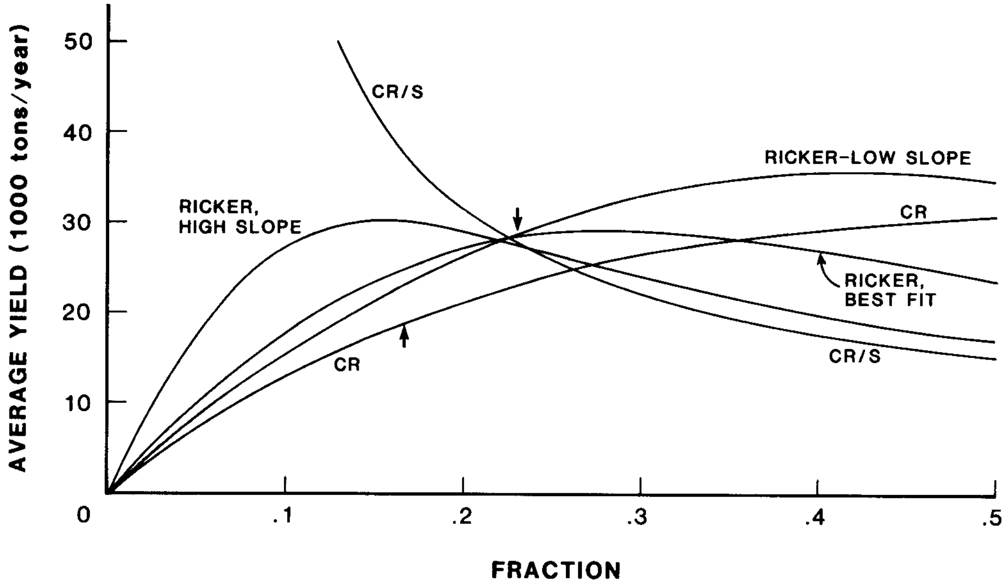

Figure 6. Comparison of average Pacific mackerel yields from linear harvest policies with a *cutoff* of 18,414 MT (20,000 short tons), and five assumed models of stock-recruitment compensation. The arrow denotes the simulations with greatest robustness, where simulated average spawning biomass is equal to the historical average.

sponding to the upper confidence limit for parameter *b* (i.e., the most compensation) tends to resemble the CR yield curve, and the lower confidence limit (i.e., least compensation) produces a yield curve closely resembling the CR/S curve at higher fishing intensities. Although the fishing intensity needed to produce the maximum average yield is sensitive to the assumed compensation model, the maximum average yield itself is much less sensitive, ranging from 29,000 to 36,000 MT (within the 90% confidence limits of the Ricker SRR).

Our simulation results are summarized by a yield isopleth diagram showing the average yields for various combinations of the *cutoff* and *fraction* parameters of the linear harvest formula (Figure 7). The region of greatest confidence in the simulation results, where average simulated spawning biomass is equal to the historical average, extends across the center of the diagram, rising slightly toward the right. Maximum average yield for a given *cutoff* appears as a ridge also rising toward the right. Maximum average yield for a zero-*cutoff* (constant effort) policy is 28,500 MT/year, whereas it exceeds 30,000 MT/year at large *cutoff* values.

In general, the standard deviation of annual harvest increases with larger *fractions*, but is nearly independent of *cutoffs* in the range of values examined here. The standard deviation of annual harvest rises in proportion to the *fraction* to about 15,000 MT at a *fraction* of 0.2, and then becomes roughly asymptotic at about 20,000 MT for *fractions* above 0.3. Because higher *cutoffs* require higher fractions to maximize yield, variability also increases with maximum average yield.

Formulas with negative *cutoffs* do not curtail harvest at low abundances, and therefore run a high risk of depleting the resource. The region of Figure 7 marked "collapse" shows those parameter values that result in total loss of the resource within the 40-year period of the simulation; the actual region of potential collapse extends to much lower *fractions*, but does not extend to positive values of *cutoff*, which serve to protect against total loss of the resource. Also, the isopleths of average yield for negative *cutoffs* do not recognize the long period of no yield following a collapse, so actual isopleths must bend downward much more sharply than is shown by the upper left section of Figure 7.

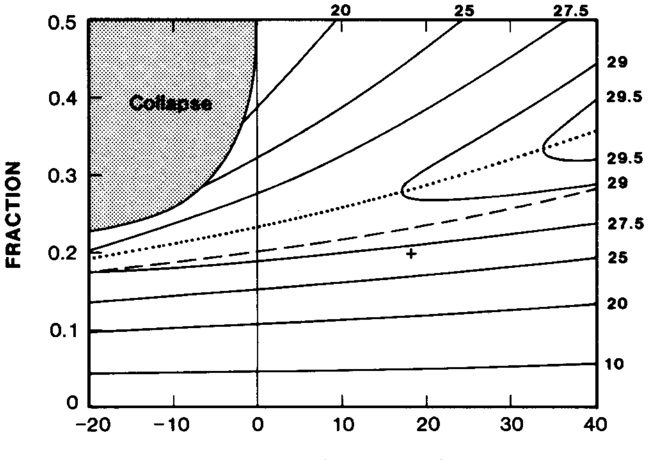

Figure 7. Average yield isopleths for linear harvest policies and the best-fitting Ricker SRR. Dotted line is maximum average yield, given the *cutoff*. Dashed line is the locus of greatest robustness, where simulated average spawning biomass is equal to the historical average. The cross denotes present management policy.

DISCUSSION

The high abundances of the 1930s and 1980s are remarkable events in the history of the fishery (Figure 1). We are now able to attempt to estimate how often these events occur. The paleosedimentary record of Pacific mackerel scales in the Santa Barbara Basin (Soutar and Isaacs 1974) shows two peak periods of deposition since 1800. One is in 1925-35, corresponding to the known abundance peak at that time. The other event occurred about 1830. Albeit imprecise, the simulated trajectory of Pacific mackerel abundances in the absence of a fishery (Figure 5) suggests that none of the post-1930 peaks would have been as large. Thus we can tentatively identify three major eruptions of the resource in the last 185 years, and conclude that the recent level of abundance is a rare event.

The ecological effects of increased Pacific mackerel abundance are confounded with other recent changes in the environment and fisheries. Mackerel extended their range far to the north during the 1980s, but the migratory effects of population pressure are difficult to separate from the influence of the strong 1982-84 oceanic warming. During 1983 and 1984 Pacific mackerel schools were reported in Puget Sound and Queen Charlotte Sound (Canada), and frequently were caught off Oregon in "blind" purse seine sets sampling nekton (W. Pearcy, Oregon State Univ., pers. comm.). Mackerel were abundant in Monterey Bay and the Gulf of the Farallons, off San Francisco. James Messersmith (CDF&G, Sacramento, California, pers. comm.) identified a very small juvenile Pacific makerel caught in 1984 in Humboldt Bay, near Eureka. This is clear evidence for at least marginally successful spawning over 400 nmi north of Point Conception, the usual northern boundary of spawning (Kramer and Smith 1970).

Mais (1981) reported a sudden change toward a much younger age composition of northern anchovies (*Engraulis mordax*) in southern California beginning about 1977. He suspected increased predation by Pacific mackerel and increased fishing pressure from the expanding Mexican anchovy fishery to be the major causes of this shift. Also, anchovy abundance has declined severely from the levels of the mid-1970s (ca. 2 million MT spawning biomass) to 1984 (ca. 0.3 million MT). In view of the Pacific mackerel abundances estimated in this paper, which are much larger than the previous estimates available to Mais, an increased mortality rate of anchovies due to mackerel predation is a very likely cause of these changes in the anchovy stock. Anchovy age composition analysis by Methot (1983) indicated large changes in the natural mortality rate of anchovies, but a conclusive statistical demonstration of this phenomenon is difficult.

The northerly extension of Pacific mackerel has been popular with commercial fishermen at Monterey, where landings have reached record levels. On the other hand, recreational fishermen seeking salmon in the Gulf of the Farallons have complained about interference and gear losses caused by mackerel. Salmon biologists in Canada have been concerned about potential increased predation on salmon smolts in Queen Charlotte Sound. To the south, recreational fishermen often spurn Pacific mackerel in the pursuit of more esteemed sportfish. Indeed, some recreational fishermen blame increased abundance of Pacific mackerel for the increased harassment of recreational fishermen by California sea lions (*Zalophus californianus*). The importance of Pacific mackerel as forage aside, these perceptions combine with the harvesting desires of southern and central California commercial fishermen to form an unusually unified public opinion that allowable catches should be increased. This opinion is strengthened by the prevailing industry opinion—confirmed by the estimates in this paper—that Pacific mackerel abundance, and hence allowable harvest, have been underestimated for several years.

Evaluation of the present management policy requires consideration of both interacting components of this policy: the harvest formula, and the abundance estimates used to implement it. Within the framework of the present linear harvest formula there is little reason to change the present *cutoff* level of 18,144 MT (20,000 short tons). This level provides sufficient protection from severe depletion while allowing a fishery in nearly all years. The latter consideration is additionally important because the present method of estimating abundance depends entirely on fishery information.

The present *fraction* of 0.2 is more amenable to change. The simulations, which assume all catches are accounted for in the harvest formula, indicate that a higher *fraction* is likely to increase average yield up to a maximum of about 29,000 MT/yr at a *fraction* of 0.28 (Figure 7). The sensitivity analysis showed that the optimal *fraction* is strongly influenced by the assumed model of compensation. However, for simplicity the following discussion will consider only the results of the best-fitting Ricker SRR, the case that best corresponds to available information.

Strict maximization of yield is often undesirable because the last increments in yield are achieved at the cost of relatively large decreases in abundance and correspondingly large increases in fishing effort. Of course, if Pacific mackerel are perceived as pests, this reduction in abundance may be desirable in its own right. Assuming we wish to conserve the resource, a popular rule of thumb is the "$F_{0.1}$" policy suggested

TABLE 5
Yield and Biomass Statistics for Various *Fractions*, Given a *Cutoff* of 18,144 MT (20,000 Short Tons), Based on Simulations Using the Best-Fitting Ricker Stock-Recruitment Model

	Yield		Biomass	
Fraction	Average	Standard deviation	Average total	Average spawning
0.00	0.0	0.0	236	160
0.01	2.14	1.02	232	157
0.20	27.1	15.4	153	90
0.24	28.6	17.3	137	78
0.28	29.0	18.7	122	67
0.30	29.0	19.2	115	63
0.40	26.7	20.4	85	44

(Values in 1000 MT).

by Gulland and Boerema (1973), whereby fishing effort should not be greater than the intensity at which the marginal yield from an additional unit of effort is ten percent of the marginal yield at very low levels of fishing. For the present case of Pacific mackerel, *fraction* may be substituted for "effort", giving a $\textit{fraction}_{0.1}$ of 0.24. Table 5 gives some values of *fraction* together with comparative statistics from the simulation results. It is important that these yield estimates assume that all catches are accounted for by the harvest formula, whereas present management policy ignores recreational catches, incidental catches during the closed commercial season, and foreign fishery catches—all of which add up to many thousand tons. Thus the effective *fraction* must be considered to be somewhat larger than the nominal *fraction* in the wording of the official management policy. Finally, the 40,000 MT harvests that have been taken from 1979 to 1984 must not be expected to continue for long under the present, or any, management policy.

ACKNOWLEDGMENTS

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AN INVERSE EGG PRODUCTION METHOD FOR DETERMINING THE RELATIVE MAGNITUDE OF PACIFIC SARDINE SPAWNING BIOMASS OFF CALIFORNIA

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ABSTRACT

The California Department of Fish and Game is required by state law to determine annually whether the spawning biomass of the Pacific sardine (*Sardinops sagax*) is more or less than 20,000 short tons[1]. The sardine biomass appears to be increasing; however, the population level is too low to be reliably estimated by existing techniques. An inverse egg production method is proposed, to allow an objective determination of the relative magnitude of the spawning biomass of Pacific sardines.

The normal egg production method estimates adult biomass by measuring daily egg production in the spawning area and specific fecundity of the population. The inverse method estimates the area over which a specified spawning biomass (20,000 tons) would be assumed to occur. Components of egg production and specific fecundity for sardines—including average female weight, batch fecundity, spawning fraction, and daily egg production rate—were estimated from previous studies. A survey was designed to cover the Southern California Bight and provide a 95% probability of encountering the calculated spawning area if the spawning biomass is at least 20,000 tons. Recommendations are made, based on possible survey results.

RESUMEN

Por ley estatal, el Department of Fish and Game de California debe determinar anualmente si la biomasa de desove de la sardina del Pacífico (*Sardinops sagax*) es menor o mayor que 20,000 toneladas cortas (1 tonelada corta = 0.907 toneladas métricas. La biomasa de la sardina parece estar aumentando; sin embargo, el nivel poblacional es demasiado bajo para poder ser evaluado fidedignamente mediante las técnicas actuales. Se propone un método inverso de producción de huevos; éste posibilitará una determinación objetiva de la magnitud relativa de la biomasa de desove de la sardina del Pacífico. La técnica de producción de huevos normal evalúa la biomasa de los adultos mediante la medición de la producción diaria de huevos en el área de desove, y la fecundidad específica de la población. El método inverso estima el área en la cual una biomasa de desove dada (20,000 toneladas) supuestamente tendrá lugar. Sobre la base de estudios previos se estimaron los componentes producción de huevos y fecundidad específica para la sardina, incluyendo el peso promedio de las hembras, fecundidad de la puesta, fracción desovante, y producción diaria de huevos. Se diseñó un estudio para cubrir la Bahía del Sur de California, ofreciendo un 95% de probabilidad de localizar el area de desove calculada si la biomasa del mismo es de, al menos, 20,000 toneladas. Sobre la base de los posibles resultados del estudio se efectúan las recomendaciones correspondientes.

INTRODUCTION

The Pacific sardine fishery increased dramatically beginning in 1915 to a maximum catch of nearly 800,000 tons landed in the 1936-37 season. Annual season catches fluctuated around 600,000 tons over the next decade, and then declined steadily (Murphy 1966). The Pacific sardine population collapsed under fishery and environmental pressure (Clark and Marr 1955) and declined from biomass levels estimated at more than 3 million tons in the mid-1930s to levels thought to be as low as 5,000 tons by the 1970s (Murphy 1966; MacCall 1979; Smith 1972) (Figure 1). California legislation enacted in 1974 (1) placed a moratorium on fishing sardines while the biomass remains below 20,000 tons, (2) allows a 1,000-ton fishery for sardines when the spawning biomass reaches 20,000 tons, and (3) requires the Department of Fish and Game to determine annually whether this biomass has been reached. The moratorium has remained in effect because the spawning biomass has been considered to be below 20,000 tons since 1974.

Signs of an increase in the Pacific sardine population have been evident in recent years (Wolf[2]; Klingbeil and Wolf 1984; Klingbeil 1981, 1982, 1983). Although information currently available is indirect

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[Manuscript received February 15, 1985.]

[1] Commercial landings, biomass estimates (Murphy 1966), tonnages specified in legislation, and tonnages in this paper are reported in short tons.

[2] Wolf, P. MS. Status of the spawning biomass of the Pacific sardine, 1984-85.

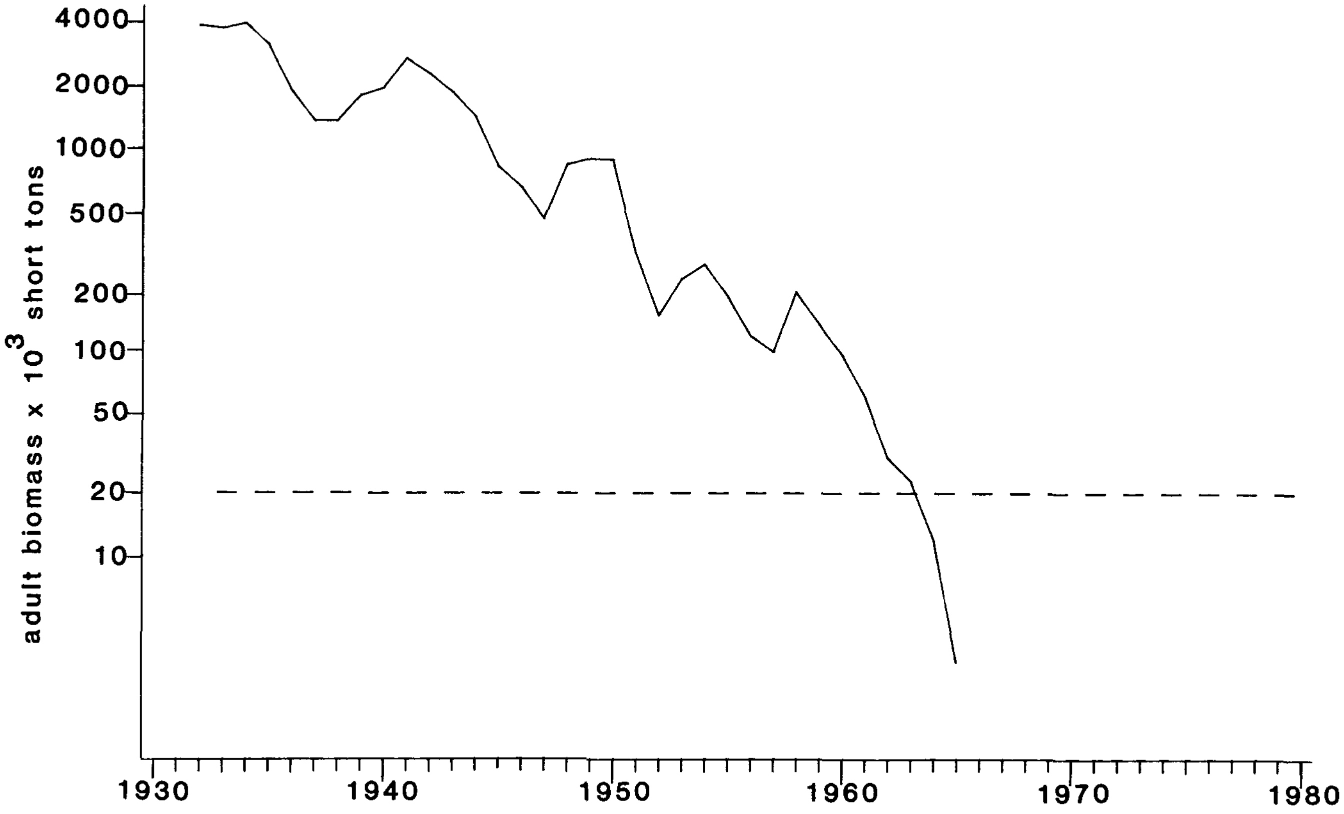

Figure 1. Time series of biomass estimates of adult Pacific sardines (fish age 2 years and older), 1932-65 (Murphy 1966; MacCall 1979). Dashed line denotes 20,000 tons.

and only indicates increases in the relative abundance of sardines, it appears that the spawning biomass could exceed 20,000 tons in the near future. Previous biomass estimates for sardines off California were based on analyses of catch data (Murphy 1966; MacCall 1979) and larval censuses (Smith 1972). The egg production method was developed by Parker (1980) and has been used to estimate the spawning biomass of anchovies off California (Picquelle and Hewitt 1983) and anchovies and sardines off Peru (Santander et al. 1982). However, no known method of biomass estimation is considered reliable at sardine biomass levels below 100,000 tons (MacCall 1984b).

The egg production method estimates spawning biomass as the quotient of the daily production of eggs in the spawning area and the daily fecundity of the population per ton of spawners (Parker 1980). The proposed inverse egg production method estimates the area over which the spawning products of a specified adult biomass could be assumed to occur, given certain conditions of average female weight, batch fecundity, spawning fraction, and daily egg production rate. These parameters were estimated from previous studies. We have designed a survey to cover the Southern California Bight and include the calculated range of spawning area if the minimum 20,000 tons of spawning biomass of Pacific sardine is present. Location and extent of the survey area, and time of year of the survey were determined from historical occurrences of sardine eggs and larvae during periods when sardine biomass levels were near 20,000 tons.

EGG PRODUCTION METHOD

The egg production method derived by Parker (1980) and applied by Picquelle and Hewitt (1983) and Hewitt (1984) estimates spawning biomass as

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

where B = spawning biomass (MT)

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

W = average weight of mature females (grams),

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

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

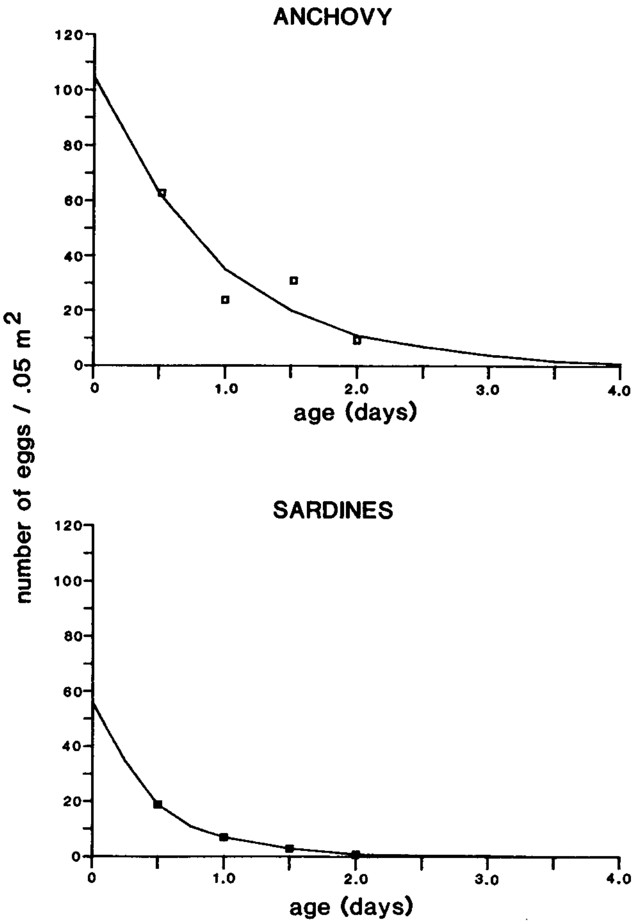

Figure 2. Exponential mortality model for estimating daily egg production rate of anchovies (*Engraulis ringens*) and sardines (*Sardinops sagax sagax*) off Peru (Smith, P.E., H. Santander, J. Alheit. MS. Comparison of the mortality and dispersal of sardine [*Sardinops sagax sagax*] and anchovy [*Engraulis ringens*] eggs off Peru.)

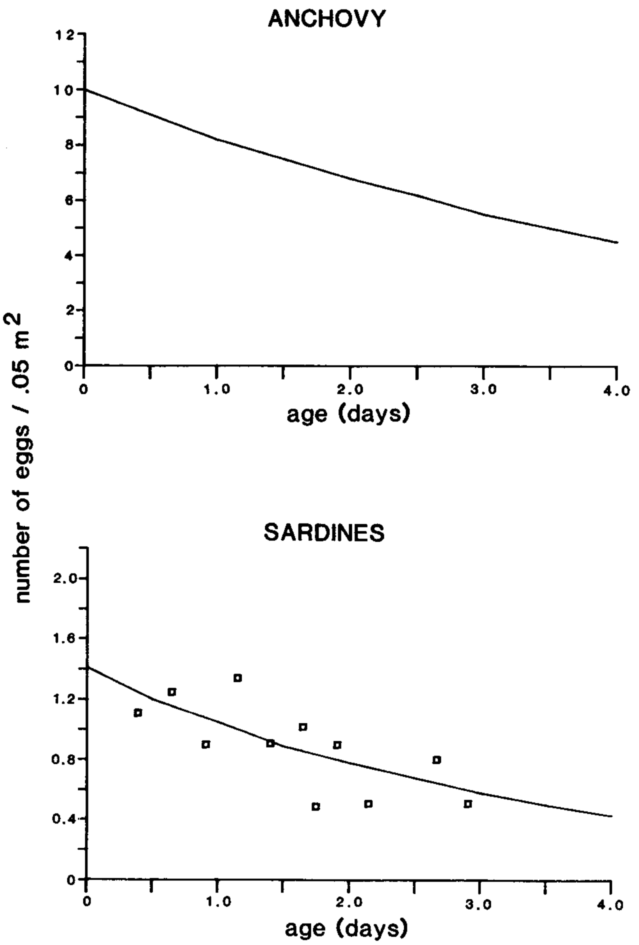

Figure 3. Exponential mortality model for estimating daily egg production rate of anchovies (*Engraulis mordax*) 1980-84, using CalVET nets, and sardines (*Sardinops sagax*), 1951-59, using oblique (CalBOBL) tows, off California.

S = fraction of mature females spawning per day,

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

k = conversion factor from grams to metric tons.

INVERSE EGG PRODUCTION METHOD

In the egg production method, the parameters of daily egg production and population fecundity are estimated by measurements collected over the duration of the survey. The parameter P_o is estimated by fitting an exponential mortality curve to counts of aged eggs collected in plankton samples and extrapolating back to the number of eggs at the time of spawning. Parameters W, F, S, and R are estimated from samples of adult fish collected during the survey.

In the inverse egg production method, the spawning biomass was specified and the equation solved for A_l:

$$A_l = \frac{B_l\, RFSm}{P_o\, k_l\, W}$$

where A_l = spawning area of biomass B_l in nautical miles^2,

B_l = spawning biomass, in short tons,

k_l = conversion factor from grams to short tons,

m = conversion factor from 0.05 meter^2 to nautical miles^2.

We propose this inverse egg production method as a preliminary, relatively inexpensive technique for identifying whether the spawning biomass has exceeded a specified level. The parameters for sardines are estimated from previous studies, rather than measured during the survey. Where no reliable parameter values are available, we use a range of values.

TABLE 1
Values of Parameters Used to Estimate Spawning Area, and Resulting Estimates

B_1	W	R	F	P_o	S	A_1
Spawning biomass (short tons)	Average female weight (g)	Sex ratio (females/total)	Batch fecundity (eggs/batch/female)	Egg production (eggs/.05m^2-day)	Spawning fraction (spawning females/ total females)	Spawning area (nautical miles^2)
20,000	120	0.5	32,000	5.0	0.02	141
					0.05	353
					0.10	706
					0.15	1058
				1.5	0.02	470
					0.05	1176
					0.10	2352
					0.15	3528

Parameters P_o, W, F, S, and R

Estimates of daily egg production for sardines and anchovies off Peru[3] indicate that egg production rates are lower for sardines than for anchovies by a factor of 1:2 (Figure 2). Applying this relationship to 1980-84 annual estimates (Hewitt 1984) of daily egg production rate for anchovies (approximately 10 eggs/ 0.05m^2) off California (Figure 3) results in an estimated sardine daily egg production rate of approximately 5 eggs/0.05m^2. CalCOFI egg surveys conducted from 1951 through 1959 yielded an estimated California sardine daily egg production rate of approximately 1.5 eggs/0.05m^2 (Figure 3). This value is thought to be low because of the sampling technique (oblique tows instead of vertical egg tows), which may have overestimated the surface area of water sampled. Both tentative values of P_o were used in the inverse egg production method. The parameter W, average weight of mature females, is estimated to be 120 grams (MacGregor 1957). The female fraction of the population by weight, R, is assumed to be one-half. Batch fecundity, F, is estimated at 32,000 eggs (MacGregor 1957). Spawning fraction, S, for other pelagic species ranges from 0.02 females spawning per day (spawning once every 50 days) for Pacific sauries (Hatanaka 1956) to 0.14 females spawning per day (spawning once every 7 days) for anchovies (Hunter and Macewicz 1980). This range of values for S was used for sardines. Setting biomass, B_1, at 20,000 tons, and using the parameters described above, we calculated a range of values for the spawning area, A_1 (Table 1).

Spawning Area

The calculated area, A_1, over which the spawning products of 20,000 tons of Pacific sardines could be expected to occur ranges from 141 to 1,058 nm^2 for a high daily egg production rate of 5 eggs/0.05m^2, and from 470 to 3,525 nm^2 for a low daily egg production rate of 1.5 eggs/0.05m^2 (Table 1). Based on these results, a useful estimate of A_1 is 500 nm^2.

PROPOSED SURVEY

We examined historical CalCOFI egg and larval survey data to determine the area and time of year over which sardine spawning would be likely to occur. Mean number of eggs/10m^2 and larvae/10m^2 in CalCOFI regions 7 and 8 from 1954 to 1960 plotted by station and by month (Figure 4) indicate that sardine spawning occurs in the Southern California Bight from April through June. CalCOFI ichthyoplankton surveys during 1981 and 1984 showed evidence of sardine spawning in this area, primarily in coastal locations (Figure 5) from April through June. Brewer and Smith (1982) reported spring occurrences of sardine larvae in nearshore areas of the Southern California Bight from 1978 to 1980, including a relatively high occurrence of larvae in the late summer and fall of 1980.

We have designed a survey that covers CalCOFI regions 7 and 8 (CalCOFI lines 80-97, stations .20-.65) during May. CalCOFI regions 7 and 8 cover an area of approximately 32,000 nm^2 (Smith et al. 1976). The critical spawning area, A_1, estimated at 500 nm^2, is approximately 2% of the survey area. Using a table for determining confidence limits of a proportion (Natrella 1963), we determined a sample size of 374 CalVET samples (vertical egg tows) to be the minimum effort required to locate the spawning area within the survey area, with 95% confidence limits. For convenience, current practices for anchovy egg production cruises were adapted for the sardine spawning area survey. These samples are 4 nm apart offshore

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[3] Smith, P.E., H. Santander, J. Alheit. MS. Comparison of the mortality and dispersal of sardine (*Sardinops sagax sagax*) and anchovy (*Engraulis ringens*) eggs off Peru.

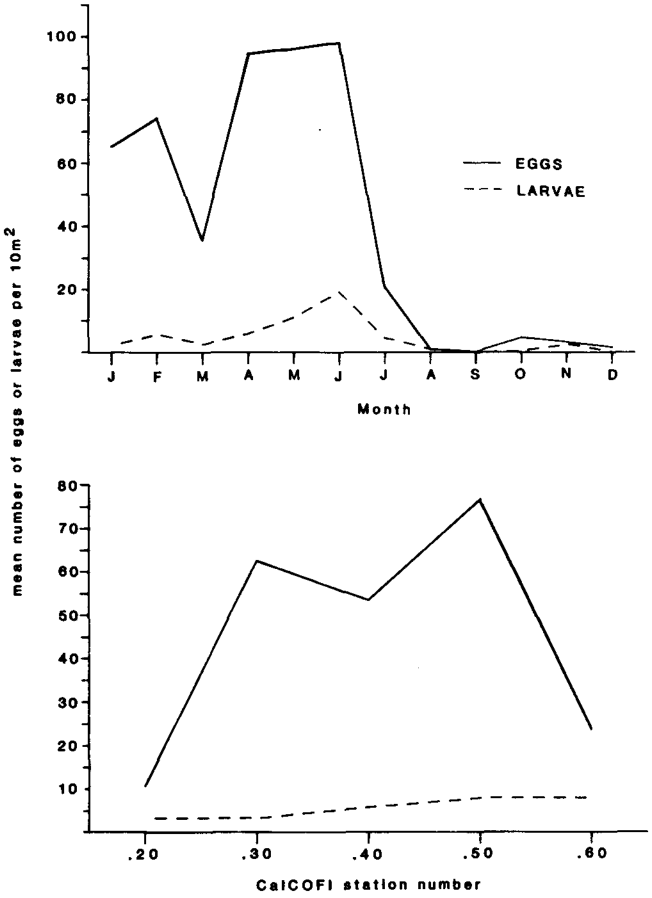

Figure 4. Occurrence of sardine eggs and larvae in CalCOFI regions 7 and 8, 1954-60, by month and by station.

and 10 nm apart alongshore for an area representative of 40 nm^2. The projected area of 500 nm^2 is therefore expected to contain 12 or 13 positive stations for 20,000 tons spawning biomass. If no positive stations result, the spawning biomass may be considered to be below 20,000 tons. Positive stations occurring over an area of 500 nm^2 would indicate that the spawning biomass of Pacific sardines is at least 20,000 tons. This proposed survey (Figure 6) is scheduled to be conducted in May 1985.

DISCUSSION

Indirect or incidental evidence of the relative abundance of sardines is adequate information for determining whether the spawning biomass is more or less than 20,000 tons only while biomass levels obviously remain very low. No estimation techniques are reliable at biomass levels as low as 20,000 tons. The proposed inverse egg production method allows an objective determination of the relative magnitude of the spawning biomass of Pacific sardines as required by state law.

The large range of values calculated for A_1 (the spawning area) resulted from using a range of values to estimate parameters P_0 (daily egg production rate) and S (spawning fraction). These parameters are not known for Pacific sardines. The low estimate for P_0 was based on California data, which were collected using an oblique tow instead of the vertical egg tow designed specifically for use in the egg production method[4]. The high estimate of P_0 depends on the relationship between egg production rate of anchovies and sardines off Peru, a relationship that has not been demonstrated for sardines off California. Daily egg production rate and spawning rate must be determined for Pacific sardines. The remaining adult parameters must be recalculated for the current California population of sardines as well.

The area parameter of the egg production method was chosen as the first indicator of population recovery because under the conditions of small numbers of positive samples it is the most reliable indicator of spawning biomass (Smith and Hewitt 1984; Smith 1973). The estimated rate of egg production is inherently the most variable (Parker 1980). The reasons for this are that the eggs are spawned in dense patches; the dispersion rate is quite slow; and rate of production is estimated from the extrapolation of an exponential mortality curve based on a small number of days of spawning. Although this approach may be useful when there are hundreds of positive samples, the results are not reliable with the few positive samples predicted for the initial years of the sardine population recovery. A simulation model of the sampling process including the initial patchiness, the historical mortality rate, and the number of observations within the spawning habitat illustrates these points (Table 2). The upper part of the table demonstrates the need for hundreds of samples to obtain a useful egg production rate; the lower part of the table establishes the small number of observations necessary to obtain a precise estimate of spawning habitat.

The first step in managing a resurgence of sardines is detecting the onset of recovery. It is recommended that Pacific sardines be surveyed annually to determine when the biomass exceeds 20,000 tons. The second management step will require measuring the extent of recovery. Several techniques of abundance estimation may be successfully applied to sardines, including the egg production method, acoustic surveys, larval census, systematic aerial surveys, or combinations of these (MacCall 1984b). Selection or development of methods will depend on management goals, performance of the resource in recovery, and fishery develop-

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[4] Smith, P.E., W. Flerx, and R. Hewitt. MS. The CalCOFI vertical egg tow (CalVET) net.

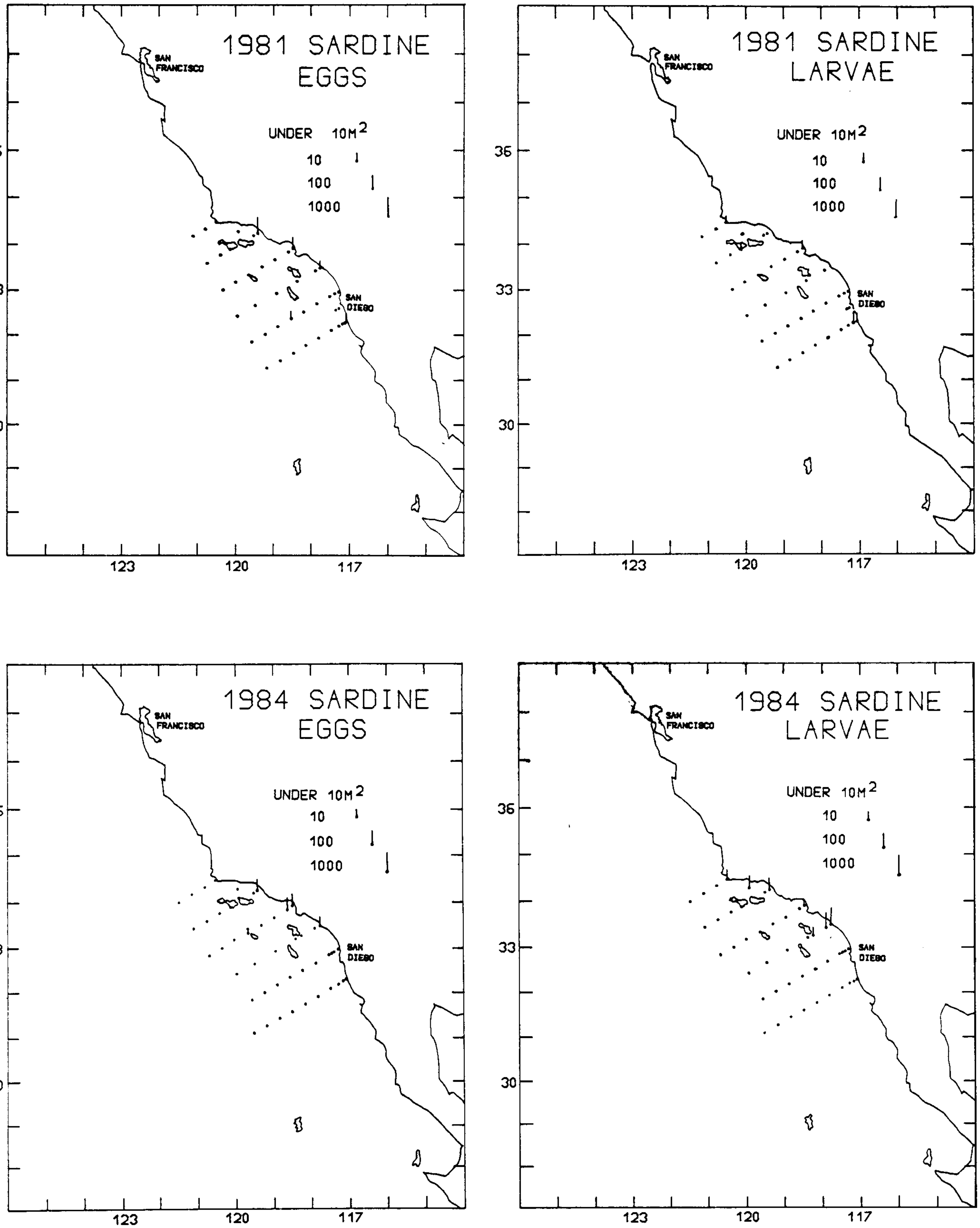

Figure 5. Abundance (total numbers) and location of sardine eggs and larvae in Southern California Bight captured during CalCOFI quarterly cruises in 1981 (January-December) and 1984 (January-July data only).

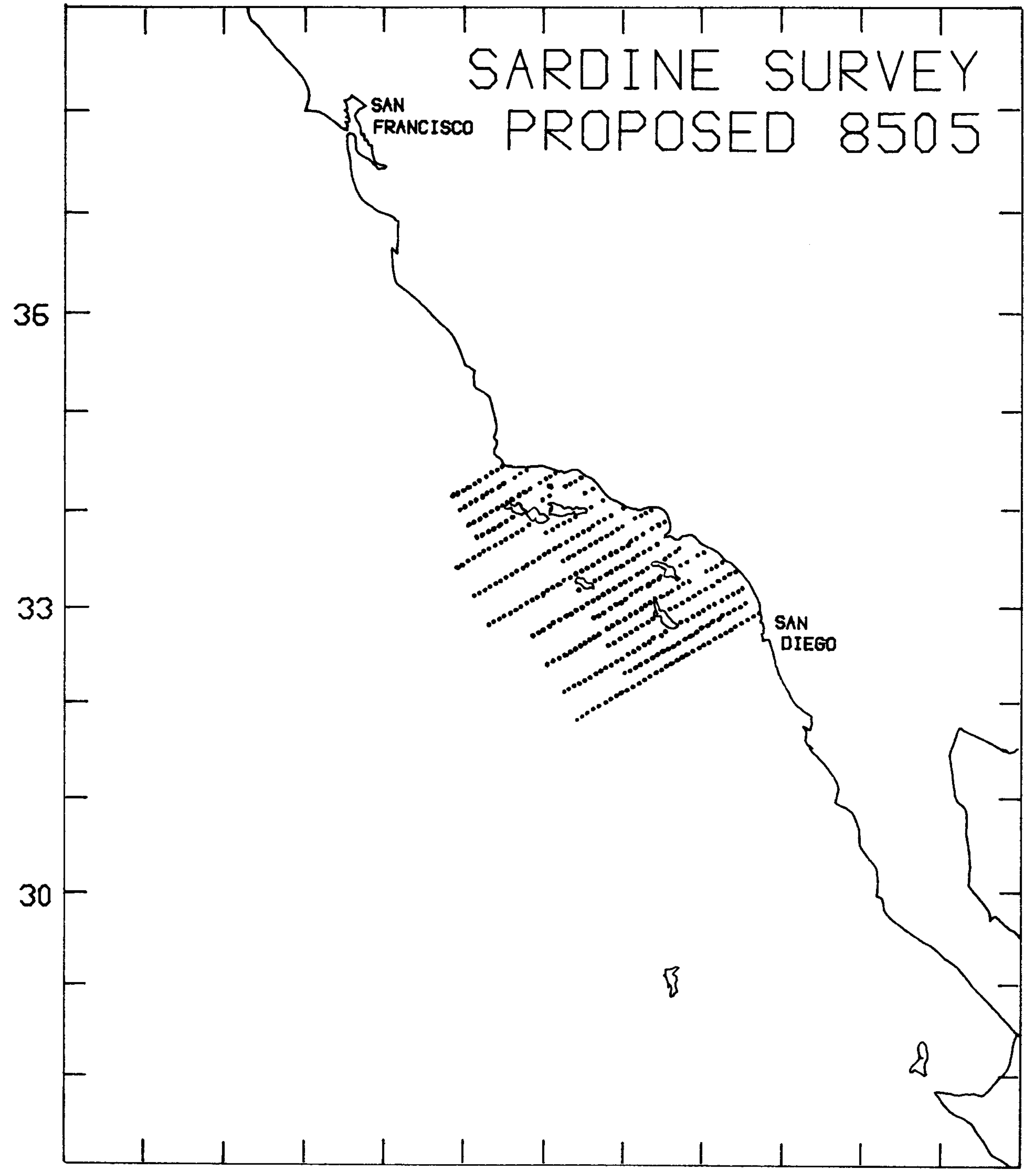

Figure 6. Proposed minimum probability sardine survey, May 1985.

ment. An inverse egg production method could be used as a regular, inexpensive technique, in combination with an alternative, periodic, absolute biomass estimation method.

ACKNOWLEDGMENTS

We would like to acknowledge the editorial assistance of Marc Mangel, Alec MacCall, and Rick Klingbeil. Terry Palmisano helped with graphics. Historical

TABLE 2
Simulation of a 20,000-Ton Spawning Biomass of Pacific Sardine Based on Historical Samples

	Number of observations within spawning area								
	1	5	10	20	50	100	200	500	1000
Estimated biomass (× 10^3 tons)									
< 0	18	8							
0 - 2	36	8	7	3					
2 - 14	18	42	38	37	30	18	18	1	
14 - 26	8	27	25	27	48	64	67	96	100
26 - 38	8	6	10	18	21	18	15	3	
38 - 50	2	2	11	6	1				
50 - 62	1	3	5	6					
62 - 74	2	1	4	1					
74 - 86	0	0	0	1					
86 +	7	3							

	Number of observations within spawning area								
	1	5	10	20	50	100	200	500	1000
Probability of zero eggs									
One-day-old	.70	.35	.09	.01	0	0	0	0	0
Two-day-old	.59	.27	.03	.01	0	0	0	0	0
Three-day-old	.53	.12	.01	.01	0	0	0	0	0
Joint probability	.22	.01	0	0	0	0	0	0	0

Simulation based on Ab (0.375 days), Bb (1.375 days), Cb (2.375) (Smith 1973), negative binomial factors (*m,k*) Ab (4.47, .093), Bb (3.31, .179), Cb (2.45, .274), and habitat egg production parameters of 5 eggs per unit observation and instantaneous mortality rate of 0.3/day.

sardine egg data were entered and edited by Cindy Meyer and Celeste Santos.

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DESCRIPTIONS OF LARVAE OF CALIFORNIA YELLOWTAIL, *SERIOLA LALANDI*, AND THREE OTHER CARANGIDS FROM THE EASTERN TROPICAL PACIFIC: *CHLOROSCOMBRUS ORQUETA*, *CARANX CABALLUS*, AND *CARANX SEXFASCIATUS*

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ABSTRACT

Larvae are described for four species of jacks, family Carangidae. Three of these, *Seriola lalandi* (California yellowtail), *Chloroscombrus orqueta*, and *Caranx caballus*, occur in the CalCOFI region. A fourth species, *Caranx sexfasciatus*, occurs from Mazatlan, Mexico, to Panama. Species are distinguished by a combination of morphological, pigmentary, and meristic characters. Larval body morphs range from slender *S. lalandi*, with a relatively elongate gut, to deep-bodied *C. sexfasciatus*, with a triangular gut mass. Pigmentation patterns are characteristic for early stages of each species, but all except *C. orqueta* become heavily pigmented in late stages of development.

RESUMEN

Se describen las larvas de 4 especies de carángidos (Carangidae). Tres de ellas, *Seriola lalandi* (jurel), *Chloroscombrus orqueta*, y *Caranx caballus* se encuentran en la región de la CalCOFI. La cuarta especie, *Caranx sexfasciatus,* se encuentra desde Mazatlán, México, hasta Panamá. Las especies se distinguen por una combinación de rasgos morfológicos, pigmentarios, y merísticos. Los Tipos de larva varían desde delgados, como *S. lalandi*, son vísceras relativamente elongadas, hasta altos, como *C. sexfasciatus*, con una masa visceral triangular. Los patrones de pigmentación son característicos para los estadios tempranos de cada especie, pero todos, excepto *C. orqueta*, se vuelven fuertemente pigmentadas en los estadios de desarrollo tardíos.

INTRODUCTION

Numerous species of carangid fishes occur in the eastern Pacific, but with the exception of jack mackerel (*Trachurus symmetricus*), these species spawn in tropical or subtropical waters. Few species spawn far enough north to occur in the CalCOFI sampling region. One species, the California yellowtail, *Seriola lalandi*, supports an important recreational fishery off southern California and Baja California, and it briefly supported a commercial fishery during the 1950s (MacCall et al. 1976). Larvae of *Seriola* species from other regions of the world have been described (see literature review in Laroche et al. 1984), but larvae of eastern Pacific *Seriola lalandi* have not previously been described[1]. This paper also describes larvae of two other carangids, *Chloroscombrus orqueta* and *Caranx caballus*, occurring in the CalCOFI region, and a third carangid, *Caranx sexfasciatus*, which occurs to the south.

MATERIALS AND METHODS

Larvae used in this work were obtained from various plankton collections made in the eastern tropical Pacific, including those of CalCOFI, EASTROPAC, the Inter-American Tropical Tuna Commission, Bureau of Sport Fisheries and Wildlife, and Scripps Tuna Oceanography cruises. In addition, specimens of *Chloroscombrus orqueta*, dipnetted near San Carlos Bay in the Gulf of California, were provided by Robert Behrstock, formerly of Humboldt State University. Several small larval *Seriola lalandi* reared at the Southwest Fisheries Center's La Jolla laboratory were also examined.

Developmental series were assembled for each species, and morphological and pigmentation changes were described using the methods and terminology of Moser and Ahlstrom (1970) and Ahlstrom et al. (1976). Body lengths given in the text and tables represent notochord length in preflexion- and flexion-stage larvae, and standard length in postflexion larvae and juveniles. Descriptions of fin formation were limited by the condition of the specimens, because many had become decalcified in preservative over prolonged storage. A limited number of specimens were successfully stained, allowing observation of meristic characters and head spination.

[Manuscript received March 8, 1985.]

[1] Seven of the illustrations in this paper originally were included in a manuscript by E.H. Ahlstrom and B.Y. Sumida entitled "Early life history studies of eastern Pacific carangids." This manuscript was prepared for a symposium held in Ensenada, Mexico, in February 1975, the proceedings of which were not published. The manuscript is a general summary of some ontogenetic and adult taxonomic characters of nine carangid genera that occur in the eastern Pacific. It is now available as Southwest Fisheries Center Administrative Report LJ-85-02.

TABLE 1
Comparative Morphometry of Five Species of Carangid Larvae

	$\frac{\text{Snout-anus length}}{\text{Body length}}$	$\frac{\text{Head length}}{\text{Body length}}$	$\frac{\text{Eye diameter}}{\text{Head length}}$	$\frac{\text{Snout length}}{\text{Head length}}$	$\frac{\text{Body depth}}{\text{Body length}}$
Seriola lalandi					
A	*59.6 ±1.34(58-61)	28.2 ±1.30(27-30)	31.0 ±1.87(28-33)	30.2 ±2.28(28-33)	19.4 ±0.55(19-20)
B	61.5 ±0.58(61-62)	31.5 ±1.00(30-32)	30.8 ±1.50(29-32)	30.5 ±1.00(29-31)	23.2 ±2.06(21-26)
C	63.8 ±1.68(62-66)	34.6 ±1.40(32-36)	30.7 ±2.14(28-34)	27.1 ±2.61(24-31)	29.7 ±1.50(27-31)
D	60	31	32	26	29
Trachurus symmetricus	calculated from Ahlstrom & Ball (1954) (Size categories were given equal weighting in calculating means; standard deviation not calculable from data as published.)				
A	56.6 (54-58)	25.2 (17-32)	41.6 (36-51)	No snout lengths measured	21.4 (16-26)
B	59.3 (58-61)	33.2 (30-35)	35.8 (34-37)		26.7 (25-28)
C	58.0 (55-60)	36.2 (35-38)	34.0 (32-37)		27.4 (26-28)
D	54.0	29.5 (28-31)	32.0 (31-33)		24.5 (24-25)
Chloroscombrus orqueta					
A	57.3 ±2.31(56-60)	32.7 ±2.52(30-35)	31.7 ±0.58(31-32)	30.7 ±3.21(27-33)	35.0 ±4.36(30-38)
B	57.2 ±0.96(56-58)	38.0 ±0.82(37-39)	36.0 ±1.82(34-38)	28.0 ±0.82(27-29)	41.5 ±3.00(39-45)
C	50.4 ±3.36(44-55)	34.8 ±2.52(30-38)	36.4 ±2.73(32-40)	25.8 ±2.09(23-28)	43.4 ±1.63(41-46)
D	40.5 ±2.12(39-42)	30.5 ±2.12(29-32)	33.0 ±1.41(32-34)	28.0 ±1.41(27-29)	42.0 ±0.00(42)
Caranx caballus					
A	59.7 ±1.53(58-61)	34.3 ±1.53(33-36)	28.3 ±0.58(28-29)	29.3 ±2.31(28-32)	34.3 ±2.31(33-37)
B	57.0 ±2.00(55-59)	35.0 ±1.73(33-36)	33.0 ±1.73(31-34)	27.0 ±2.00(25-29)	42.0 ±1.73(41-44)
C	55.0 ±1.76(52-58)	35.9 ±1.60(33-38)	34.8 ±2.78(30-40)	25.1 ±3.48(21-32)	43.9 ±1.73(42-46)
D	52	36	35	26	39
Caranx sexfasciatus					
A	54.6 ±1.14(53-56)	32.0 ±3.08(29-37)	31.6 ±2.30(28-34)	29.0 ±2.34(27-33)	35.4 ±4.93(29-42)
B	58.3 ±1.53(57-60)	35.3 ±2.52(33-38)	33.3 ±2.08(31-35)	29.0 ±1.73(27-30)	50.3 ±5.51(45-56)
C	57.1 ±3.81(51-62)	37.6 ±1.84(34-40)	34.8 ±1.69(33-38)	25.5 ±2.88(20-28)	53.2 ±2.20(49-57)
D	48.0 ±2.83(46-50)	32.5 ±2.12(31-34)	33.5 ±2.12(32-35)	25.0 ±1.41(24-26)	43.5 ±3.54(41-46)

*Mean, standard deviation, and range expressed as percentage of body length or head length. A, preflexion; B, flexion; C, postflexion; D, juvenile.

DESCRIPTIONS

Seriola lalandi

Literature. Brownell (1979) illustrated an egg and two reared yolk-sac larvae, which he tentatively identified as *S. lalandi*, from waters off South Africa. The egg measured 1.44 mm in diameter with an oil globule diameter of 0.32 mm.

Distinguishing features. Seriola lalandi larvae are slender-bodied and heavily pigmented, lack a supraoccipital crest, and develop the largest number of dorsal fin rays (31-39) among eastern Pacific carangids. The combination of these characters distinguishes *S. lalandi* from all other carangid larvae in the CalCOFI region except for larvae of *Seriola rivoliana*, which co-occur with *S. lalandi* in the southernmost extent of its range, and are presently undescribed.

Morphology and meristics. Early larvae of *S. lalandi* are slender-bodied; body depth at the base of the pectoral fin averages 19% to 23% in preflexion and flexion stages, increasing to about 30% in postflexion and juvenile stages (Table 1). Early stages of *S. lalandi* <10.0 mm are more slender than those of jack mackerel (*Trachurus symmetricus*), in which body depth ranges from 21% to 27% of body length (Table 1, Figure 1).

The gut is comparatively elongate; it increases in length relative to total body length during the larval period, then becomes relatively shorter in juveniles (Tables 1 and 2; Figure 2). The slender gut of early *S. lalandi* differs from the rounded mass found in *Caranx* and *Chloroscombrus*, and from the intermediate robust but somewhat elongate form in *T. symmetricus*. The intestinal coil begins to form at the end of the yolk-sac period at a position about one-fourth of the cleithrum-anus distance. The posterior margin of the

TABLE 2
Measurements (mm) of *Seriola lalandi*

Station	Body length	Snout-anus length	Head length	Eye diameter	Snout length	Body depth at pectoral fin base
6706-S-130.35	4.2 yolk-sac	2.2	0.52	0.26	0.10	0.36
5707-P-107.60	4.4	2.6	1.2	0.38	0.36	0.84
5708-B-113.35	5.2	3.0	1.4	0.46	0.40	1.0
6007-H-133.30	5.9	3.6	1.7	0.47	0.48	1.1
5707-P-107.60	6.1	3.7	1.8	0.56	0.60	1.2
6007-H-133.30	6.4	3.8	1.8	0.56	0.58	1.3
5909-B-133.25	6.6	4.0	2.1	0.64	0.66	1.5
5707-0-110.70	6.9	4.2	2.2	0.64	0.68	1.6
6007-H-133.30	7.2	4.5	2.2	0.70	0.64	1.5
6608-J-123.40	8.6	5.3	2.8	0.90	0.86	2.2
5608-B-130.45	8.9	5.6	3.1	0.92	0.92	2.4
7205-JD-130.80	9.8	6.5	3.5	1.1	0.88	3.0
Baja Calif.	10.9	7.2	3.8	1.3	1.0	3.2
8108-NH-106.7.45	13.7	8.8	4.9	1.6	1.2	4.2
6008-B-137.30	17.9	11.2	6.1	1.8	1.7	5.5
Mazatlan Proj.	20.0	12.9	6.8	1.9	2.1	6.1
Mazatlan Proj.	22.4	14.0	7.2	2.1	1.9	6.5
Cr. 79-DSJ	26.7 juv.	16.0	8.2	2.7	2.2	7.8

Specimens between dashed lines are undergoing notochord flexion.

loop extends posteriad gradually to reach about two-thirds of the cleithrum-anus distance at the beginning of notochord flexion. During this process the gut mass becomes somewhat deeper, tapering posteriad, but retains its elongate shape. By completion of notochord flexion the loop has reached the rectum, about three-fourths of the cleithrum-anus distance, and the entire gut region has become covered by well-developed body-wall musculature.

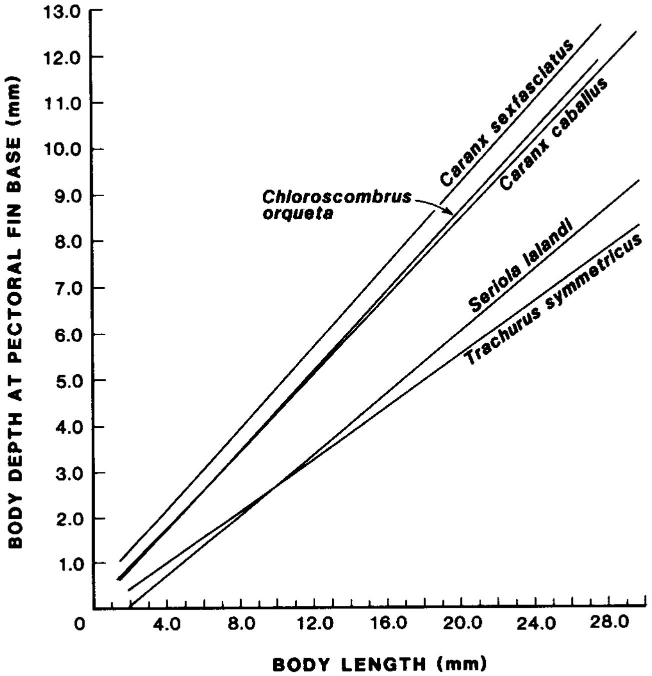

Figure 1. Regression of body depth at pectoral fin base on body length in five species of carangid larvae.

Relative head length increases gradually during larval development ($\bar{x}$ = 28% of body length in preflexion and 35% in postflexion stages) and decreases slightly in early juveniles. Relative eye diameter changes little during development, and relative snout length decreases slightly.

Head spines develop on the following bones: preopercle, frontal, posttemporal, and supracleithrum. Two series of spines develop on the preopercle, one along its posterior margin and one along a ridge just anterior to the margin. The first spine forms at the angle of the posterior margin at about 4.3 mm body length. This becomes the largest preopercular spine, its length reaching 9% of the body length at about 10 mm SL. At about 4.6 mm the first spine in the anterior series forms on the ridge in a position directly anterior to the angle spine of the posterior preopercular series.

Larvae about 5 mm long have developed two additional spines on the posterior margin of the preopercle, one on either side of the angle spine. A second spine forms on the ridge in association with the margin spine below the angle. The spines on either side of the angle spine are about one-half the length of the latter. Also at this stage the frontal bone begins to project above

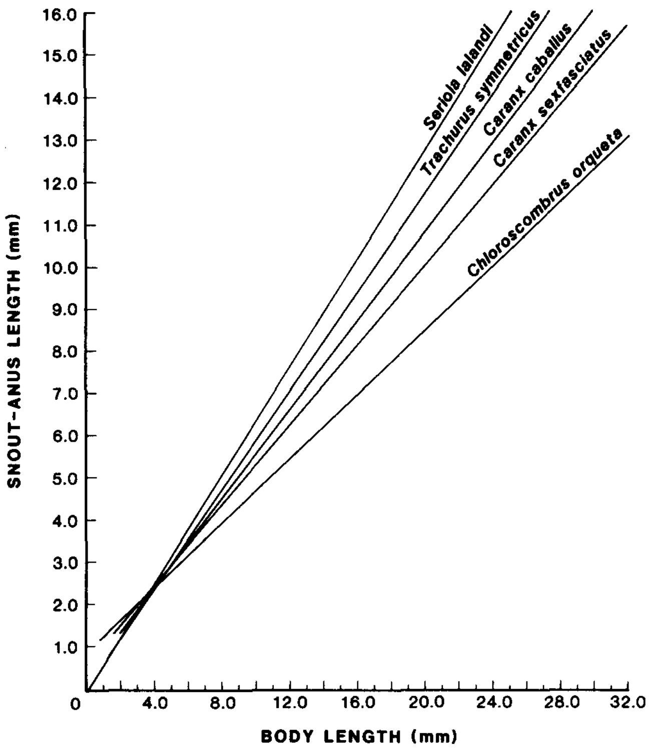

Figure 2. Regression of snout-anus length on body length in five species of carangid larvae.

the eye, forming a supraocular crest, which bears a spine.

Larvae about 6 mm long have added a small spine to each end of the preopercular margin series and begin to develop a single spine on the posttemporal and on the supracleithrum about midway between the posttemporal spine and the pectoral fin base. Also, a prominent longitudinal ridge is present on the pterotic bone.

At the completion of notochord flexion (~8.6 mm), an additional spine is present at each end of the preopercular series, and two more posttemporal spines have developed, one adjacent to the original spine and the other anteroventral to them. At this stage the full head-spine complement is present, and the spines remain prominent until about 13 mm SL, when most of them begin to diminish in size. The two spines on the preopercular ridge are the first to be lost, followed by the outer spines of the preopercular margin series and the supraocular spine. By 26 mm SL only the preopercular spines near the angle are prominent.

Meristic counts of stained specimens are presented in Table 3.

Pigmentation. Seriola lalandi is moderately pigmented in early stages, becoming heavily pigmented during the larval period. Serial melanophores outline the dorsal and ventral body margins of approximately 80% of the length of the body in yolk-sac larvae (Figure 3A-C). These melanophores become expanded and prominent in the preflexion stage (~4.5 mm), extending anteriorly over the snout and posteriorly around the tip of the tail. The melanophores along the tail tip are minute, dispersing outwardly onto the finfold of the developing caudal fin with ensuing growth. Other pigmentation in preflexion larvae includes a lateral midline series on the body and a series on the ventral midline along the isthmus in a continuum with melanophores below the gut (Figure 3D, E). Pigmentation increases rapidly over much of the head and body in early flexion larvae >6.6 mm, and these areas become almost completely covered with melanophores, except for the fin membranes and the posteriormost portion of the body. In larvae ≥7.0 mm, melanophores appear along the edge of the developing dorsal and anal fin pterygiophores. The melanophore pattern undergoes little change in postflexion larvae except for augmented pigmentation on the dorsal, anal, and pelvic fin membranes (Figure 4). By 14.0 mm, melanophores extend over most of the caudal peduncle, which is completely pigmented by 18.0 mm.

The strongly banded pattern exhibited by juveniles apparently forms rapidly, since it is lacking in a 22.4-mm specimen but present in a 24.5-mm specimen (Figure 4C).

Chloroscombrus orqueta

Literature. Larvae of *Chloroscombrus orqueta* have not been described previously.

Distinguishing features. Early *Chloroscombrus orqueta* larvae closely resemble some *Caranx* species in body morph and pigmentation, but have a diagnostic melanophore pattern on the dorsal body margin composed of four melanophores positioned on myomeres 1, 3, 9, and 14. Another feature is a small spine on the pterotic bone in larvae 7.5-11.0 mm. Larvae of *C. orqueta* also develop more dorsal and anal fin rays (25-30 rays for each fin) than any other *Caranx* species in the eastern Pacific.

Morphology and meristics. Chloroscombrus orqueta larvae are deep-bodied, increasing in body depth during all stages of larval development (Table 4; Figure 1). Relative body depth averages 35% in preflexion larvae, and about 42% in later stages (Table 1). Snout-anus distance is about 57% of body length in preflexion and flexion larvae. This is similar to other species described herein; however, in postflexion stages and juveniles the terminal segment of the gut in *C. orqueta* curves more anteriad, resulting in the shortest mean snout-anus length among the species discussed (Table 1; Figure 2). The gut loop is well

TABLE 3
Meristics of Stained *Seriola lalandi*

Station	Body length (mm)	Dorsal fin	Anal fin	Pectoral fin	Caudal fin	Pelvic fin	Branchiostegals
7808-VA-137.35	3.2	—	—	—	—	—	—
5707-B-120.75	3.9	—	—	—	—	—	—
6907-G-117.50	4.1	—	—	—	—	—	—
5609-B-120.45	4.3	—	—	—	—	—	—
5707-0-110.70	4.6	—	—	—	—	—	—
5408-C-130.45	4.9	—	—	—	—	—	4
5807-93.50	5.2	—	—	—	—	—	—
6007-H-133.30	5.6	—	—	—	—	—	4
5707-P-110.55	5.7	—	—	—	0+1+1+0	—	6
5906-0-123.60	6.0	—	—	—	0+1+1+0	—	7
5408-C-117.35	6.3	—	—	—	0+2+2+0	—	7
5707-0-110.70	6.9	10	12	6	0+6+5+0	—	7
6007-H-133.30	7.2	16	7	7	0+6+5+0	—	7
6608-J-123.40	8.6	VII,27	I+I,16	13	1+9+8+1	—	7
7205-J-130.80	9.8	VI,36	II+I,21	14	4+9+8+4	I,4	7
Off Baja Calif.	10.9	VII+I,35	II+I,21	19	5+9+8+5	I,5	7
8108-NH-106.7.45	13.7	VII+I,34	II+I,21	20	9+9+8+9	I,5	7
6008-B-137.30	17.9	VII+I,33	II+I,20	21	12+9+8+12	I,5	7
Mazatlan proj., 6-3-S	20.0	VII+I,36	II+I,22	21	12+9+8+12	I,5	7
RV/DSJ Cr. 79	26.7 juv.	VII+I,31	II+I,21	22	10+9+8+10	I,5	7

Specimens between dashed lines are undergoing notochord flexion.

formed in our smallest larvae (2.7 mm), and the posterior edge of the loop extends to about 60% of the cleithrum-anus distance. During this stage the gut mass lies in a longitudinal plane. By 3 mm, the ascending portion of the loop extends above the gut mass, and the rectal portion descends ventroposteriad at about a 45° angle. The loop portion increases in diameter and in relative mass and occupies most of the perivisceral cavity by about 4.0 mm. At this stage the rectal portion is oriented vertically and curves around the posterior edge of the coil. The gut and the prominent gas bladder above it form a triangular mass with sides of about equal length. The gut mass becomes more rounded with continued development, and by 8.0 mm the body-wall musculature is well developed.

Relative head length increases during preflexion and flexion stages ($\bar{x}$ = 33%-38% of body length), but decreases ($\bar{x}$ = 35%-30%) thereafter. Relative eye diameter increases during larval development and decreases slightly in juveniles. Relative snout length decreases in progressive larval stages but increases slightly in the juvenile stage (Tables 1 and 4).

Head spines develop on the following bones: preopercle, frontal, posttemporal, supracleithrum, and pterotic. Small larvae (2.7 mm) bear a large spine at the angle of the preopercular margin and three smaller spines below the angle. By 3.0 mm, larvae have two more spines above the angle. Larvae >3 mm have a fourth and fifth spine below the angle and a third spine above the angle. By 4 mm, a sixth spine is added below the angle and a fourth above the angle. By 5 mm, larvae have a fifth spine above the angle. Larvae larger than 8.0 mm have 8-10 spines below the angle and 6-7 above the angle. The angle spine reaches a

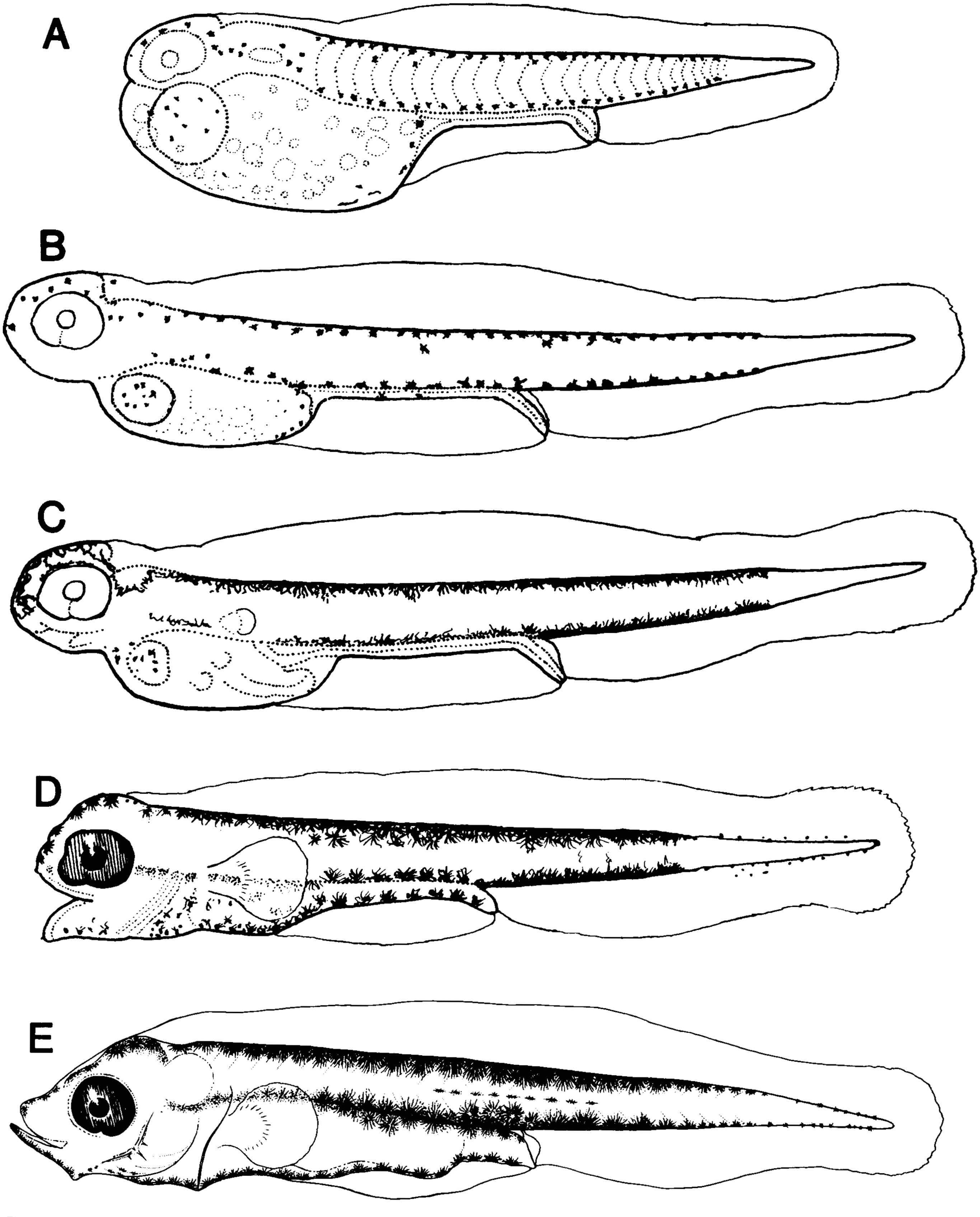

Figure 3. Early larvae of *Seriola lalandi*: *A*, 2.8 mm; *B*, 3.8 mm; *C*, 3.8 mm; *D*, 3.5 mm; *E*, 4.6 mm.

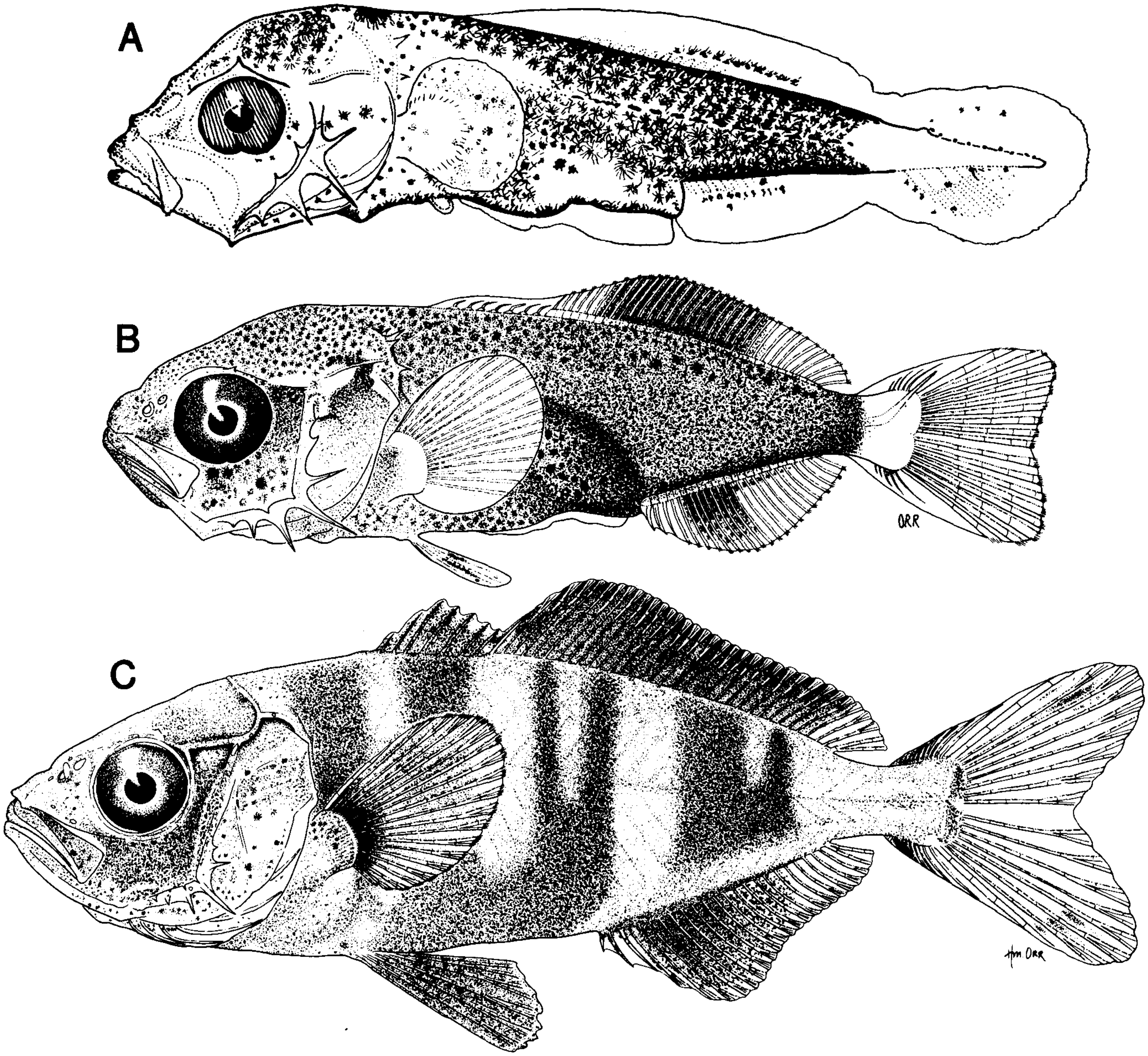

Figure 4. Larvae and early juvenile of *Seriola lalandi*: *A*, 7.0 mm; *B*, 11.7 mm; *C*, 24.5-mm juvenile.

maximum relative length of about 15% of the body length in 3-mm larvae, is reduced to 8%-11% of body length in 4-7-mm larvae, and then decreases abruptly in relative size. The spines above and below the angle spine are about one-half its length, and the others decrease in size gradually toward each end of the series. The uppermost margin spines begin to disappear at about 13 mm; by 16 mm only the spine adjacent to the angle remains in the upper series. Specimens larger than 20 mm retain only the angle spine.

Larvae <3.0 mm have 4 small spines on the lower part of the preopercular ridge. These spines increase in number to a maximum of 9-11 on the lower limb and 3-4 on the upper limb of the ridge in 6-11-mm larvae. Thereafter they decrease in number and are absent by 15 mm.

By about 3.0 mm, larvae have single spines on the posttemporal, supracleithrum, and on the supraocular shelf (frontal bone). Additional posttemporal spines appear by 5 mm, and in larvae >6.6 mm there are 4 spines arranged in an arc on the lower region of the bone. Larvae ≥7.0 mm form additional supracleithral spines, and larvae >8.0 mm have 4 spines arranged in a vertical series on the upper region of the bone. Larvae 8-11 mm in length have a maximum of 9-11

TABLE 4
Measurements (mm) of *Chloroscombrus orqueta*

Station	Body length	Snout-anus length	Head length	Eye diameter	Snout length	Body depth at pectoral fin base
B-5608-137.23	2.7	1.5	0.80	0.26	0.26	0.82
B-5608-137.23	3.0	1.8	0.98	0.30	0.32	1.1
B-5608-137.23	3.4	1.9	1.2	0.38	0.32	1.3
ETP 13.019	3.7	2.1	1.4	0.54	0.38	1.6
ETP 13.019	4.0	2.3	1.5	0.56	0.44	1.8
TO 59-1 #46	4.1	2.4	1.6	0.54	0.44	1.6
TO 59-1 #46	4.6	2.6	1.7	0.60	0.48	1.8
ETP 13.019	5.1	2.7	1.8	0.70	0.48	2.1
ETP 13.019	5.3	2.9	2.0	0.72	0.54	2.2
ETP 13.019	5.9	3.2	2.2	0.76	0.60	2.5
TO 59-1 #46	6.6	3.3	2.3	0.84	0.64	2.8
TO 59-1 #35	7.2	3.6	2.4	0.92	0.60	3.1
TO 59-1 #35	8.0	4.2	2.9	1.0	0.66	3.6
ETP 13.021	8.3	4.3	3.1	1.0	0.72	3.6
ETP 13.019	9.8	5.0	3.5	1.2	1.0	4.2
RAB S-14	11.4	5.5	4.0	1.6	1.0	5.2
ETP 13.019	13.4	6.2	4.0	1.5	1.1	6.0
RAB 71-III (a,b)	15.2	6.7	4.7	1.9	1.1	6.8
Rab S-14	23.5 juv.	9.8	7.5	2.4	2.2	9.8
RAB S-2	29.7 juv.	11.5	8.6	2.9	2.3	12.4

Specimens between dashed lines are undergoing notochord flexion.

spines on the supraocular shelf. Specimens >15 mm lack supraocular spines, and the posttemporal and supracleithral spines become obsolescent at about the same stage.

Small larvae <3.0 mm possess a supraoccipital crest with a scalloped margin. By about 3.0 mm it has developed to its maximum relative size, extends from the midregion of the optic lobes to the second myoseptum, and has formed 10-12 rounded projections. By about 8.0 mm it is much reduced in size and is restricted to the occipital region, and is lost by 13.0 mm.

A small spine-bearing ridge develops on the pterotic bone at about 7.5 mm. A maximum of two spines appear on the ridge. The ridge is absent in specimens larger than 11.0 mm.

Meristic counts of stained material are presented in Table 5.

Pigmentation. Chloroscombrus larvae are lightly pigmented and resemble larvae of some *Caranx* species; however, they may be distinguished by characters discussed below. Pigmentation on preflexion and flexion larvae (~2.6-4.6 mm) is found in the following areas: (1) head—region of the midbrain and jaws; (2) abdomen—over the gas bladder, dorsally over the free portion of the gut terminus, ventrally on the gut wall, and along the margin of the preanal finfold; (3) body—dorsally and ventrally on the body margin, along the lateral midline, internally above the notochord medial to the midline pigment, and a melanophore or two below the developing caudal fin (Figure 5A-C). This is a typical pattern for many early carangid larvae, but a diagnostic melanophore pattern for preflexion and early flexion *C. orqueta* is the dorsal body margin pigment consisting of four melanophores positioned over myomeres 1, 3, 9, and 14 (Figure 5A, B). This character occurs in other *Chloroscombrus* species—*C. cosmopolita* in the eastern Atlantic (Aboussouan 1968) and *C. chrysurus* in the western Atlantic and Gulf of Mexico[2].

Pigmentation gradually increases in postflexion larvae (>5.0 mm), particularly in the head and trunk region (Figures 5D and 6A). Melanophores along the dorsal body margin increase in number to form a continuous dashed line of pigment by 7.2 mm. Myoseptal pigmentation on the ventral surface of the body is first evident at about 5.0 mm (Figure 5D), positioned below the lateral midline streak; internal

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[2] Laroche, W.A., D. Ruple, and S.L. Richardson. MS. Young carangid fishes from the Gulf of Mexico: a generic diagnosis of larvae, with additional descriptive notes including early development of three species. Gulf Coast Research Lab., Ocean Springs, MS 39564.

TABLE 5
Meristics of Stained *Chloroscombrus orqueta*

Station	Body length (mm)	Dorsal fin	Anal fin	Pectoral fin	Caudal fin	Pelvic fin	Branchiostegals
5608-B-137.23	2.7	—	—	—	—	—	6
Cabo Blanco, Costa Rica 10 miS	2.9	—	—	—	—	—	6
5608-B-137.23	3.0	—	—	—	—	—	7
P-42-130.30	3.2	anlagen	anlagen	—	—	—	7
5608-B-137.23	3.4	anlagen	anlagen	—	0+2+2+0	—	7
P-42-130.30	3.7	anlagen	anlagen	—	0+4+4+0	—	7
ETP 13.019	4.0	VII+I,11	II+I,16	5	0+8+7+0	—	7
ETP 13.019	4.3	VII+I,18	II+I,18	7	0+8+7+0	—	7
ETP 13.019	4.5	VIII+I,22	II+I,23	10	2+9+8+2	—	7
ETP 13.019	5.1	VIII+I,23	II+I,20	12	2+9+8+2	—	7
ETP 13.019	5.6	VIII+I,22	II+I,22	12	2+9+8+2	—	7
TO 59-1 #46	5.9	VIII+I,26	II+I,25	15	3+9+8+3	I,2	7
TO 59-1 #46	6.6	VIII+I,26	II+I,25	14	4+9+8+4	I,2	7
ETP 60.295	7.5	VIII+I,28	II+I,28	20	6+9+8+6	I,3	7
TO 59-1 #35	7.7	VIII+I,26	II+I,25	19	7+9+8+7	I,4	7
TO 59-1 #35	8.0	VIII+I,26	II+I,25	20	6+9+8+6	I,4	7
ETP 13.021	8.3	VIII+I,27	II+I,26	20	8+9+8+8	I,5	7
Cabo Blanco, Costa Rica 10 miS	8.7	VIII+I,27	II+I,28	20	9+9+8+9	I,5	7
RABMEX S-13	9.5	VIII+I,28	II+I,28	21	9+9+8+9	I,5	7
RABMEX 71 III (a,b)	10.2	VIII+I,28	II+I,27	20	9+9+8+9	I,5	7
RABMEX S-14	11.0	VIII+I,27	II+I,26	20	9+9+8+9	I,5	7
RABMEX S-14	12.2	VIII+I,28	II+I,26	21	10+9+8+10	I,5	7
RABMEX S-13	13.2	VIII+I,28	II+I,26	21	9+9+8+9	I,5	7
RABMEX 71 III (a,b)	15.2	VIII+I,28	II+I,29	20	10+9+8+9	I,5	7
RABMEX S-10	15.7	VIII+I,28	II+I,27	21	9+9+8+9	I,5	7
RABMEX S-14	23.5	VIII+I,28	II+I,26	20	9+9+8+9	I,5	7
RABMEX S-2	29.7	VIII+I,28	II+I,28	20	9+9+8+9	I,5	7

Specimens between dashed lines are undergoing notochord flexion.

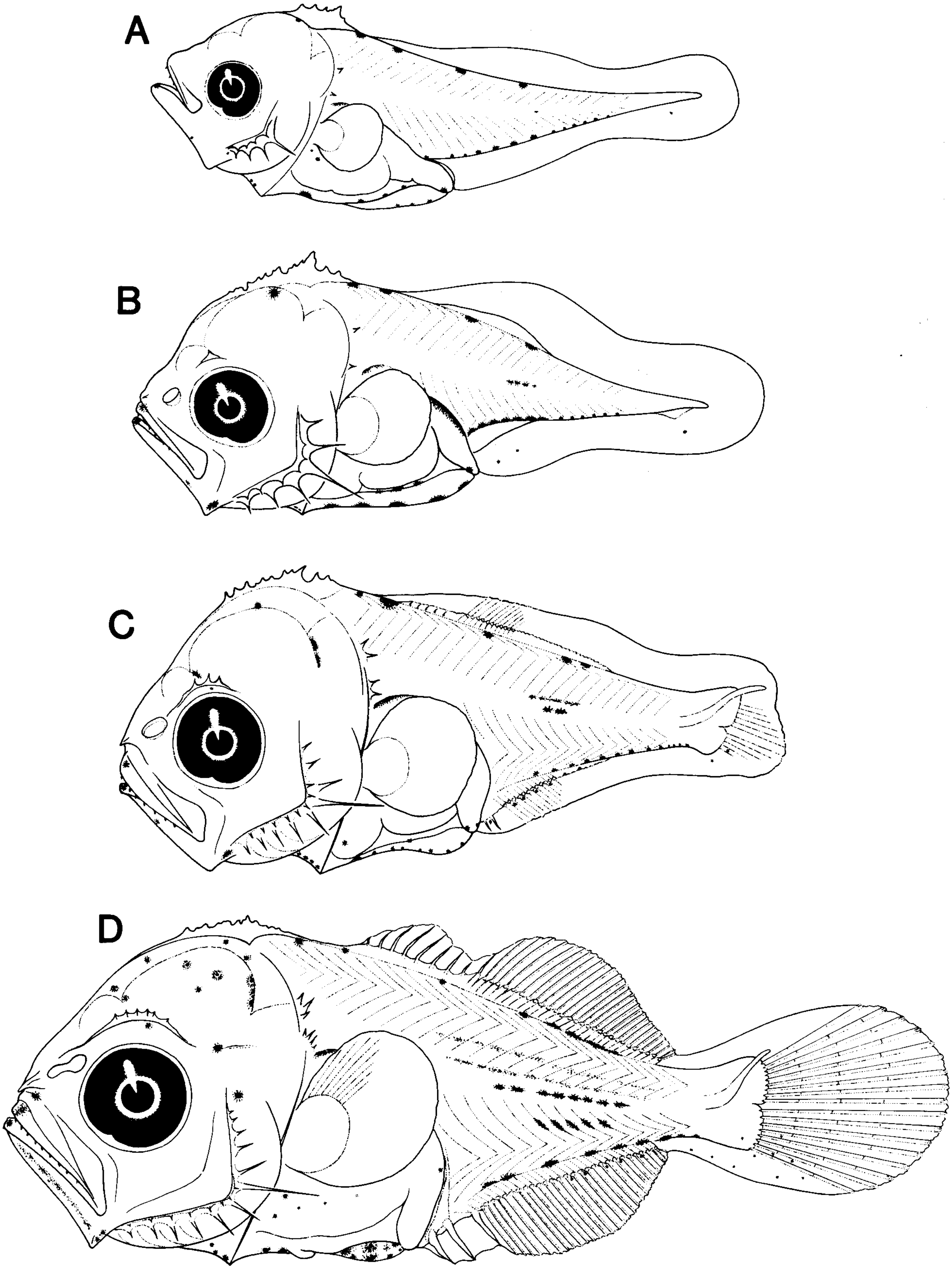

Figure 5. Larvae of *Chloroscombrus orqueta*: *A*, 2.7 mm; *B*, 2.9 mm; *C*, 3.7 mm; *D*, 5.1 mm.

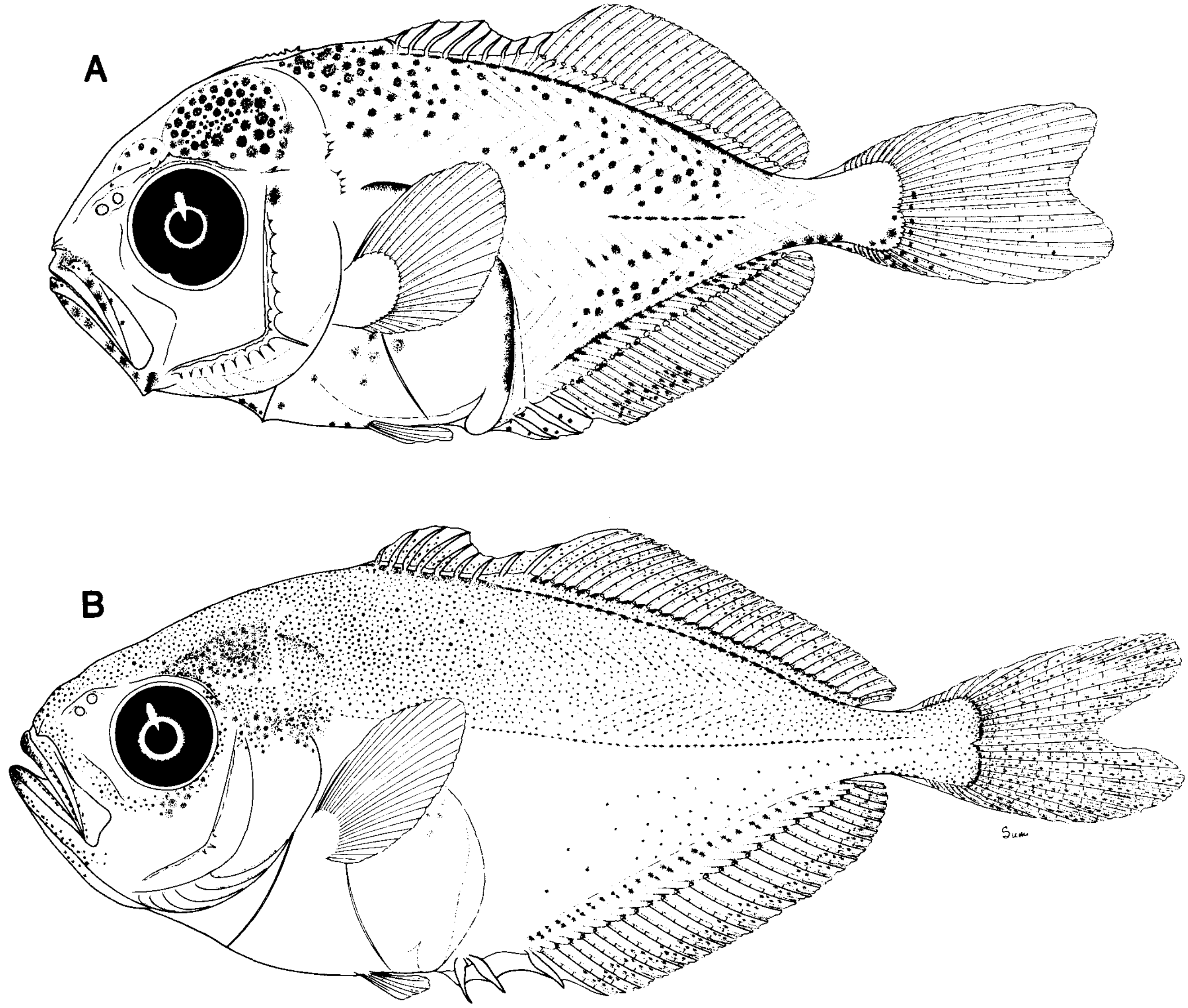

Figure 6. Postflexion larva and early juvenile of *Chloroscombrus orqueta*: *A*, 10.2 mm; *B*, 23.5-mm juvenile.

pigmentation above the spinal column also develops at this time, but is obscured by overlying body musculature. Myoseptal pigmentation on the dorsal surface of the body as well as melanophores in the shoulder region appear later, at about 7.2 mm.

By the early juvenile stage (~23.5 mm; Figure 6B), pigmentation is confined to the dorsolateral half of the head and body region, and remains sparse or lacking on the ventrolateral half. Fin pigmentation initially develops on the anal and caudal fins by about 10.0 mm, and concentrates on the musculature overlying the pterygiophores of the dorsal and anal fins and on the distal margins of the dorsal, anal, and caudal fins in early juvenile stages (Figure 6A, B). The pectoral fins lack pigment throughout the larval and juvenile period.

Caranx caballus

Literature. Larvae of *Caranx caballus* have not been previously described.

Distinguishing features. Caranx caballus larvae are distinguishable by their pigmentation pattern and meristic count of 25 vertebrae. The body morph of early larvae resembles that of *Chloroscombrus orqueta*; however, differences in pigmentation, particularly on the dorsal body margin, differentiate the species. Small *Caranx caballus* (to ~4.0 mm) possess opposing dorsal, lateral, and ventral pigmentation streaks on the body and lack the four characteristic melanophores on the dorsal body margin of early *Chloroscombrus orqueta* larvae.

Morphology and meristics. Relative body proportions of *Caranx caballus* larvae are similar to those of

TABLE 6
Measurements (mm) of *Caranx caballus*

Station	Body length	Snout-anus length	Head length	Eye diameter	Snout length	Body depth at pectoral fin base
ETP 46.135	3.0	1.8	1.0	0.28	0.32	1.0
ETP 46.135	3.6	2.2	1.3	0.36	0.36	1.2
Cabo Blanco, Costa Rica	3.8	2.2	1.3	0.38	0.36	1.4
Cabo Blanco, Costa Rica	3.9	2.3	1.4	0.44	0.38	1.7
" "	4.4	2.5	1.6	0.54	0.40	1.8
TO 59-1 #38 surf.	4.9	2.7	1.6	0.54	0.46	2.0
Cabo Blanco, Costa Rica	5.0	2.7	1.7	0.56	0.46	2.1
" "	5.4	3.0	2.0	0.60	0.64	2.3
Mazatlan 8, Sta. 6	6.3	3.5	2.2	0.76	0.64	2.8
ETP 47.040	7.8	4.4	2.9	1.0	0.68	3.6
67-2, N19	9.3	5.2	3.4	1.2	0.72	4.2
67-2, N19	10.9	6.0	4.2	1.5	1.0	5.0
ETP 47.019	11.7	6.8	4.3	1.4	1.1	5.4
67-2, N19	13.2	7.2	4.8	1.7	1.2	5.7
67-2, N50	16.7	8.9	5.5	2.2	1.2	7.0
67-2, N50	18.4	9.5	6.4	2.4	1.4	7.7
RABMEX S-13	21.7 juv.	11.4	7.7	2.7	2.0	8.5

Specimens between dashed lines are undergoing notochord flexion.

Chloroscombrus orqueta at equivalent stages of development (Tables 1 and 6). Larvae are deep-bodied (Figure 1); relative body depth increases throughout the larval period and decreases slightly in juveniles. Relative snout-anus distance decreases throughout the larval period. Gut development is similar to that described for *C. orqueta*. Relative head length and eye diameter increase during the larval period, while relative snout length decreases.

Spines develop on the preopercle, posttemporal, and supracleithrum. By 3.0 mm, larvae have a large spine at the angle, three below the angle, and one above the angle on the preopercular margin. Larvae 5-6 mm have up to 5 spines below the angle, 7-17-mm larvae have 6-7 spines, and 18-24-mm larvae have 8-9 spines below the angle. The number of spines above the angle increases to about 2 in 4-mm larvae, 4 in 5-8-mm larvae, and 5-6 in larger larvae. The angle spine is relatively largest in 3-mm larvae (10% of body length) and becomes relatively smaller gradually in later larval stages. Larvae ≤3.0 mm develop 3 spines below the angle of the preopercular ridge, and 4-8-mm larvae have 5 spines. Larvae 3-8 mm have only a single spine above the angle. Larvae larger than 8 mm resorb all preopercular ridge spines.

By 3 mm, larvae form a single posttemporal and a supracleithral spine, and develop no additional posttemporal spines; however, by 5.0 mm, a second supracleithral spine appears. Larvae lose both types of spines at about 10 mm.

By 3 mm a supraoccipital crest is present. It extends from the midregion of the optic lobes to the second myoseptum and has wide irregular serrations. After notochord flexion it is restricted to the occipital region and is absent in larvae larger than 8.0 mm. Postflexion larvae develop a supraocular shelf and pterotic ridge, but they do not develop spines.

Table 7 provides meristic counts of stained specimens.

Pigmentation. Pigmentation on *C. caballus* larvae is sparse in early stages, with a generalized pattern of opposing dorsal, lateral, and ventral streaks on the body, and melanophores on the top of the head and over the abdominal region (Figure 7). Preflexion and flexion larvae are characterized by a few melanophores in the ventral region of the gut. These mela-

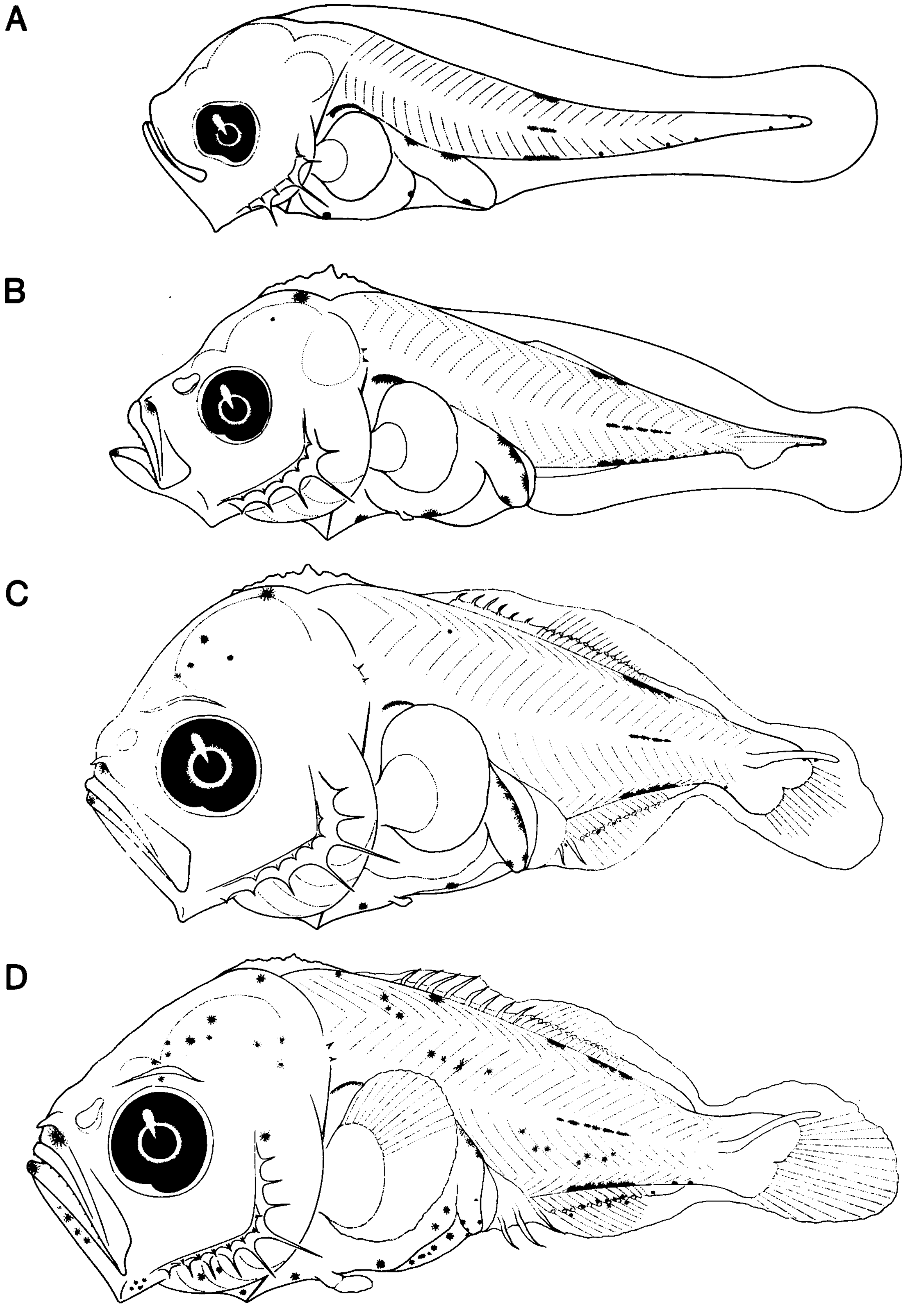

Figure 7. Larvae of *Caranx caballus*: *A*, 2.3 mm; *B*, 3.6 mm; *C*, 3.9 mm; *D*, 4.4 mm.

TABLE 7
Meristics of Stained *Caranx caballus*

Station	Body length (mm)	Dorsal fin	Anal fin	Pectoral fin	Caudal fin	Pelvic fin	Branchiostegals
ETP 46.135	3.0	—	—	—	—	—	5
TO 58-1 #59	4.0	V,13	II+I,10	—	0+4+4+0	—	7
#59	4.2	anlagen	anlagen	—	0+5+5+0	—	7
Cabo Blanco, Costa Rica	4.4	VIII+I,20	II+I,14	9	2+9+8+2	I,2	7
Cabo Blanco, Costa Rica	5.0	VIII+I,21	II+I,19	13	3+9+8+2	I,4	7
67-2 #19	6.2	VIII+I,21	II+I,18	16	4+9+8+5	I,5	7
Cabo Blanco, Costa Rica	6.7	VIII+I,23	II+I,19	17	5+9+8+5	I,5	7
Cabo Blanco, Costa Rica	7.7	VIII+I,22	II+I,20	20	6+9+8+6	I,5	7
67-1, N-22	8.6	VIII+I,22	II+I,19	20	8+9+8+8	I,5	7
67-2, #19	9.3	VIII+I,22	II+I,19	22	9+9+8+9	I,5	7
67-2, #19	10.9	VIII+I,22	II+I,19	22	9+9+8+9	I,5	7
ETP 47.019	11.7	VIII+I,23	II+I,20	22	9+9+8+9	I,5	7
67-1, N-2	13.0	VIII+I,23	II+I,19	22	9+9+8+9	I,5	7
67-2, #27A	13.9	VIII+I,23	II+I,20	22	9+9+8+9	I,5	7
ETP 14.014	16.9	VIII+I,23	II+I,19	22	9+9+8+9	I,5	7
67-2, N-50	18.4	VIII+I,23	II+I,19	22	9+9+8+9	I,5	7
ETP 14.014	23.5 juv.	VIII+I,24	II+I,20	22	9+9+8+9	I,5	7

Specimens between dashed lines are undergoing notochord flexion.

nophores are usually in an anterior, median, and posterior (next to the anus) position along the ventral margin of the gut area, with additional pigmentation along the upper section of the terminal segment of the gut.

During notochord flexion (~3.9-4.9 mm), melanophores become lightly scattered over the head and body (Figures 7C, D and 8A) in contrast to the dense pigmentation that covers all but the posterior sections of the tail in postflexion specimens. Postflexion larvae (6.3-8.5 mm) develop a cluster of pigment around the lateral midline streak (Figure 8B), which is obscured in later stages by heavy pigmentation over the trunk. Beginning at about 13.0 mm, melanophores begin forming in the middle of the caudal peduncle, and subsequently spread to the margins of the peduncle.

Bars of pigmentation are first evident on the body in specimens about 17.0 mm long (Figure 8C), persisting into the juvenile stage. Because of the heavy background pigment over the entire surface of the body, these bars are not as prominent as those in *C. sexfasciatus*.

Fin pigmentation is heavy and conspicuous on the fin membranes of the spinous dorsal, spinous portion of the anal, and the pelvic fins in postflexion larvae from about 10.5 mm through the juvenile stage. Pigment first appears on the anal and pelvic fins by about 5.5 mm and on the spinous dorsal fin by about 6.2 mm.

Caranx sexfasciatus

Literature. Larvae of *Caranx sexfasciatus* have not been previously described.

Distinguishing features. A unique feature of

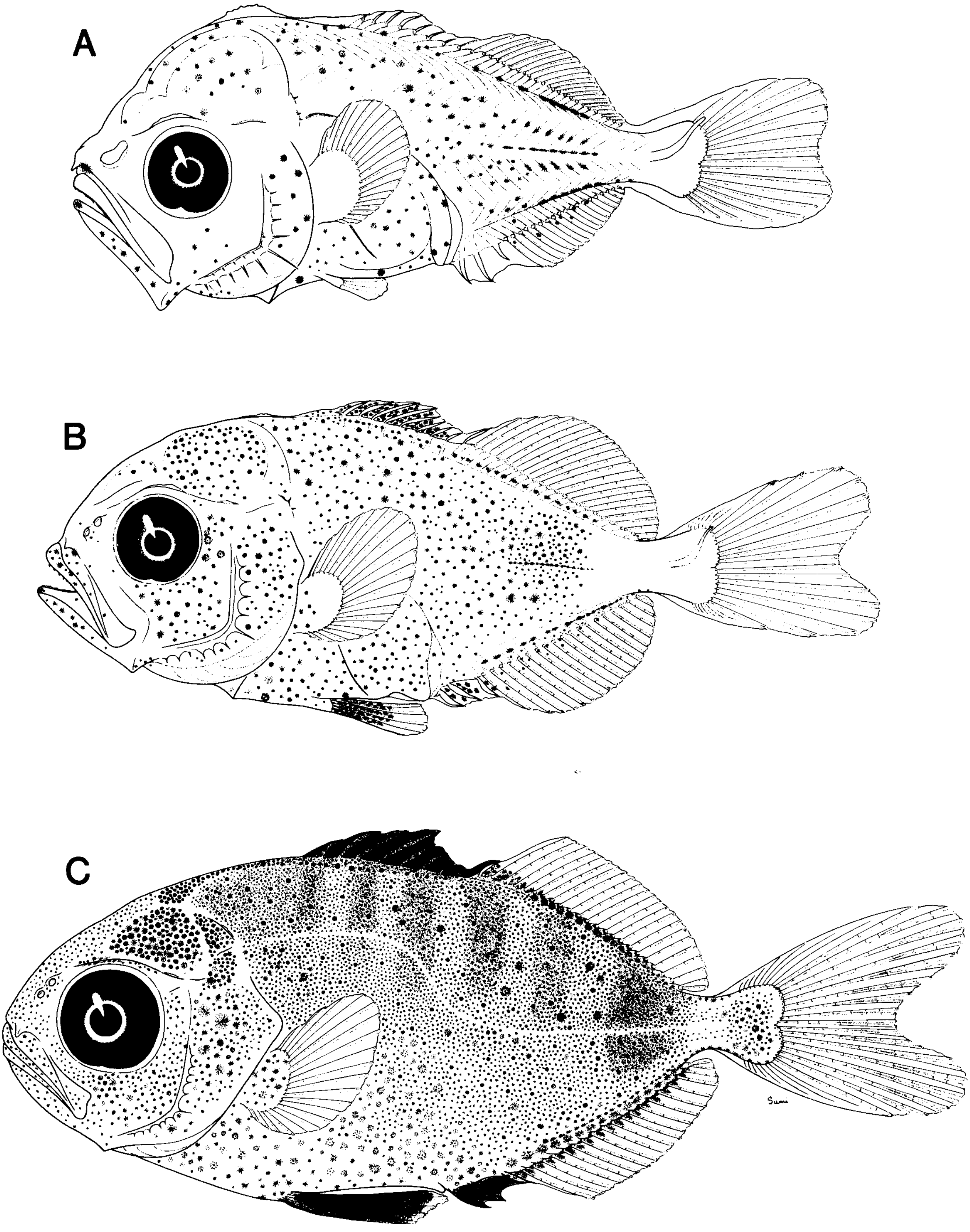

Figure 8. Postflexion larvae of *Caranx caballus*: *A*, 4.9 mm; *B*, 8.4 mm; *C*, 17.0 mm.

TABLE 8
Measurements (mm) of *Caranx sexfasciatus*

Station	Body length	Snout-anus length	Head length	Eye diameter	Snout length	Body depth at pectoral fin base
7205-JD 157G.150	2.6	1.4	0.76	0.24	0.22	0.76
ETP 13.019	3.0	1.6	0.90	0.30	0.24	1.0
7205-157G.150	3.1	1.7	1.0	0.34	0.28	1.1
7205-157G.150	3.4	1.9	1.1	0.34	0.36	1.3
TO 58-1 #69	3.8	2.1	1.4	0.40	0.40	1.6
ETP 13.019	4.0	2.3	1.4	0.44	0.42	2.0
Cabo Blanco, Costa Rica	4.2	2.4	1.4	0.48	0.42	1.9
TO 59-1 #35	4.5	2.7	1.7	0.60	0.46	2.5
TO 58-1 #69	4.6	2.8	1.8	0.60	0.50	2.5
Mazatlan 5-14-0	4.8	2.8	1.7	0.60	0.46	2.5
Cabo Blanco, Costa Rica	5.3	3.3	2.1	0.70	0.50	2.8
ETP 12.033	5.9	3.3	2.0	0.72	0.56	2.9
ETP 46.134	6.6	4.0	2.6	0.88	0.68	3.6
ETP 30.114	7.7	4.2	2.9	1.0	0.80	4.4
7205-G-157G.150	8.5	5.1	3.2	1.2	0.76	4.6
ETP 47.019	9.4	5.1	3.6	1.3	0.80	5.2
ETP 14.232	12.5	6.4	4.6	1.5	0.91	6.6
TO 5801 #141	15.4	8.4	5.8	2.1	1.6	7.8
SIO 64-140	22.8 juv.	11.4	7.7	2.5	2.0	10.5
67-2, N51	30.4 juv.	14.0	9.5	3.3	2.3	12.4

Specimens between dashed lines are undergoing notochord flexion.

Caranx sexfasciatus larvae is a conspicuously pigmented supraoccipital crest. All other described carangid larvae with a supraoccipital crest lack pigment on this structure. Another distinctive character in larvae larger than about 3.4 mm is a preanal finfold that is covered with pigment until resorption of the finfold at about 10.0 mm. Larvae are considerably deep-bodied following notochord flexion, and possess the smallest number of anal fin rays (15-17) among *Caranx* species in the eastern Pacific.

Morphology and meristics. Preflexion larvae of *C. sexfasciatus* are of moderate body depth, but become markedly deep-bodied in later stages (Tables 1 and 8; Figure 1). Body depth averages 35% of body length in preflexion larvae, but increases to over 50% of body length in flexion and postflexion larvae, diminishing to about 44% in early juveniles.

Relative gut length, head length, and eye diameter increase slightly in the larval period, but diminish in juveniles. Relative snout length remains constant at about 29% in preflexion- and flexion-stage larvae, decreasing to about 25% in postflexion larvae and juveniles. Gut development is similar to that described for *C. orqueta*.

As in *C. caballus*, spines develop on the preopercle, posttemporal, and supracleithrum. Small larvae <3 mm have a large spine at the angle of the preopercular margin, 2 below the angle, and 1 above the angle. Postflexion larvae up to about 8.5 mm develop 4 spines below the angle; 9-12-mm larvae have 5 spines; and specimens larger than 13 mm have 6 spines. The number above the angle increases to 3-4 in postflexion larvae up to about 9.0 mm and is reduced to 1 or none in specimens larger than 12 mm. The angle spine is relatively largest in 3-mm larvae (maximum of 15% of body length) and subsequently decreases gradually in relative size. Larvae ≤3 mm develop 4 spines below the angle of the preopercular ridge; by 6.0 mm, 4-5 spines are present. These spines are lost in larvae >6.0 mm. A single spine is present above the angle of the ridge until the completion of notochord flexion (~4.5 mm), after which there is none.

By 4.0 mm, larvae have a single spine on the su-

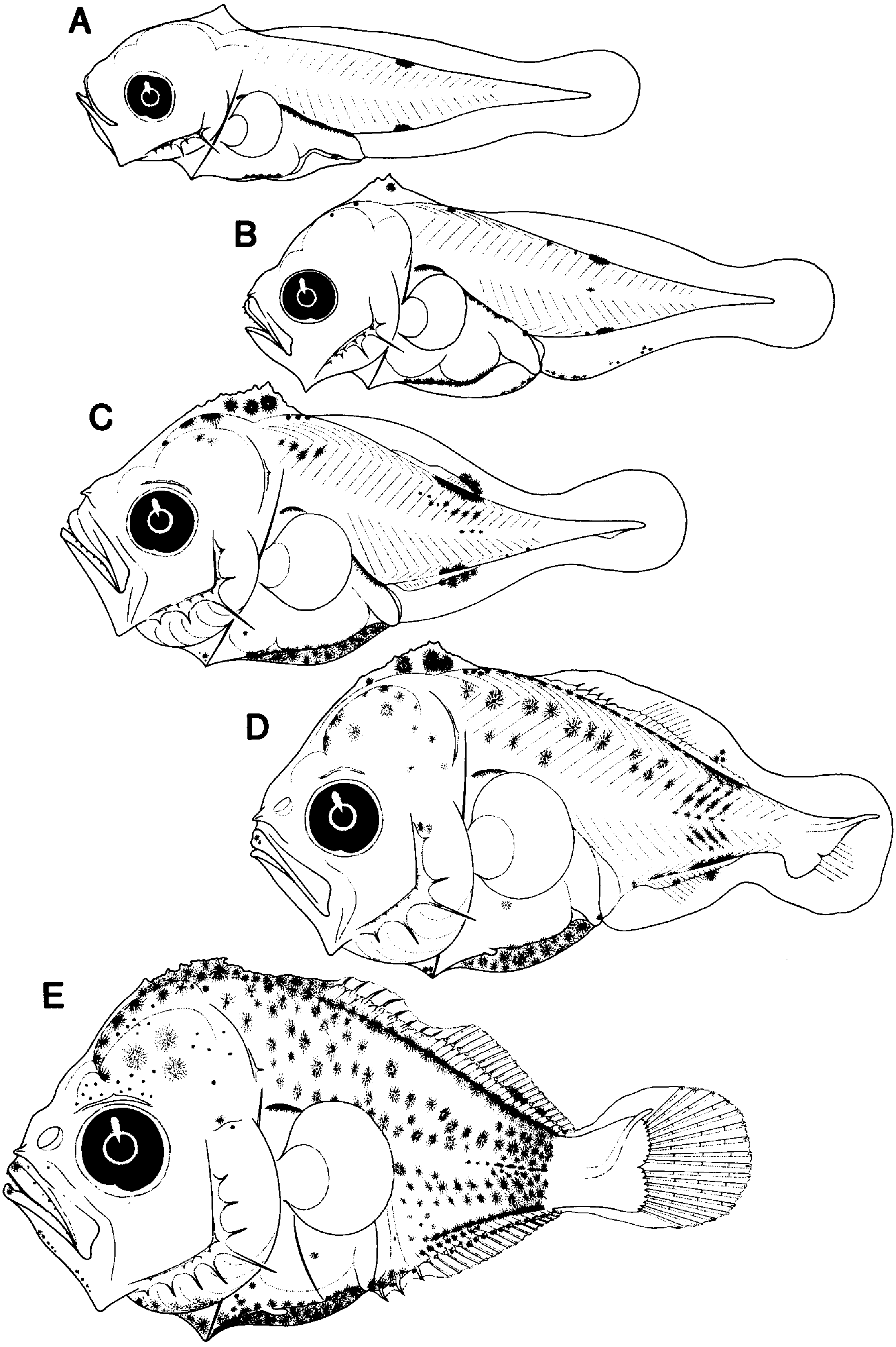

Figure 9. Larvae of *Caranx sexfasciatus*: *A*, 2.6 mm; *B*, 3.0 mm; *C*, 3.4 mm; *D*, 4.0 mm; *E*, 4.2 mm.

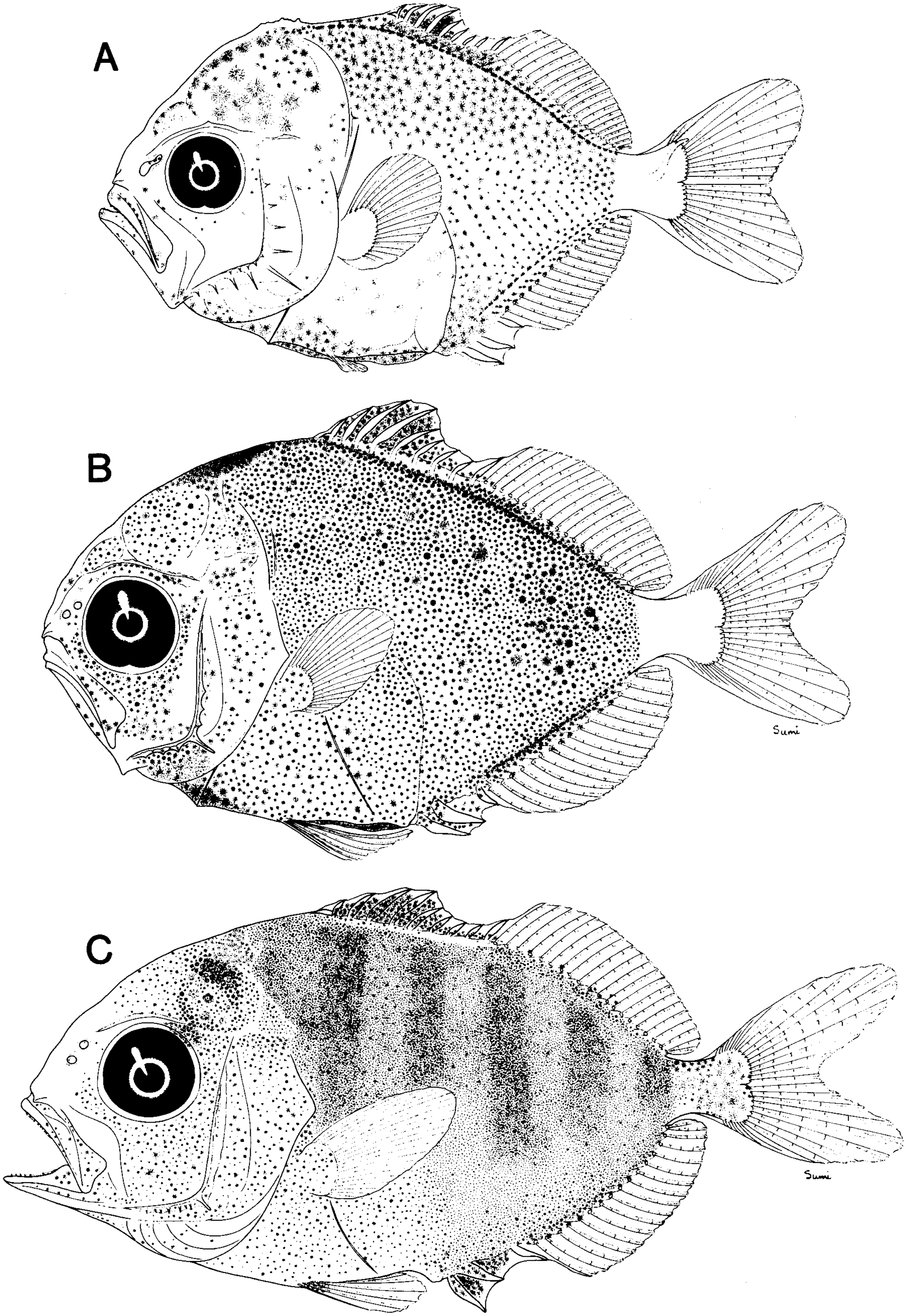

Figure 10. Postflexion larvae of *Caranx sexfasciatus*: *A*, 5.5 mm; *B*, 9.4 mm; *C*, 15.4 mm.

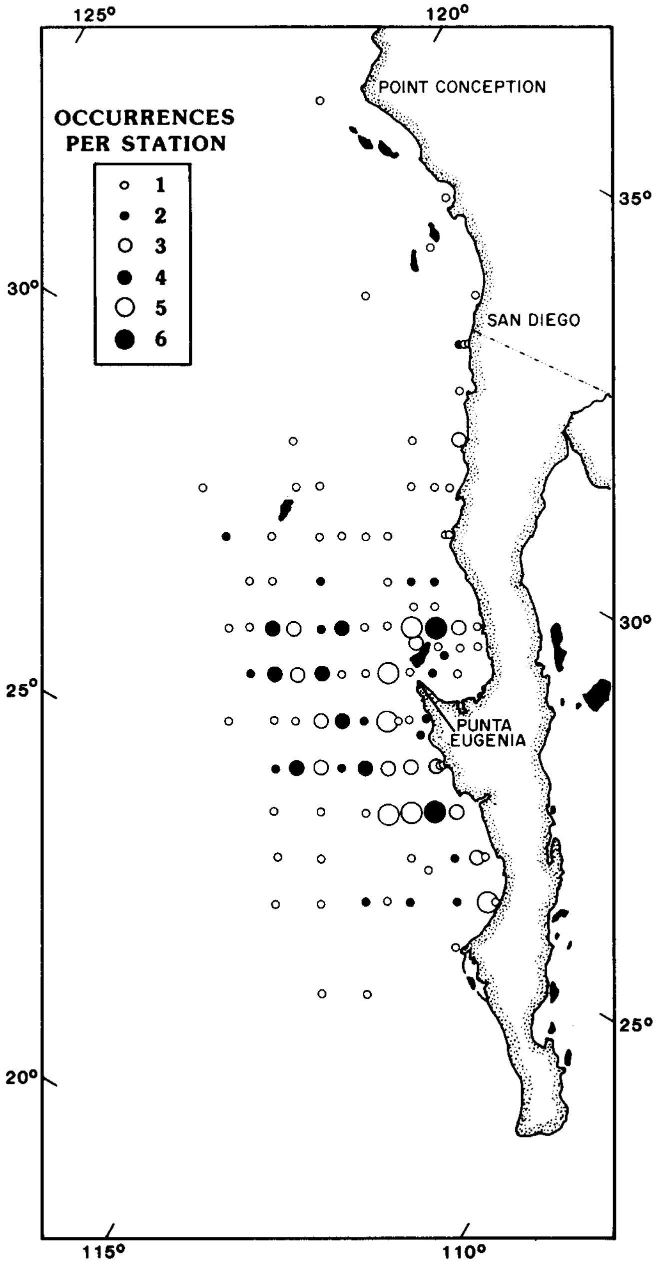

Figure 11. Pooled numbers of occurrences of larvae of *Seriola lalandi* in standard CalCOFI tows taken from 1954 to 1969.

pracleithrum; it remains until about 12.0 mm. At about 4.5 mm, a single posttemporal spine forms directly above the supracleithral spine and is variously present or absent in larvae up to about 8.5 mm, after which it is absent.

Our smallest larvae, <3.0 mm long, have developed a small supraoccipital crest. It enlarges rapidly to its maximum development at about 3.0 mm. It is triangular, with a peak above the occipital region and a convex forward margin, sometimes with minute serrations. It becomes flat and inconspicuous during notochord flexion and is absent in larvae larger than 8.0 mm. An inconspicuous supraocular crest and pterotic ridge develop in postflexion larvae, but these do not develop spines.

Meristic counts of stained specimens are presented in Table 9.

Pigmentation. Caranx sexfasciatus larvae possess striking melanistic pigment on the supraoccipital crest, a character unique among larval carangids that have been described. Our smallest specimens, 2.4-2.6 mm in length, have no pigmentation on the supraoccipital crest, but a single melanophore appears there by 3.0 mm (Figure 9A, B). Melanophores on the crest increase in number and intensity during the larval period until the crest is completely resorbed by 8.0 mm (Figures 9 and 10).

Another distinctive character in larvae larger than about 3.4 mm is a preanal finfold that is completely pigmented until resorption of the finfold at about 10.0 mm. Other pigmentation on early *C. sexfasciatus* consists of a pattern typical for many carangid larvae, with opposing dorsal, lateral, and ventral streaks on the body, as well as pigment on the head and abdominal region. Pigmentation spreads rapidly on the head and body in postflexion larvae (Figures 9E and 10), resulting in a very heavily pigmented body, with the exception of the caudal peduncle. By 15.4 mm, the caudal peduncle is pigmented, and the body exhibits the dark vertical stripes characteristic of the juvenile stage (Figure 10C).

Fin pigmentation remains sparse except for the spinous dorsal fin, which is pigmented early in the larval period, at about 5.5 mm. Pigmentation on this fin persists and intensifies to the late juvenile stage. The anterior portion of the anal fin is also pigmented in the early stages, but the pigment is transitory.

DISTRIBUTION

Seriola lalandi is reported to range from southern Washington to Chile, including the Gulf of California (Miller and Lea 1976); however, the larval distribution is limited to warmer waters. Within all CalCOFI plankton tows taken from 1954-69, *S. lalandi* larvae occurred in 206 samples. The northernmost occurrence was off Point Conception in July 1965; incidence was highest off central Baja California, where larvae were found in a broad band from nearshore to about 200 miles offshore (Figure 11). Incidence of yellowtail larvae was low off southern California (4% of occurrences) compared to Baja California, which had 96% of the occurrences.

Yellowtail larvae were collected from April to October, with 83% of the occurrences in July and

TABLE 9
Meristics of Stained *Caranx sexfasciatus* Larvae

Station	Body length (mm)	Dorsal fin	Anal fin	Pectoral fin	Caudal fin	Pelvic fin	Branchiostegals
7205-157G.150	2.5	—	—	—	—	—	—
7205-157G.150	2.7	—	—	—	—	—	4
7205-157G.150	3.0	—	—	—	—	—	6
75.04 Sta. 8	3.5	—	—	—	—	—	7
TO 59-1 #35	4.7	IX,15	II+I,11	8	1+9+8+1	—	7
Cabo Blanco, Costa Rica	5.3	VIII+I,19	II+I,15	14	4+9+8+4	bud	7
ETP 12.033	5.9	VIII+I,19	II+I,16	15	3+9+8+3	bud	7
75.04 Sta. 2	6.1	VII+I,19	II+I,15	15	5+9+8+5	bud	7
ETP 30.114	7.7	VIII+I,19	II+I,16	18	7+9+8+7	I,3	7
Costa Rica 37-2	9.0	VIII+I,20	II+I,15	20	8+9+8+8	I,5	7
ETP 14.232	12.5	VIII+I,19	II+I,16	21	9+9+8+9	I,5	7
TO 58-1 #69	13.7	VIII+I,20	II+I,17	21	9+9+8+9	I,5	7

Dashed line separates preflexion from postflexion larvae.

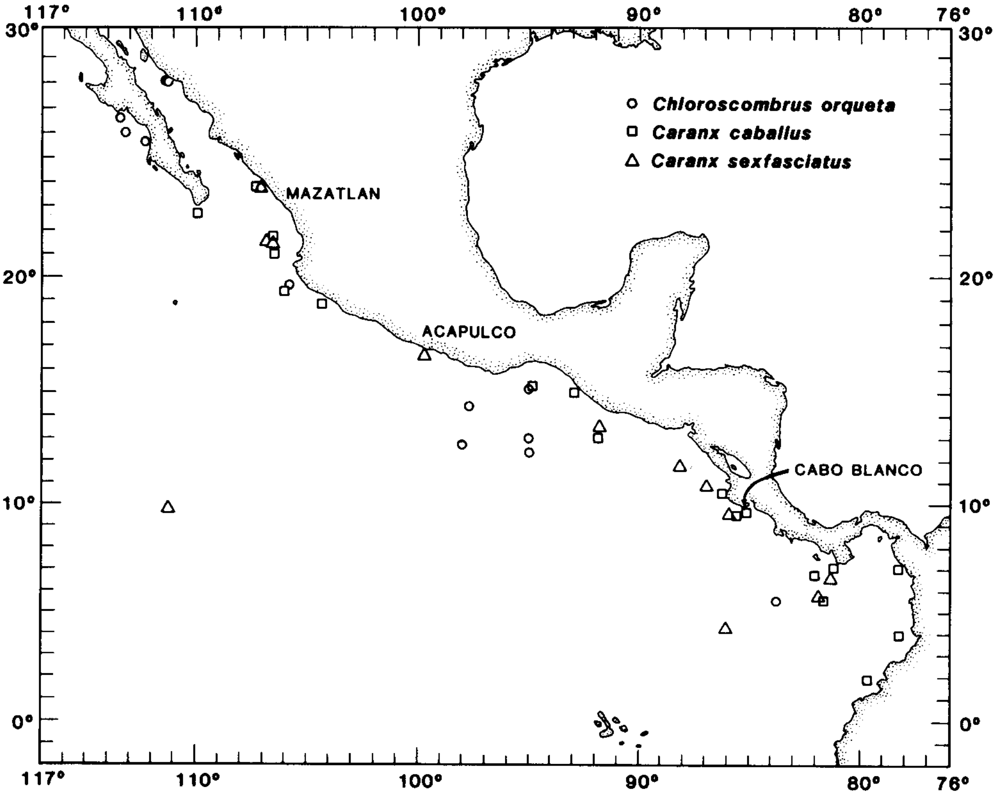

Figure 12. Occurrences of larvae of *Chloroscombrus orqueta*, *Caranx caballus*, and *Caranx sexfasciatus*. Omitted in this figure are a cluster of *Chloroscombrus orqueta* occurrences near San Carlos Bay, Gulf of California, and clusters of occurrences of the above three species off Cabo Blanco, Costa Rica.

August. This seasonal pattern correlates with the spawning period, reported to be in the spring and summer (Walford 1974). In their observations of maturing ova, Smith and Paul (1960) concluded that spawning generally begins in July and continues until October.

The size-frequency distribution of yellowtail larvae collected in CalCOFI samples in 1954-69 was narrow, with a mean length of 4.1 mm ± 1.16 SD and a range of 2.8-17.9 mm for the 429 larvae measured.

Figure 12 shows localities where larvae of *Chloroscombrus orqueta*, *Caranx caballus*, and *Caranx sexfasciatus* were taken. Of these three species, *Chloroscombrus orqueta* and *Caranx caballus* range as far north as southern California (Hubbs et al. 1979; Miller and Lea 1976), but none of our larvae was taken north of Baja California.

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EVALUATION OF SOME TECHNIQUES FOR PRESERVING NUTRIENTS IN STORED SEAWATER SAMPLES

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ABSTRACT

We examined the effects of freezing, acidification, and acidification plus freezing on the concentrations of nitrate, phosphate, and silicate in seawater samples. We compared polyethylene and polystyrene containers, and determined preservation effects after storage periods of 1, 3, 6, and 12 months.

Because of the magnitudes of the concentration changes and their variability, none of the tested procedures was judged satisfactory for our purposes. Interpretation of results was complicated by strong interactions among treatments and between treatments and water sources. If nutrient preservation is necessary, the effects of preservation should be determined for the specific conditions of the study.

RESUMEN

Examinamos los efectos de la congelación, la acidificación y acidificación más congelación sobre las concentraciones de nitratos, fosfatos y silicatos en muestras de agua marina. Comparamos recipientes de polietileno y poliestireno, y determinamos los efectos de la preservación al cabo de 1, 3, 6, y 12 meses de almacenamiento.

Debido a las magnitudes y variabilidad de los cambios en la concentración ninguno de los procedimientos examinados se consideró satisfactorio para nuestros propósitos. La interpretación de los resultados se vió complicada por las intricadas interacciones entre tratamientos y entre lugares de origen de las muestras. Si la preservación de nutrientes es necesaria, sus efectos deben ser determinados para las condiciones específicas de cada estudio.

INTRODUCTION

In 1982, when planning for the 1984 CalCOFI surveys began, the planning committee agreed about the importance of adding measurements of chlorophyll and primary production to the standard data set. We recognized, however, that these additions would not be financially feasible without some cutbacks in other areas. As one possible cost reduction, we considered eliminating the shipboard analyses of nutrients by postponing analyses until the samples were returned to the facilities at Scripps Institution of Oceanography (SIO), thereby eliminating sea pay and overtime for the chemists. The feasibility of this move depended upon our ability to preserve the nutrient samples in a simple and effective manner for at least one month.

In January 1983 we began a series of nutrient preservation experiements within the central North Pacific and the California Current. We examined the effects of three different preservation procedures (freezing, acidification, and freezing plus acidification) on the concentration of three nutrients (nitrate, phosphate, and silicate) in two container types (polyethylene bottles and polystyrene tubes). We determined the preservation effects after storage for periods of 1, 3, 6, and 12 months. The effects of storage on nitrite were also determined. Because initial nitrite concentrations were always low, concentration changes were examined only in relation to concomitant changes in nitrate.

We ran five separate experiments, using water samples from different depths and different locations (Table 1), providing a variety of nutrient concentrations and, presumably, a variety of chemical and biological histories. All samples were oceanic; none were from upwelled or turbid waters.

The effectiveness of various preservation strategies has been examined previously; reviews are given by Riley (1975) and Grasshoff (1976). The definition of "effective procedure" undoubtedly varies from study to study depending on the degree of accuracy and/or precision required by the investigator. Freezing at $-10°$ to $-20°C$ has been demonstrated to successfully preserve phosphate, nitrate, and silicate (Collier and Marvin 1953; Strickland and Parsons 1968; Thayer 1970; Truesdale 1971; MacDonald and McLaughlin 1982); however, recommendations as to the necessity for prefiltration or quick-freezing vary. Numerous other workers have reported inferior results with frozen samples unless they are chemically stabilized (Murphy and Riley 1956; Gilmartin 1967; Jenkins 1968; Charpiot 1969). Depression of silicate levels in frozen samples caused by the polymerization of reactive silicate has been reported (Kobayashi 1967). This may be reversed by extended periods of thawing. Polymerization is not expected in samples of high

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[Manuscript received December 9, 1984.]

TABLE 1
Origin of Samples Used in Study

Experiment #	Date (Jan. 1983)	Location		Depth of sample (m)	Initial concentration µmol/l		
					NO_3	PO_4	SiO_3
1.	13	24°52.4'N	156°13.4'W	15	0.02	0.060	0.62
2.	14	27°16.9'N	155°16.3'W	995	44.32	3.020	131.04
3.	18	27°57.7'N	141°38.6'W	140	1.50	0.155	3.90
4.	22	28°49.4'N	127°14.4'W	180	1.86	0.320	4.60
5.	26	33°11.3'N	118°22.8'W*	90	9.58	1.006	11.16

*CalCOFI 90.37

(oceanic) salinities (Burton et al. 1970), at least not for storage periods less than 5 months (MacDonald and McLaughlin 1982), and, at present, there is no accepted protocol for the length and means of thawing samples.

An alternative preservation strategy is to reduce the pH of the sample sufficiently to preclude biological activity. Acidification of samples with hydrochloric acid has been reported to preserve silicate (Mullin and Riley 1955), and sulfuric acid has been used to preserve silicate (Grasshoff 1976) and phosphate (Charpiot 1969). Other workers have warned against the acidification of phosphate samples because of the hydrolysis of labile organic phosphate (Jenkins 1968; Grasshoff 1976). At SIO hydrochloric acid has been used to stabilize samples in several studies, particularly when nitrate is to be analyzed (J. Gieskes, pers. comm.). The combination of acidification and freezing was recommended by Riley (1975), but no experimental justification was presented.

Although plastic containers are essential for preserving silicate (Mullin and Riley 1956), a number of workers have reported loss of phosphate from samples stored in polyethylene, especially soft polyethylene (Murphy and Riley 1956; Heron 1962; Hassenteufel et al. 1963). Other workers have stored samples for phosphate analysis in polyethylene containers without noticeable loss of phosphate (Charpiot 1969; Thayer 1970), and samples are briefly held in polyethylene tubes during autoanalyzer use. Acidification of samples should prevent the absorption of phosphate by polyethylene (A. Mantyla, pers. comm).

The disparity of the conclusions in previous studies suggests that the results of specific studies may have limited general applicability (e.g., Gilmartin 1967; Thayer 1970), both because of differences in the biological and chemical systems being studied and because of differences in the needs of various workers. The present investigation was specific to the requirements of the CalCOFI program. Since we could not expect to analyze nutrients less than one month after collection, this was the shortest storage period considered. Also, preservation is cost-effective only if it does not greatly increase the cost of analysis ashore and if the shipboard treatment is rapid and does not require skilled chemists or special materials. This latter requirement precluded many preservation procedures, such as those requiring filtration before preservation or quick-freezing in dry ice.

METHODS

Analytical procedures were those routinely used on CalCOFI surveys by the Physical and Chemical Oceanographic Data Facility (PACODF; Atlas et al. 1971). Control samples consisted of four or five replicate subsamples drawn into standard autoanalyzer tubes that had been rinsed with 1N HCl and triple-rinsed with distilled water. Nutrient concentrations were determined with an Hitachi autoanalyzer within 24 hours of collection. The same autoanalyzer was used for all subsequent analyses.

Preservation Methods

Frozen samples. We drew four replicate subsamples into each container type and placed them in a blast freezer at − 10°C within one hour of collection. Samples remained frozen until the night before anlysis, when they were defrosted at room temperature.

*Acidified samples.*We drew four replicate subsamples into each container type. To each subsample we added 0.1 ml of concentrated HCl, using an Eppendorf pipette. Samples were capped and stored at room temperature. Prior to determining nutrients, we checked the pH of the samples with Hydrion paper to ascertain that acid had been added, and then neutralized them with the addition of 60 mg of sodium carbonate, returning the pH to 7-8. Controlled neutralization is essential because the subsequent nitrate analysis is sensitive to pH values outside this range.

Acidified and frozen samples. We drew four replicate subsamples into each container type and acidified them before freezing. Prior to analysis, we thawed and neutralized samples as described above.

Container Types

Polystyrene tubes. These were 16-ml, disposable, screw-capped test tubes. Because they are sterilized by the manufacturer, preliminary rinsing was not necessary.

Polyethylene bottles. These were 50-ml bottles, which were rinsed with 1N HCl and triple-rinsed with distilled water before use. In experiment 5, we substituted 60-ml autoanalyzer tubes like those routinely used to collect and hold nutrient samples at sea. Because we were depending upon materials at hand, we did not standardize the type of polyethylene used. In experiments 1 and 3, bottles were soft polyethylene; in the others they were linear polyethylene. In retrospect, this lack of control was a mistake.

Because we added a constant volume of acid to sample containers of varying sizes, the resultant pH of the preserved sample varied. In all cases it was below 2.

Simulated Catastrophes

In addition to the treatments described above, we simulated two types of catastrophe and determined their effects after one month. For these, we stored samples in tubes, except in experiment 4, when we used bottles.

No preservation. We stored samples at room temperature without acidification.

Accidental thaw. We simulated the effects of a power failure by removing samples from the freezer and allowing them to thaw at room temperature overnight before refreezing. We were particularly interested to see whether acidification of frozen samples would buffer them against the effects of an accidental thaw.

Performance Criteria

We used three criteria to evaluate the performance of the various preservation procedures.

Quality of the autoanalyzer output. One unexpected consequence of sample preservation was an increase in the noise of the autoanalyzer output signal, which made it difficult to accurately determine the peak height. In some cases, particularly phosphate and nitrite stored for 12 months, the noise was severe enough to completely prevent estimation of peak height, resulting in loss of data. In order to quantify this effect, we ranked the output traces for each sample from one to three, with one signifying a normal trace, two a noisy trace that could still be read with some degree of certainty, and three a trace that could not be interpreted with any degree of assurance.

Accuracy. We measured the accuracy of the preservation procedure as the absolute value of the deviation of the mean concentration of the four preserved replicates from the mean of the four or five replicates analyzed on board ship.

Precision. We measured the precision of the four preserved samples by their variance. Change in precision was evaluated by comparing the variance of the preserved replicates with the variance of the four or five replicates analyzed on board ship.

Statistical Analysis

The experimental design was originally intended for a single, multidimensional analysis of variance. Unfortunately, the data showed significant heteroskedasticity, which could not be removed by simple data transformation. In addition, there were significant interaction terms, which complicated interpretation of the results. Ultimately, we reorganized the data into a series of two-way designs and analyzed with the Friedman nonparametric two-way analysis of variance (Tate and Clelland 1959; Conover 1971). Under the assumption of no significant differences between primary effects (preservation method, container type, or preservation time) the test statistic, W, can be approximated by

$$W = \text{observed SS } \left(\sum_{i=1}^{m} R_i\right) \Big/ \text{ maximum SS } \left(\sum_{i=1}^{m} R_i\right)$$

where

$$\text{observed SS } \left(\sum_{i=1}^{m} R_i\right) = \sum_{j=1}^{n} \left[\sum_{i=1}^{m} R_{ij} \right]^2 - \left\{ \frac{\left[\sum_{j=1}^{n} \sum_{i=1}^{m} R_{ij} \right]^2}{n} \right\}$$

and

$$\text{maximum SS } \left(\sum_{i=1}^{m} R_i\right) = (m^2)\,(n^3 - n)/12$$

where items are ranked 1 through n across the factor being tested, and m = the number of sets of ranks.

For large values of m or n, the chi-square approximation was used:

$$x^2_{n-1} = m(n\text{-}1)\,(W)$$

We retained outlying values in the analyses and, unless otherwise noted, used only complete experiments.

For example, in the case where the effect of storage time on nitrate concentration is being tested ($n = 5$, $m = 17$), the appropriate sum of squares has components caused by storage time within samples frozen in tubes, within samples frozen in bottles, within samples acidified in tubes, etc. Thus the total sum of squares may be decomposed to examine the effect of storage time on samples stored in bottles, regardless of preservation method, or the effect of time on frozen samples regardless of container type. Or the effect of storage time on samples frozen in tubes may be compared with the effect on samples acidified in tubes. In this way, the components of the primary analysis may be examined for interaction effects, which cannot be tested directly. The calculated "probability" values associated with ANOVAs performed on subsidiary units have uncertain statistical meaning, but they indicate the relative strength of the primary effect within the various subunits. In addition, since accuracy and precision are independent measures of performance, they can be combined into a single measure for each nutrient, and the statistics for all nutrients may be combined to give an overall estimate of the relative success of the three preservation methods.

We are concerned with three factors: preservation procedure (freezing, acidification, and acidification plus freezing), container type (polystyrene tubes and polyethylene bottles), and storage time (1, 3, 6, and 12 months). To reduce the effects of multiple testing, effects of the preservation procedure, which we consider our major concern, were tested for significance at $P = .05$. The effects of container type were considered to be significant at $P = .025$, and the effects of storage time at $P = .01$.

When we obtained a significant ANOVA between three or more factors, we tested differences between specific levels of the primary factor by means of an a posteriori test (Nemenyi 1963), carried out at $P = .05$. Results are indicated by the pattern of underlining in Tables 2-4. For instance, in Table 2, the accuracies of the nitrate determinations changed significantly with time of storage according to the Friedman ANOVA ($P < .01$). The four storage times are listed from left to right in order of decreasing accuracy. The results of the Nemenyi analysis indicate that samples stored for 1 month are significantly more accurate than samples stored for 6 and 12 months, but are not significantly different from samples stored for 3 months; samples stored for 3 months are significantly more accurate than samples stored for 12 months, but are not different from samples stored for 1 or 6 months; samples stored for 6 months are not significantly more accurate than samples stored for 12 months. These relationships are indicated by a series of three overlapping underlines.

We examined the effects of the simulated catastrophes with a Friedman two-way ANOVA in which the six levels of the primary factor were the three preservation procedures, together with the three catastrophes: samples stored without preservation; samples frozen, thawed, and refrozen; and samples acidified and frozen, thawed, and refrozen. Secondary factors were the initial conditions of the five experiments.

RESULTS

The experimental results are summarized in Tables 2 to 4. The complete data set is available on request from the senior author.

Nitrate and Nitrite (Table 2)

There was no detectable increase in the noise of the nitrate signal caused by preservation. However, increased signal noise did result in loss of nitrite data, and consequently in nitrate data, especially in acidified samples stored for 12 months.

For nitrate there was a significant difference between preservation procedures only among the samples stored in autoanalyzer tubes in experiment 5, where there was a strong tendency ($P < .01$, accuracy and precision combined) for acidified samples to be best and frozen samples worst. When this subset was removed from the analysis, there was a tendency for frozen samples to be superior ($P < .10$, accuracy and precision combined).

For all procedures and all containers, there was a significant increase in the concentration of nitrate with time, accompanied by a loss of accuracy and decrease in precision.

There were also significant changes of nitrite over time ($P < .05$). However, no general trend of increase or decrease with time could be detected. There was no evidence of correlation between concentrations of nitrite and nitrate, either within or between experiments. Thus, changes in nitrate concentration could not be explained solely as reduction to or oxidation of nitrite.

Phosphate (Table 3)

For all samples, there was a significant increase in the noise of the phosphate autoanalyzer signal over time. The signal quality of samples run on board ship or stored for only one month was significantly better than that of samples stored for longer periods of time. The increase in noise with time was strongest in samples acidified or acidified and frozen and stored in tubes. Regardless of storage time, signals from frozen

TABLE 2
Summary of Nitrate Changes in Stored Seawater Samples

Factor	Criterion	ANOVA probability	Performance Best Worst	
Preservation method	q	>.20	F A A+F	
F: frozen	a	<.20	F A+F A	
A: acidified	p	>.20	F A A+F	
	a+p	>.20	F A+F A	
Container type	q	>.20	B T	
T: tube	a	>.20	T B	
B: bottle	p	>.20	B T	
	a+p	>.20	T B	
Storage time in months	q	=.10	12 1 3 C 6	
C: control	c	<.01*	C 1 3 6 12	(increase)
	a	<.01*	1 3 6 12	
	p	<.05	C 1 3 12 6	

q: quality of the autoanalyzer signal
a: accuracy of the preserved samples
p: precision of the preserved samples
c: nitrate concentration in the preserved samples

Treatments are listed according to performance, left to right from best to worst. Underlining indicates the results of a posteriori tests, performed only when ANOVA results are significant (*).

samples had significantly less noise than did samples that were acidified and frozen, whereas signals from acidified samples were intermediate. There was no effect of container type.

The chemists who did the analyses believe that much of the problem can be attributed to the release of carbon dioxide in the sample when it is neutralized prior to analysis. Such bubbles are known to interfere with the proper operation of the autoanalyzer. The problem is more severe with phosphate because of the small diameter of the phosphate tube and because, unlike the other nutrients, the sample is not diluted with distilled water during analysis. However, if signal deterioration results solely from the production of bubbles, we would expect it to be independent of storage time, but dependent upon the volume of the sample (since the absolute amounts of acid and base added were the same for all volumes). Neither was the case in our samples, suggesting that other factors may be involved.

The precision of the phosphate determination is affected by the accuracy with which the autoanalyzer traces can be read. However, in most cases, changes in precision were greater than could be explained by uncertainty in the signal alone.

The preservation procedure affected neither the accuracy nor the precision of phosphate determinations, except for samples stored in tubes, where the procedure did influence precision ($P < .05$). Frozen samples were more precise than samples acidified and

TABLE 3
Summary of Phosphate Changes in Stored Seawater Samples

Factor	Criterion	ANOVA probability	Performance Best Worst
Preservation method	q	<.02*	F A A+F
F: frozen	a	>.20	F A+F A
A: acidified	p	>.20	F A A+F
	a+p	>.20	F A A+F
Container type	q	>.20	B T
T: tube	a	=.05	T B
B: bottle	p	<.10	T B
	a+p	<.01*	T B
Storage time in months	q	<.01*	C 1 3 12 6
C: control	c	<.025	C 3 1 6 (increase)
	a	<.01*	1 6 3
	p	<.01*	C 1 6 3

q: quality of the autoanalyzer signal
a: accuracy of the preserved samples
p: precision of the preserved samples
c: phosphate concentration in the preserved samples

Treatments are listed according to performance, left to right from best to worst. Underlining indicates the results of a posteriori tests, performed only when ANOVA results are significant (*).

frozen; precision of acidified samples was intermediate. This effect was not evident among samples stored in bottles and may in part reflect the deterioration of the autoanalyzer signal resulting from neutralization of the acid in the smaller-volume tubes.

When both accuracy and precision were considered together, pooling all storage procedures, the performance of tubes was significantly better than that of bottles. However, this effect was greatest in samples that were either frozen or acidified; samples that had been acidified and frozen showed no difference between container types.

The statistical analysis of length of storage time on accuracy and precision did not include the samples stored for 12 months because of the small number of these samples available. In all experiments, there was a tendency for the phosphate concentration to increase with time of storage, accompanied by a significant loss of accuracy and precision. Since this occurred both in frozen and in acidified samples, it did not appear to be solely related to the acidification of the sample and the resultant breakdown of organic material. Moreover, since the concentration increased in both container types, there was no evidence of differential adsorption of phosphate by the plastics, as has been suggested by previous workers (Murphy and Riley 1956; Heron 1962; Hassenteufel et al. 1963).

In general, these data indicate that the best phosphate results may be obtained from samples frozen in polystyrene tubes and analyzed within one month.

TABLE 4
Summary of Silicate Changes in Stored Seawater Samples

Factor	Criterion	ANOVA probability	Performance
			Best Worst
Preservation method	q	>.20	A+F A--F
F: frozen	a	>.20	A+F A F
A: acidified	p	>.20	A+F F A
	a+p	>.20	A+F F A
Container type	q	>.20	T B
T: tube	a	=.01*	T B
B: bottle	p	<.05	T B
	a+p	<.01*	T B
Storage time in months	q	>.20	1 3 12 6 C
C: control	c	>.20	C 1 3 12 6 (decrease)
	a	<.01*	$\underline{\text{C 1 3 12 6}}$
	p	<.01*	$\underline{\text{C}}$ $\underline{\text{1 3 6 12}}$

q: quality of the autoanalyzer signal
a: accuracy of the preserved samples
p: precision of the preserved samples
c: silicate concentration in the preserved samples

Treatments are listed according to performance, left to right from best to worst. Underlining indicates the results of a posteriori tests, performed only when ANOVA results are significant (*). Dash indicates ties.

Silicate (Table 4)

Both accuracy and precision of samples stored in polystyrene tubes were greater than those of samples stored in polyethylene bottles.

In all experiments, there was a significant loss of accuracy with increased storage time, related to a tendency for the concentration of silicate to decrease. This tendency was strongest for samples acidified and frozen in tubes ($P < .05$). A similar decrease with time was not evident in samples stored in bottles. Within tubes and bottles there was a significant decrease in precision over time, with the major period of decrease occurring during the first month of storage.

Interaction Effects

Numerous interaction effects were apparent in the results of this experiment. The more easily interpretable have been pointed out. In addition, there frequently appeared to be interactions between the storage procedure or the container type and the initial concentration of the nutrient. For instance, in the case of phosphate frozen in tubes (Figure 1), after one month there was a significant decrease in concentration in experiment 1, where the initial phosphate concentration was low (Mann Whitney U test, $P < .01$). However, in experiment 2, where initial concentration was high, there was a significant increase in concentration ($P < .01$).

The effect of time on the nutrient concentration of stored samples was confounded with any differences in the day-to-day standardization and operation of the autoanalyzer. This latter source of variability is not

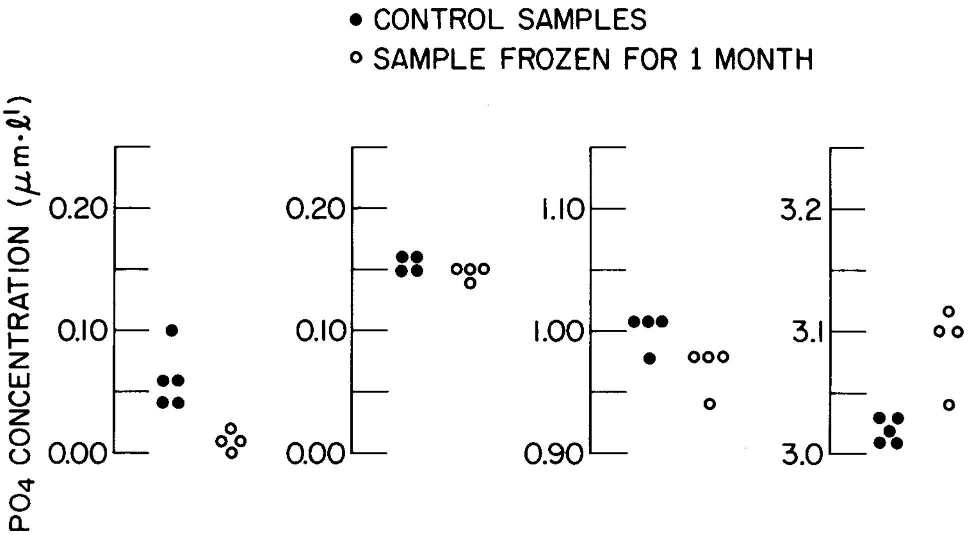

Figure 1. Interaction between initial concentration of phosphate and the change in concentration after freezing for one month in polystyrene tubes. Experiments 1, 3, 5, and 2, from left to right.

expected to have any temporal trend. However, it is not appropriate to blame operator error for any variability that does not exhibit a linear trend with time. The frozen samples generally showed highest concentrations of all nutrients after 6 months of storage. This pattern was not apparent in samples that had been acidified or acidified and frozen. Although all 6-month samples were analyzed by the same chemists, frozen samples were run the day before the others. We initially suspected that the high concentrations in the frozen samples were due to operator variability rather than true temporal changes. However, we are unable to postulate a source of operator error of such magnitude. In fact, the graphs for nitrate and phosphate from experiment 2, after 6 months, were off scale for the only time during the entire experiment.

The numerous interaction effects, especially those involving initial nutrient concentration or time of storage, make precise predictions about preservation of future samples risky.

Simulated Catastrophes

When the three simulated catastrophes were considered and compared with the three preservation procedures for both nitrate and phosphate, there were significant differences between treatments ($P < .05$). The primary outliers were related to the absence of treatment, which caused phosphate concentrations to decrease in all samples, and nitrate concentrations to increase in samples with very high or low initial concentrations but to decrease in samples with intermediate concentrations. There were no significant differences in precision. There was no evidence of treatment effect on either accuracy or precision of silicate determinations; silicate preserved as well in untreated samples as in preserved samples.

We could detect no decrease in accuracy or precision resulting from an accidental overnight thawing. Thus there is no evidence that adding acid before samples are frozen protects them from deterioration during a thaw.

CONCLUSIONS

When the data from all nutrients are weighted equally and combined, the most accurate and precise storage procedure is freezing; acidification, without freezing is the least satisfactory. The differences, however, are not significant ($P < .25$). Storage of samples in polystyrene tubes gave significantly better results than storage in polyethylene bottles ($P<.01$).

With respect to this latter result, we cannot distinguish between the effect of the smaller volume and the polystyrene material. From a technical standpoint, 16 ml represents an absolute minimum needed for the autoanalyzer. A second analysis, should the need arise, is not possible, and any loss of sample may preclude adequate rinsing. While the smaller volume may have advantages in terms of rapid freezing and thawing, the tubes were also superior to the bottles when samples were acidified. Thus, circumstantial evidence suggests that the difference between the performances of tubes and bottles was due primarily to the container material. A better container may be a 50-ml polystyrene bottle. More research into this is warranted.

The purpose of this study was not only to identify the best preservation procedure, but to determine whether any would be an adequate substitute for shipboard analyses. The error introduced by preservation was small relative to the range of values found within the California Current, and data from preserved samples would be adequate for mapping major horizontal and vertical distributions. However, general distributions within the California Current have been described in the past, and it is now the details and anomalies that are receiving most attention. Unfortunately, the relatively large error at the lowest values (e.g., after one month > ± 100% for nitrate, > ± 33% for phosphate, and > + 200% for silicate) would complicate the use of these data for investigations into the relationships between the depth or slope of the nutricline and the biomass or productivity of the euphotic layer (e.g., Eppley et al. 1978, 1979; King and Devol 1979; Hayward and McGowan 1985). Moreover, the error introduced at higher concentrations, although relatively small, is equivalent to the variance observed at 300 m at a single station over a 28-year period, and this error would hinder calculations such as long-term anomalies of mass transport (e.g., Haury and Shulenberger 1982). Thus, because the magnitude of the error introduced by any of the storage procedures tested was sufficient to preclude many of the uses which we anticipated for the data, we concluded that nutrient storage during the 1984 CalCOFI surveys could not be justified.

When our results are considered in the context of previous studies of this sort, the only conclusion is the impossibility of valid generalization. The results of different nutrient storage procedures appear to depend strongly upon the type of water being sampled and upon specific details of the analytical techniques employed. Preservation of nutrient samples should be considered a strategy of last resort. However, any program that depends upon preservation of water samples for future nutrient analysis must independently determine the error expected to be introduced by the specific procedures selected. The question of whether the additional analytical error is acceptable can then be addressed.

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SIZE DISTRIBUTIONS AND SEX RATIOS OF RIDGEBACK PRAWNS (*SICYONIA INGENTIS*) IN THE SANTA BARBARA CHANNEL (1979-1981)

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ABSTRACT

Ridgeback prawns (*Sicyonia ingentis*) were sampled monthly over two years (1979-81) at offshore stations, and less frequently onshore. Size distribution and sex ratios of samples were determined. Data from the offshore station indicate a unimodal size distribution (23-47 mm CL), from which age structure could not be discerned. Data from onshore samples provided evidence that prawns enter the fishery at age 1. The sex ratio of monthly samples fluctuated during 1981, in contrast to 1980, when a 1:1 ratio was observed in all months except during the fall.

RESUMEN

Durante más de dos años (1979-81) se realizaron muestreos mensuales del langostino *Sicyonia ingentis* en estaciones alejadas de la costa y, menos frecuentemente, en estaciones costeras. Se determinaron la distribución de tallas y las proporciones de sexos. Los datos de las estaciones alejadas de la costa indicaron una distribución de tallas unimodal (longitud del caparazón: 23.47 mm), de la cual no pudo discernirse la estructura de edades. Los datos de las estaciones costeras aportaron evidencias de que los langostinos comienzan a participar de la pesquería a la edad 1. En 1981 la relación de sexos en las muestras mensuales fue fluctuante, a diferencia de 1980, cuando se observó una relación de 1:1 durante todos los meses, excepto en el otoño.

INTRODUCTION

A small commercial fishery for the ridgeback prawn (*Sicyonia ingentis*) has recently developed in the Santa Barbara Channel, and a concomitant increase in oil and gas exploration in the channel has produced a need for information about the prawn's life history. This species is also of general interest because there are few abundant free-spawning crustaceans on the west coast of the United States. Only a few studies of this species have been conducted since its description by Burkenroad (1938). Herkelrath (1977) examined some aspects of *S. ingentis*, including growth, but field observations were few. Herkelrath (1977) also examined salinity and temperature tolerance of these prawns. Wicksten (1980) recorded distributional notes on *S. ingentis*, and Frey (1971) indicated that the ridgeback prawn had the potential to support a fishery. More recently, commercial landings, catch-effort data, and size distributions were examined by Sunada (1984). He found a declining catch per unit of effort (CPUE) from a high of 60 kg/hr in 1979, the first year of heavy fishing, to 20 kg/hr in 1982. He concluded from the size distribution data that individuals were recruited at age 1; the catch consisted mainly of ages 2 and 3, with a maximum at age 4.

Molt and reproductive periodicity in populations of *S. ingentis* in the Santa Barbara Channel from 1979 to 1982 are described by Anderson et al. (1985). They found that females (26-44 mm CL) did not molt in the summer but rather progressed synchronously through a single molt cycle with a peak of activity in late fall. Another such peak occurs in April. Females were capable of repeated spawning throughout the spawning season from July through September (Anderson et al. 1984; Anderson et al. 1985).

The purpose of this paper is to document findings on size distributions and sex ratios of *S. ingentis* in the Santa Barbara Channel from 1979 to 1981. These data provide important baseline information on the ridgeback prawn during a critical period of increasing exploitation, and they provide new information for preliminary estimation of growth rates during certain life stages.

MATERIALS AND METHODS

Monthly samples were collected using shrimp semiballoon trawl gear at one fixed station in the Santa Barbara Channel off Santa Barbara, California (Figure 1). Occasionally, additional samples were taken at random trawl sites. Nets used were approximately 30 m long and 7 m wide at the mouth, with 11.5-cm mesh (diagonal, not stretched) on the cod end and a 2.5-cm mesh on the belly. Trawls made at the harbor station (Figure 1) used a 2.5-cm mesh net. Carapace length (CL) was measured from the posterior margin of the orbit to the posterior border of the carapace.

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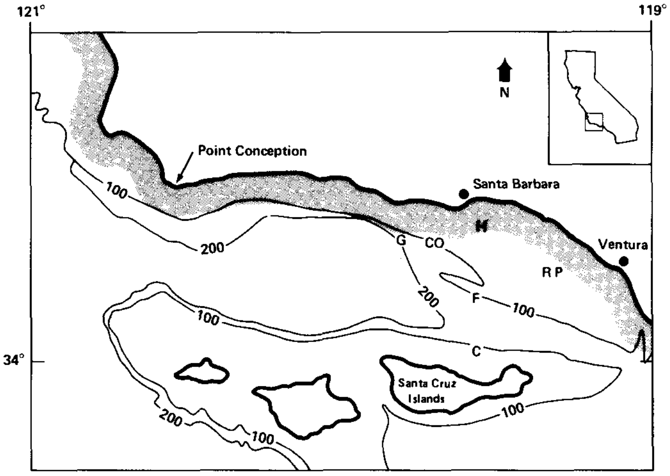

Figure 1. Map of the study area in the Santa Barbara Channel. Inset shows the location of the Santa Barbara Channel along the coast of California. Depths are in meters. The three-mile limit is indicated by shading. F = fixed station (34°18′N × 119°43′W); R = Rincon Point (34°17′N × 119°32′W); P = Pitas Point (34°18′N × 119°34′W); G = Gaviota area (34°23′N × 120°08′W); CO = Coal Oil Point (34°21′N × 119°52′W); C = China Cove (34°06′N × 119°40′W); H = harbor area (34°22′N × 119°42′W).

Males were distinguished from females by the presence of a petasma in the former.

Molt increments were measured in the laboratory for prawns collected in November 1982. We judged prawns to be in advanced premolt (stage D_2-D_4) at the time of collection (Anderson et al. 1985). They were kept in individual compartments in troughs containing running seawater of 12° to 15°C. Ecdysis occurred from 6 to 13 days after collection. We measured premolt CL on the cast exoskeleton. Postmolt CL was measured approximately 24 hours after ecdysis.

RESULTS

Size Distributions

Size distributions of prawns varied with sex and depth. Monthly sampling of prawns at 145-m depth over 2 years revealed a narrow size range (23-47 mm CL) offshore (Figures 2 and 3). The maximum size of females was consistently greater than the maximum size of males. Size composition of the catch at the deep station did not change markedly throughout the sampling period (Figure 2), and few individuals were collected that were smaller than 25 mm CL (Figure 3). In contrast, samples taken at 60-m depth contained more prawns in smaller size classes of approximately 25 mm CL and below (Figure 4). Sampling at 40 m yielded the smallest prawns observed in this study (Figure 5). For animals collected at that depth in December 1982, we observed a unimodal peak over the range of 6 mm CL to 15 mm CL (Figure 5). Samples at some onshore stations in May 1983 showed a unimodal peak (Figure 5) at a slightly larger size—10 to 27 mm CL; the maximum size of females was greater than the maximum size of males.

Molt increments were measured in laboratory in late fall because *S. ingentis* populations undergo a synchronous molt at this time (Anderson et al. 1985); thus it was relatively easy to obtain field specimens in late premolt. Molt increments measured in the laboratory were small (Table 1) and variable. The change between premolt CL and postmolt CL ranged from 1% to 8%, with means of 4.1% for females and 4.6% for males. Prawns examined measured from 21.2 to 24.6 mm CL for males and 25.7 to 28.4 mm CL for females.

Sex Ratios

Sex ratios during the two years of study showed two different patterns (Figure 6). In 1979 to 1980, ratios were consistently 1:1 until the spawning season, when females were more numerous in the trawl. In 1980 to 1981, sex ratios fluctuated throughout the year.

DISCUSSION

Although the data presented do not permit a definitive discussion of growth rates for *S. ingentis*, some preliminary estimates are possible. The 6-mm-CL-to-15-mm-CL prawns collected in December 1982 (Figure 5) are probably the annual cohort of juveniles. This compares favorably with the identification by Kennedy et al. (1977) of 4-to-5-mm *S. brevirostris* as the smallest juvenile recruits. If the sample taken in May 1983 (with a mode between 14 mm CL and 21 mm CL) also represents the year class that settled in the fall of 1982, growth between December and May was slightly greater than 1 mm/mo. Since prawns collected in trawls at 145 m were as small as 23 mm, it appears possible that individuals enter the fishery one year after settlement. Although the lowest age can be approximately established, it is not possible to determine the number of age classes present in the catch. Growth in crustaceans depends on molt frequency and molt increment. Both of these factors may be affected by sex, and usually decline with age (Hartnoll 1982). Effects of variability in molt increment and molt frequency on size distributions have been examined recently (Hartnoll 1982; Botsford, in press). In general, small increments together with variability in increment or period tend to obscure age-class modes in size distributions. For *S. ingentis*, apparent offshore movement (Figures 2-4) and small, variable molt increments in the laboratory (Table 1) make it difficult to follow distinct age-classes. Variability in molt frequency throughout the year and

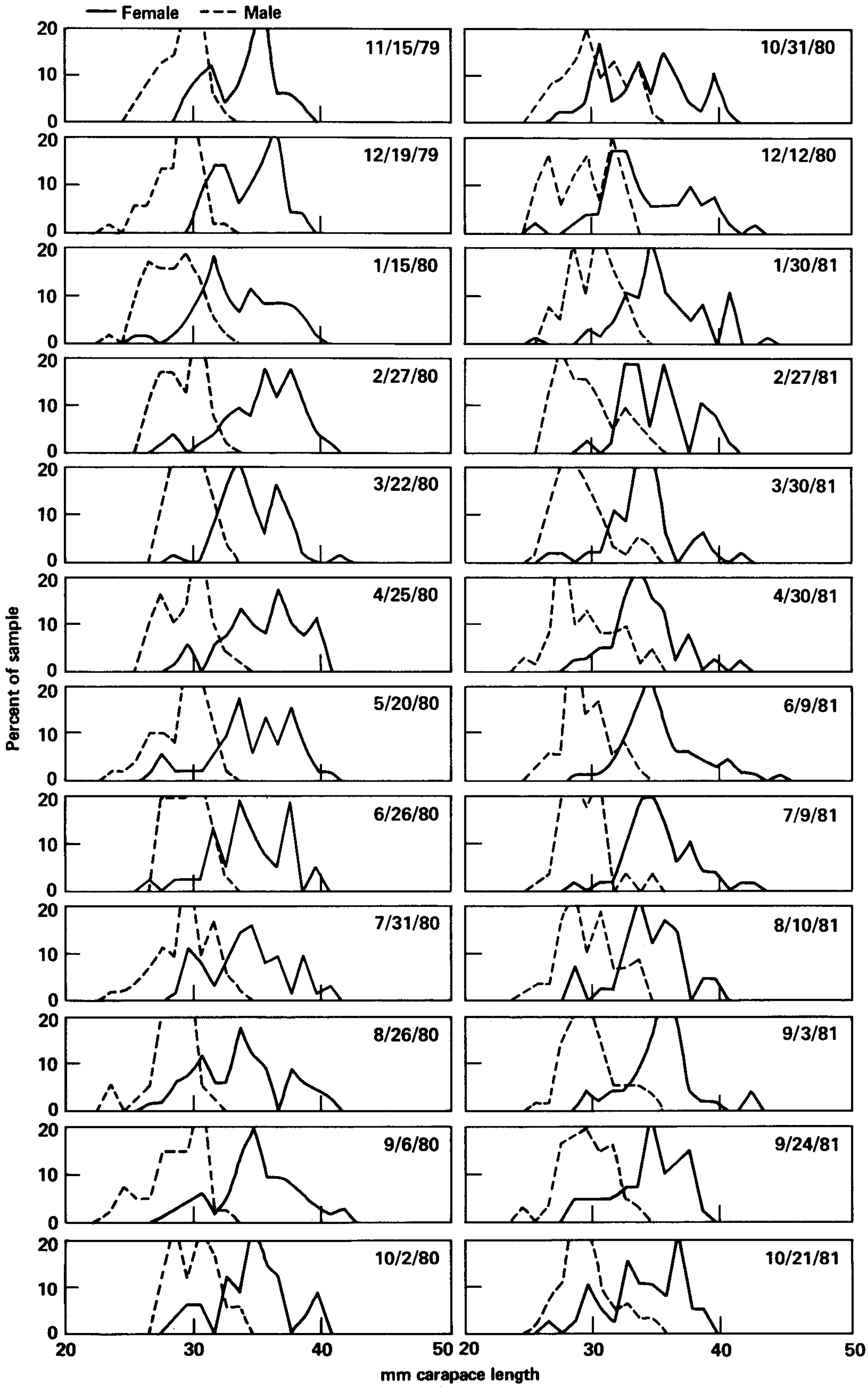

Figure 2. Size-class distribution of *S. ingentis* males and females in 24 monthly trawls at one fixed station (145-m depth). The range in number of animals observed was 50 to 118. The number observed in any single trawl is given in Figure 6.

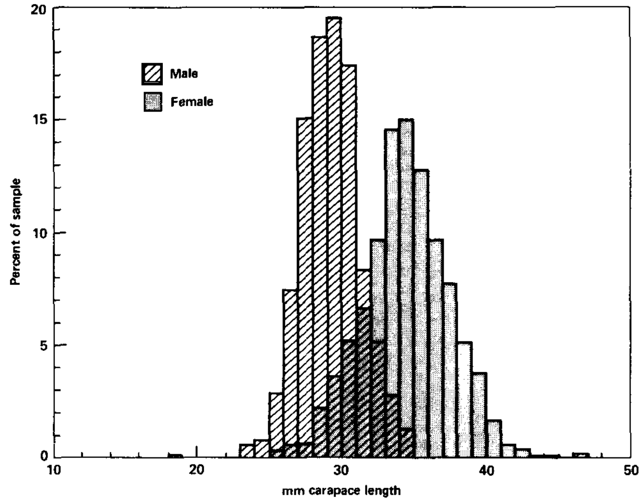

Figure 3. Size-class distribution of male and female *S. ingentis* in all monthly trawls combined for two years at one fixed station (145 m). n = 2452.

between sexes (Anderson et al. 1985) may also affect our ability to distinguish age-classes.

An estimate of crustacean growth patterns can usually be obtained from knowledge of the molt increment and frequency. The laboratory molt increment data reported here were taken for this purpose; however, the fact that molt increments were small leads to suspicion that they do not represent true natural molt increments. They may be a laboratory artifact or may be small because they were measured in November following the reproductive season. Use of these low increments would lead to a high maximum age in the fishery. For example, if these molt increments were the natural molt increments, and molting occurred a minimum of twice per year (Anderson et al. 1985), it would take 14 molts or 7 years to grow from a size of 25 mm to a size of 45 mm, growing at 1.041 mm per molt—the average of the measured increments for females (Table 1). Since 25 mm is near the size at age one, and 45 mm is near the maximum size of females in the trawls, this would imply a maximum age of 8 years. More reasonable estimates will require measurement of natural increments and molting frequencies. This information reflects natural mortality rate, and hence is critical for management of this fishery.

Kennedy et al. (1977) observed distinct modal progressions of size classes in populations of *S. brevirostris* from eastern Florida. They found that 8-to-10-mm-CL recruits grew to approximately 22 mm CL in 6 months after recruitment. This is twice the growth

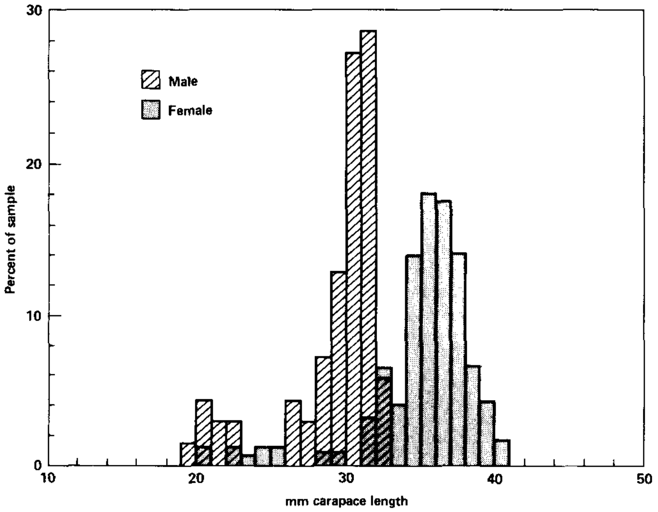

Figure 4. Size-class distribution of male and female *S. ingentis* in a representative trawl at 60 m (Rincon Point, 9/10/79). n = 191.

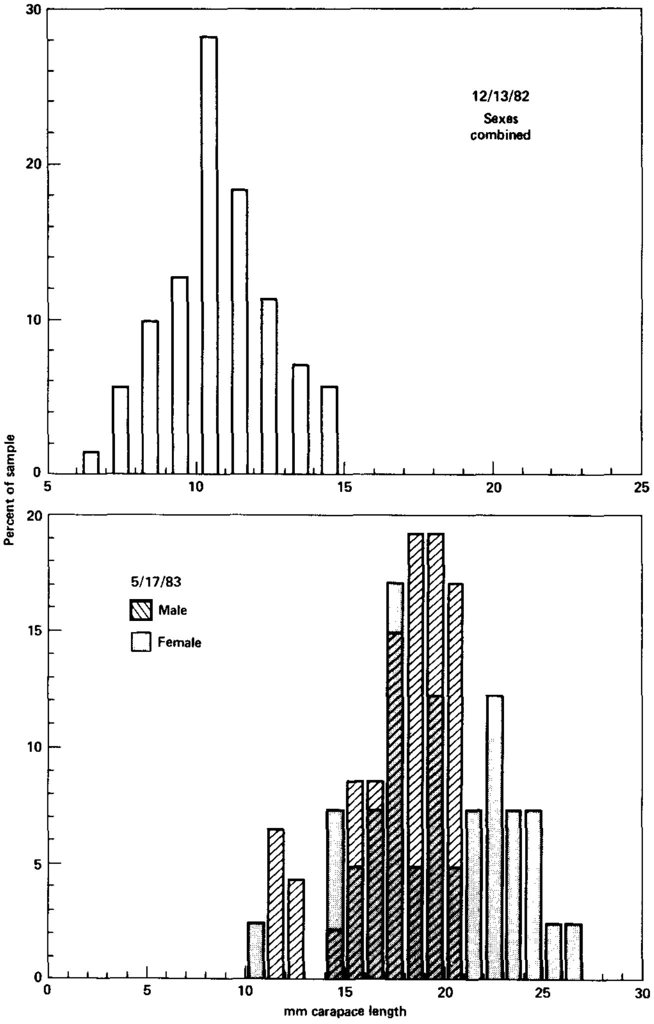

Figure 5. Size-class distribution of juvenile and small adult *S. ingentis* taken on 12/13/82 (n = 71) and 5/17/83 (n = 87). Sexes are combined on 12/13/82 because sexual differentiation as evidenced by the presence of a petasma was noted in only a few of the larger animals. Trawls were made in approximately 40 m of water due west of Santa Barbara Harbor (site H in Figure 1).

TABLE 1
Molt Increments of Adult Ridgeback Prawns, Taken at the Fall Molt

Females				Males			
Initial CL (mm)	CL after molt (mm)	Difference (mm)	Percent change	Initial CL (mm)	CL after molt (mm)	Difference (mm)	Percent change
25.7	26.9	1.2	5	21.2	21.5	0.3	1
25.8	27.6	1.8	7	21.4	21.8	0.4	2
26.6	26.8	0.2	1	22.1	23.8	1.7	8
26.6	27.3	0.7	3	22.2	23.2	1.0	5
26.9	27.6	0.7	3	22.4	24.3	1.9	8
27.9	29.2	1.3	5	22.5	23.4	0.9	4
28.4	29.7	1.3	5	22.5	23.3	0.8	4
			$\bar{x} = 4.1$	22.8	24.2	1.4	6
			$\sigma = 1.95$	23.4	24.3	0.9	4
				23.6	24.1	0.6	3
				23.9	25.1	1.2	5
				24.2	25.5	1.3	5
				24.2	25.3	1.1	5
				24.4	25.4	1.0	4
				24.4	26.1	1.7	7
				24.4	25.0	0.6	2
				24.4	25.3	0.9	4
				24.6	26.2	1.6	7
							$\bar{x} = 4.6$
							$\sigma = 2.06$

rate we observed for *S. ingentis* at the same age. In agreement with our data on *S. ingentis*, male *S. brevirostris* appeared to grow slightly slower, and they reached a smaller maximum size (30 mm for males versus 38 mm for females). The maximum lifespan of *S. brevirostris* is 22 months (Kennedy et al. 1977).

Kennedy et al. (1977) and Cobb et al. (1973) showed seasonal cycles in prawn abundance at various stations. Kennedy et al. demonstrated a seasonal offshore migration of *S. brevirostris*. Recruitment occurs at 26 m. In June and July, highest CPUE occurs at 40 m and then shifts to 60 m by October. A similar migration pattern may occur in *S. ingentis* populations.

To date, there is no explanation for the variability we observed in sex ratio. It may be due to the fact that fishery exploitation was in its third heavy year, but there is no direct evidence as yet. Sex-ratio changes may well reflect different migration patterns in the two years studied. Sex ratios in *S. brevirostris* populations are close to unity, but females are slightly more numerous (Cobb et al. 1973; Kennedy et al. 1977). In each of these studies, it is not known whether sex ratios in the catch reflect the true sex ratio of the population or sex-specific differences in catch rate.

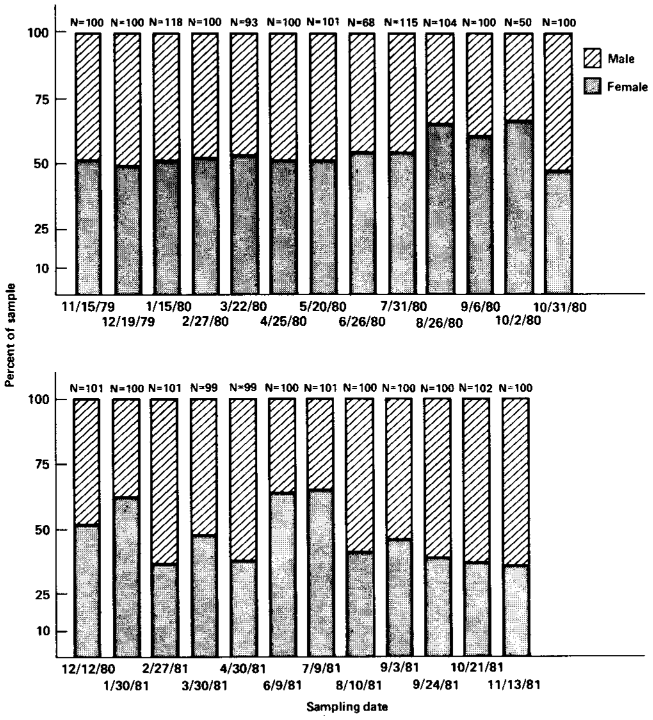

Figure 6. Sex ratios of populations of *S. ingentis* at one fixed station (145 m) in the Santa Barbara Channel. Observations were made monthly for two years.

Further studies are required for a complete understanding of recruitment, growth rates, and population movement for *S. ingentis.* Such studies would be important not only because this species is of local interest, but because very little is known about growth and recruitment of any free-spawning crustacean on the west coast of the United States. Perhaps one of the most significant factors influencing *S. ingentis* distribution is the presence of closed gyral circulations in the Southern California Bight. North of Point Conception, strong upwelling throughout most of the year results in strong offshore surface transport. This would cause tremendous loss of larvae for a free-spawning species with a long pelagic phase. Circulation patterns in the bight minimize loss of epipelagic fish larvae, and many migrating species apparently have increased spawning success in the bight for this reason (Parrish et al. 1981). Eggs of *S. ingentis* are demersal or neutrally buoyant if agitated slightly (personal observation); this means that deep currents may also play an important role in recruitment. Very little is known about deepwater currents in the Santa Barbara Channel, but it has been shown that some Penaeidae larvae and postlarvae actively discriminate between currents and current directions (Hughes 1972).

ACKNOWLEDGMENTS

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STOMACH CONTENTS OF ALBACORE, SKIPJACK, AND BONITO CAUGHT OFF SOUTHERN CALIFORNIA DURING SUMMER 1983

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ABSTRACT

Three species of scombrids were troll-caught off southern California for a food habits study during Cruise 166 of NOAA research vessel *David Starr Jordan* in August 1983, to examine effects of the anomalous oceanography (El Niño) of that period. The stomachs of 94 albacore (*Thunnus alalunga*), 31 skipjack (*Katsuwonus pelamis*), and 42 bonito (*Sarda chiliensis*) were examined. Chi-square analysis for homogeneity showed highly significant differences in types of prey and proportions consumed by the three species. Albacore consumed 96.8% fish, 35.1% cephalopods, and 52.1% crustaceans by frequency of occurrence, and 82.4% fish, 1.7% cephalopods, and 15.9% crustaceans by numerical frequency. Skipjack consumed 19.4% fish, 12.9% cephalopods, and 54.8% crustaceans (45.2% euphausiids) by frequency of occurrence, and 11.1% fish, 2.6% cephalopods, and 86.3% crustaceans (76.5% euphausiids) by numerical frequency. Bonito consumed 71.4% fish and 26.2% crustaceans (11.9% euphausiids) by frequency of occurrence, and 32.1% fish and 67.9% crustaceans (63.4% euphausiids) by numerical frequency. A comparison to historical data during similar and dissimilar environmental conditions suggests that the scombrids are opportunistic predators, and that prey availability was partly a function of the oceanographic conditions. The index of relative importance and mean volumetric ratio measurement of northern anchovy (*Engraulis mordax*) in the diet of albacore is presented.

RESUMEN

Con el fin de examinar los efectos oceanográficos anómalos (El Niño) en el período de agosto de 1983, durante la campaña 166 del buque de investigación de la NOAA "David Starr Jordan" para un estudio de hábitos alimentarios, se capturaron con línea tres especies de escómbridos a la altura del sur de California. Se examinaron 94 contenidos estomacales de albacora (*Thunnus alalunga*), 31 de listado (*Katsuwonus pelamis*), y 42 de bonito (*Sarda chilensis*). Análisis de chi-cuadrado para homogeneidad demostraron diferencias altamente significativas en los tipos y proporciones de presas consumidas por las 3 especies. Por frecuencia de registro, la albacora consumió un 96.8% de peces, 35.2% de cefalópodos, y 52.1% de crustáceos; mientras que por frecuencia numérica los valores fueron, peces: 82.4%, cefalópodos: 1.7%, y crustáceos: 15.9%. El listado consumió 19.4% de peces, 12.9% de cefalópodos, y 54.8% de crustáceos (45.2% de eufáusidos) por frecuencia de registro; en frecuencia numérica los valores fueron, peces: 11.1%, cefalópodos: 2.6%, y crustáceos: 86.3% (76.5% de eufáusidos). El bonito consumió 71.4% de peces, y 26.2% de crustáceos (11.9% de eufáusidos) por frecuencia de registro, y 32.2% de peces y 67.9% de crustáceos (63.4% de eufáusidos) por frecuencia numérica.

La comparación con datos históricos similares durante condiciones ambientales semejantes y diferentes sugiere que los escómbridos son predadores oportunísticos, y que la disponibilidad de presas era, parcialmente, el resultado de las condiciones oceanográficas. Se presentan el índice de importancia relativa y medidas de la tasa volumétrica media de la anchoveta del norte (*Engraulis mordax*) en la dieta de la albacora.

INTRODUCTION

The limitations of single-species models in fisheries management have been recognized and well documented (Anderson and Ursin 1977; Laevastu and Larkins 1981; and Livingston MS[1]). That predation mortality can control year-class strength of a given prey species has been established and deserves further examination (Laevastu and Larkins 1981; Rothschild and Forney 1979). We conducted a multispecies comparison by examining stomach contents of three species of scombrids—skipjack (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), and Pacific bonito (*Sarda chiliensis*)—collected in the California Current during the 1983 El Niño. Food habits studies from El Niño and other periods are also reviewed here.

[Manuscript received February 4, 1985.]

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We found significant amounts of young-of-the-year anchovies, *Engraulis mordax*, in the diet of these scombrids, especially albacore. A number of animals prey on the northern anchovy, including at least 33 species of fish, seabirds, marine mammals, and man (Radovich 1979). The impact of predation and adverse environmental conditions on a commercially important fish like the northern anchovy could have far-reaching economic repercussions.

Prior to Iversen's (1962) study on albacore in the central and northeast Pacific Ocean, food habits studies on albacore were largely nonquantitative (Clemens and Iselin 1963; McHugh 1952; Powell and Hildebrand 1949; Hart 1942; and Hart and Hollister 1947). In the 1970s, more quantitative studies were undertaken, including those by Pinkas et al. (1971) and Iversen (1962). Both studies were conducted when El Niño events were mild or absent.

Most food habits studies on skipjack have taken place in the central and eastern tropical Pacific Ocean (Alverson 1963; Nakamura 1965; and Waldron and King 1963). However, Alverson's study in the eastern tropical Pacific Ocean includes the region between Point Conception and 20°N, between 123° to 115°W during another strong El Niño (1957-59).

There is a paucity of literature on bonito's food habits in the California Current. One other study, spanning two years of collection (1968 and 1969—mild El Niño years), was available for comparison (Pinkas et al. 1971).

METHODS

The three scombrid species (94 albacore, 41 Pacific bonito, and 21 skipjack) were caught by hand-operated jig lines with artificial lures trolled at an average speed of 6 knots, during Cruise 166 of NOAA research vessel *David Starr Jordan*. In addition, 1 bonito and 10 skipjack were caught in gill nets deployed at night. Size of fish caught was fairly homogeneous within each species (Table 1). The albacore and bonito were caught in water approximately the same temperature (17.8°C and 17.3°C); the skipjack were caught in the warmer water (21.2°C) of the Southern California Bight (Table 1).

The albacore and bonito were caught in close association with each other, within 100 miles of shore, between 33°59′ to 36°44′N and 121°19′ to 122°30′W. The skipjack were all taken south of Point Conception in the Southern California Bight between 32°38′ to 33°46′N and 117°57′ to 119°16′W (Figure 1).

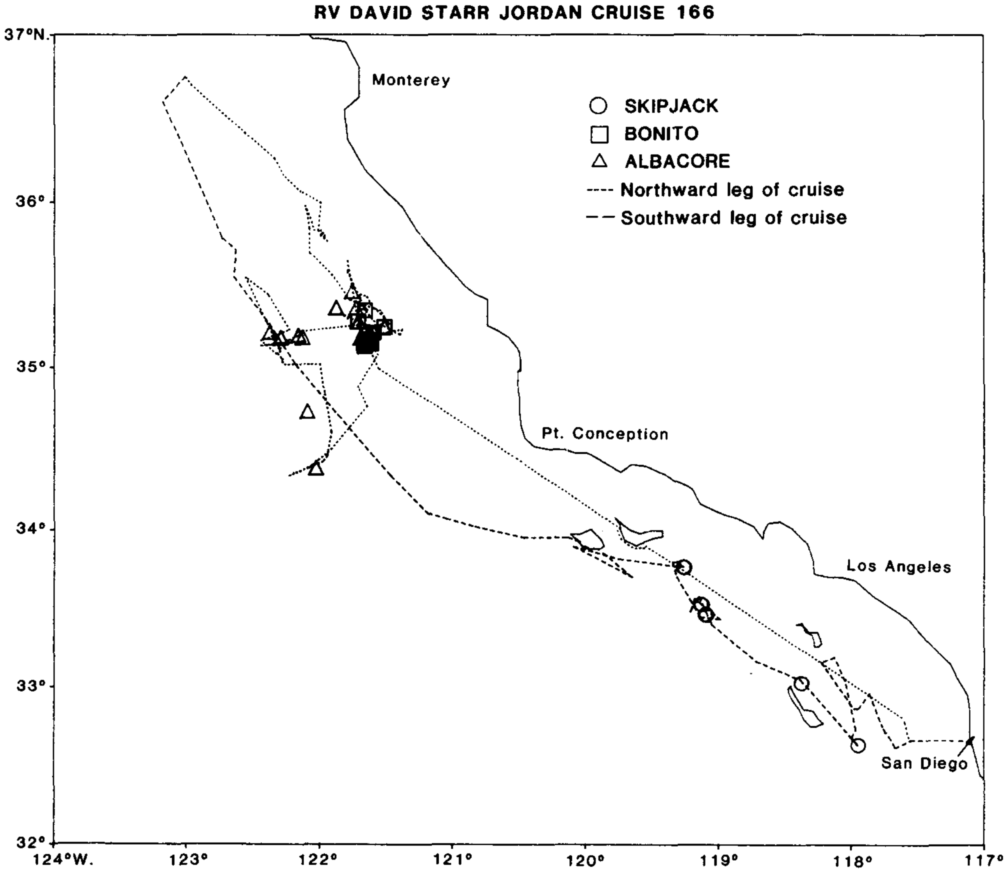

Figure 1. Capture locations of albacore, skipjack, and bonito during Cruise 166 of R/V *David Starr Jordan*, August 15-September 1, 1983.

TABLE 1
Mean Fork Lengths and Standard Deviations, and Mean Water Temperatures at Time of Catch

		Albacore ($n=94$)	Skipjack ($n=31$)	Bonito ($n=42$)
FL. (cm)	$\bar{x}$	69.3	48.7	59.9
	(s)	(8.817)	(2.031)	(1.902)
Temp. (°C)	$\bar{x}$	17.77	21.17	17.32
	(s)	(0.624)	(0.442)	(0.252)

Stomachs were removed aboard the ship and frozen. Contents were thawed in the laboratory and rough-sorted. Because many prey items in the stomachs in this study have not yet been identified, they were pooled into gross taxonomic categories, usually at the class level, except where otherwise indicated. In order to compare our data with previous studies, we pooled (whenever possible) the data from those studies to correspond to our fewer categories.

Percent frequency of occurrence (number of stomachs in which a particular prey occurred as a percentage of the total number of stomachs = %FO) and percent numerical frequency (%NF) were determined for all three species. Additionally, anchovies were separated from the other fish found in the albacore stomachs. The percent volumes of anchovies and other fish prey were determined.

We calculated a measure of relative importance (Pinkas et al. 1971) for the fish consumed by 85 albacore. This value, termed index of relative importance (IRI), is the product of the sum of the numerical plus volumetric percentages of a given prey item and percent frequency of occurrence of that prey [IRI = %FO(%NF + %VF)]. It is used here for comparison of anchovies consumed relative to all other fish prey combined and not as a total IRI for all prey items.

The data from the 85 albacore stomachs that contained fish were also examined individually to determine the importance of a given prey to an individual predator. Individual stomach analysis is similar in principle to an IRI calculation; however, instead of pooling prey from all of the stomachs of a given predator, one evaluates the distribution of fractional volumes and numbers of prey for each stomach. In contrast to the IRI, these data make it possible to determine the variance, mean, and standard deviation, and to perform statistical tests. The mean volumetric or numerical ratio measurement (MVRM, MNRM) was based on the percentages or proportions of prey in relation to total stomach volume or total numbers of all prey in individual stomachs (Ankenbrandt, in press). We calculated the MVRM for anchovies in the diet of albacore by the following equation (and MNRM can be calculated similarly):

$$\bar{r}_j = \frac{\sum_{i=1}^{N} r_{ij}}{N} = \text{mean volumetric ratio of prey } j \text{ to the total volume of } N \text{ stomachs}$$

where N = number of stomachs examined

$$r_{ij} = \frac{V_{ij}}{\left[\sum_{j=1}^{n} V_{ij}\right]} = \text{ratio of prey } j \text{ to the total volume of stomach } i$$

and where V_{ij} = volume of prey type j in stomach i

n = number of prey items

In an attempt to determine if the albacore were consuming anchovies at random, we performed a runs test (Sokal and Rohlf 1969) to test the null hypothesis that the frequency of occurrence of anchovies within the albacore stomachs is random.

It appeared that the three predator species were not eating the same kinds of prey items in the same proportions. We used Crow's (1982) suggestion for showing differences in feeding habits by analysis of stomach contents using a 2-way, $R \times C$, contingency table, where R is the number of prey categories and C is the predator species.

RESULTS

Scombrid Feeding Habits

Chi-square analysis for homogeneity showed highly significant differences in types of prey and proportions consumed by the three scombrid species (Table 2).

TABLE 2
Observed Frequency

Prey	Predator			
	Skipjack	Albacore	Bonito	Total
Unident. Crust.	6	71	13	90
Pleuroncodes	4	84	0	88
Amphipods	8	20	19	47
Hyperiidae	1	18	0	19
Euphausiids	148	916	449	1513
Fish	22	5741	228	5991
Cephalopods	5	117	0	122
Total	194	6967	709	7870

Minimum estimated expected value is 0.47
Independence of prey occurrence was tested, and the null hypothesis of homogeneity was rejected. Chi-square value = 1,641.721, probability <0.0001.

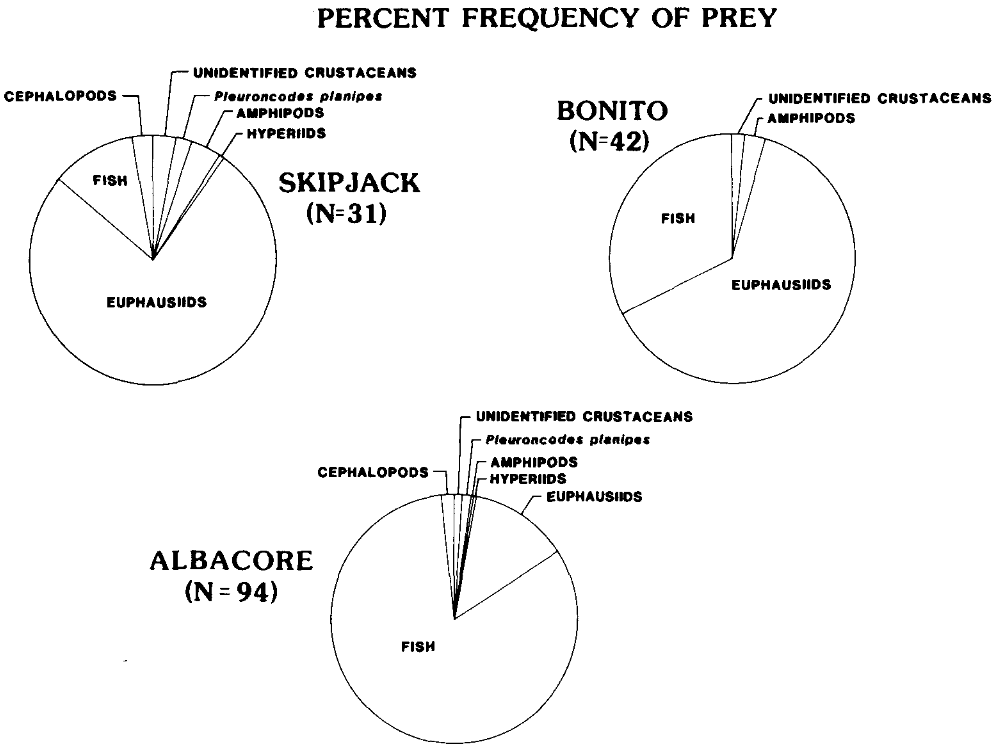

Figure 2. Percent numerical frequency of prey consumed by three scombrids (skipjack, albacore, and bonito) caught during Cruise 166.

Skipjack consumed crustacea most frequently (FO = 54.8%) and in greatest numerical frequency (NF = 86.3%). Bonito consumed fish most frequently (FO = 71.4%), but crustacea were highest in numerical frequency (NF = 67.0%) (Figures 2 and 3). The crustacean most important to both skipjack and bonito was the euphausiid *Nyctiphanes simplex*.

The primary prey of albacore was fish (FO = 96.8%, NF = 82.4%) (Figures 2 and 3). The IRI for anchovies in the diet of albacore was 7,630; for all

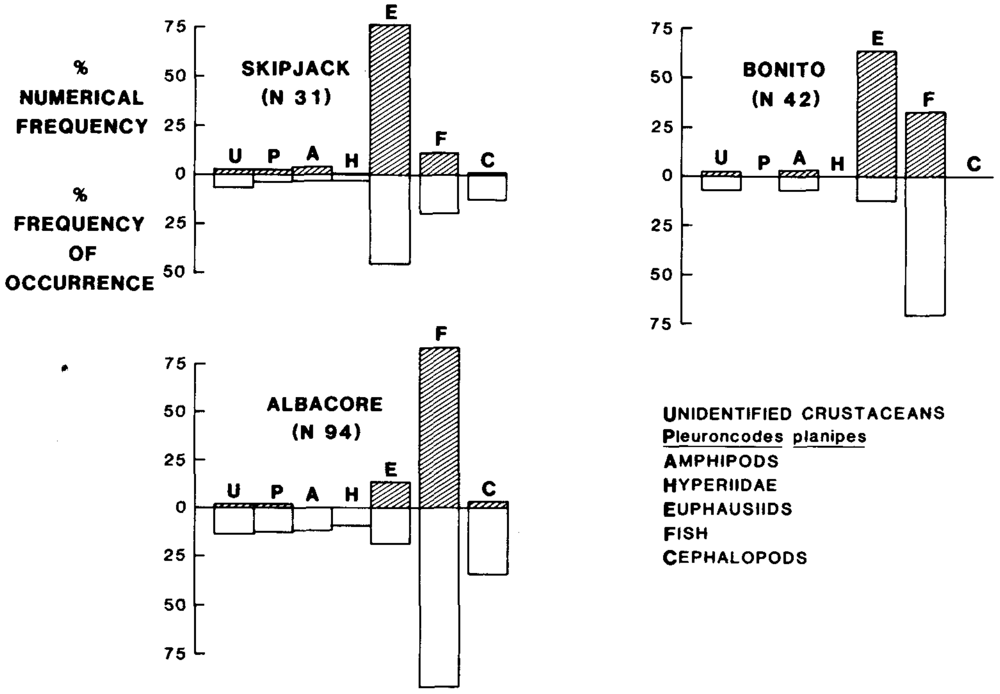

Figure 3. Percent numerical frequency and percent frequency of occurrence of prey consumed by skipjack, albacore, and bonito caught during Cruise 166.

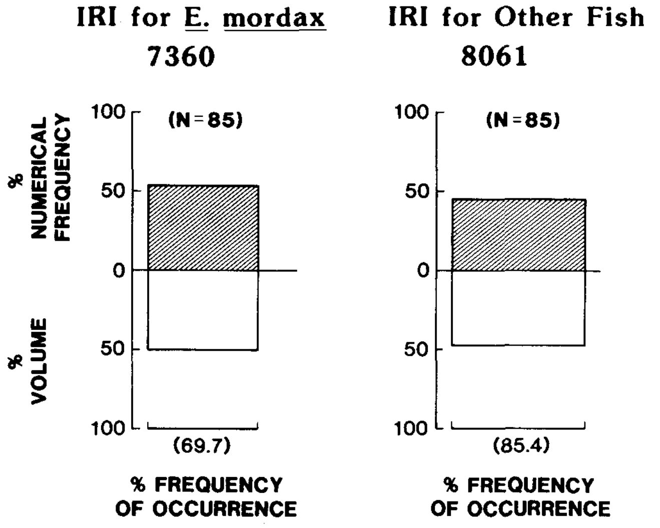

Figure 4. Index of relative importance and percent numerical frequency, percent volumetric frequency, percent frequency of occurrence for anchovies and other fish consumed by albacore caught during Cruise 166.

other fish combined, the IRI was 8,061 (Figure 4). The anchovies found in the albacore stomachs were young-of-the-year, from 22-47 mm SL, with a mean of 33.6 mm and a standard deviation of 4.97 (Figure 5). Albacore stomachs can be a source for verifying the existence or abundance of the anchovy size classes that are underrepresented in the California reduction fishery sampling program used for anchovy population studies (Mais 1981).

The presence of *Pleuroncodes planipes*, pelagic red crab, in the diets of skipjack and albacore is notable because the crab's northern limit in most years appears to be 28°N, in Sebastian Viscaino Bay (Longhurst 1967).

Individual Stomach Analysis

The mean volumetric ratio measurement for anchovies in albacore stomachs (0.092) was only a little less than the mean volumetric ratio measurement for all other fish combined (0.11) (Table 3).

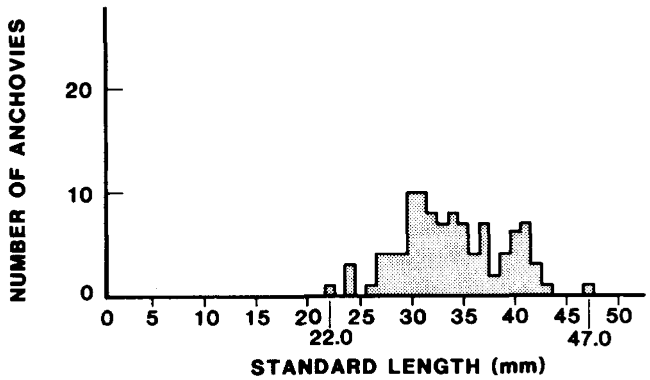

Figure 5. Length-frequency distribution of anchovies found in albacore stomachs caught during Cruise 166.

TABLE 3
Mean Volumetric Ratio Measurements (MVRM) and Standard Deviations of Anchovies and All Other Fish Consumed by 85 Albacore

	E. mordax	Other fishes
MVRM	0.092	0.110
(*s*)	0.144	0.207

The mean numerical percentage of anchovies in albacore stomachs is somewhat less ($\bar{x}$ = 42.4%) than all other fish combined ($\bar{x}$ = 57.6%), as was the mean volumetric percentage of anchovies ($\bar{x}$ = 44.1%) to all other fish combined ($\bar{x}$ = 55.9%) (Table 4).

The mean volumetric and numerical percentages of anchovies from individual stomach analyses were also less than the numerical and volumetric percentages of anchovies in the IRI calculation (Table 5).

Cumulative frequency plots showing the proportions of percent numerical and volumetric frequencies of anchovies in albacore stomachs (Figures 6 and 7) demonstrate that there were more albacore stomachs containing fish other than anchovies than stomachs containing anchovies alone.

The runs test resulted in rejection of the null hypothesis of random distribution of anchovies in albacore stomachs at the 5% significance level. Ancho-

TABLE 4
Mean Volumetric and Numerical Percentages and Standard Deviations of Anchovies and Other Fish Consumed by 85 Albacore

	E. mordax	Other fishes
Numerical percentage		
$\bar{x}$	42.4%	57.6%
(*s*)	39.7	39.7
Percent volume		
$\bar{x}$	44.1%	55.9%
(*s*)	41.2	41.2

TABLE 5
Percentages Used in IRI Calculation

	E. mordax	Other fishes
Numerical percentage	53.9%	46.1%
Percent volume	51.7%	48.3%
Frequency of occurrence	69.7%	85.4%

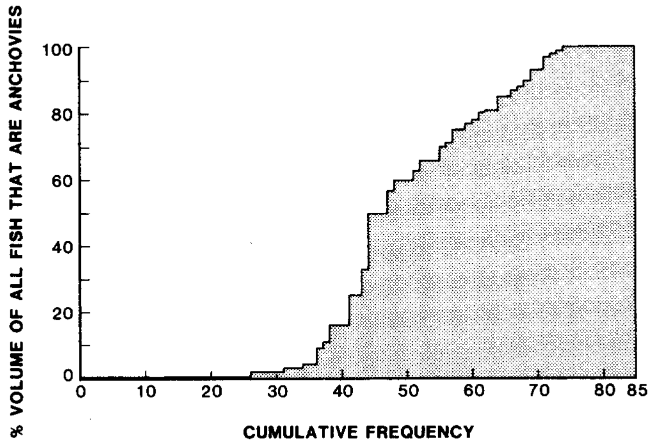

Figure 6. Cumulative frequency plot of volumetric percentage of all anchovies in 85 albacore stomachs.

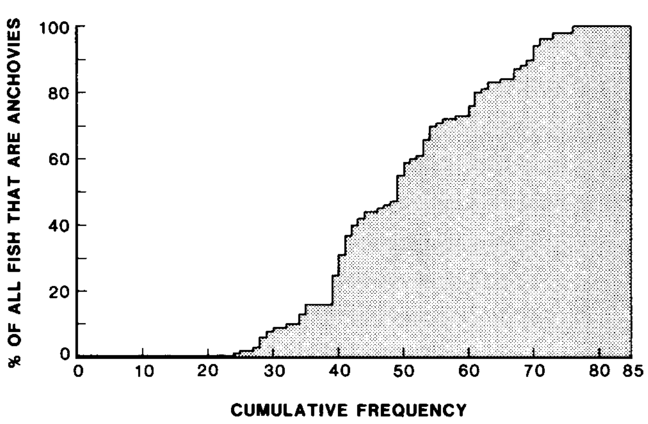

Figure 7. Cumulative frequency plot of numerical percentage of all anchovies in 85 albacore stomachs.

vies were present in some of the albacore stomachs in large quantities; and some stomachs did not contain any anchovies. This finding is not necessarily a reflection of active selection, but more likely an indication of the patchy distribution of the anchovy schools.

DISCUSSION

There are significant differences in types of prey and proportions consumed among the three scombrids. Bonito and skipjack consumed more euphausiids than any other type of prey. Albacore consumed more fish than any other prey, and the northern anchovy, *Engraulis mordax*, was consumed nearly as much as all other fish combined.

The 1983 El Niño event resulted in, among other things, a marked decrease in the southward transport of the California Current. The decreased transport correlates with a decrease in zooplankton biomass (Chelton et al. 1982) and a decrease in the occurrence of cephalopods off the California coast. In addition, fauna endemic to more southerly ranges (e.g., *Pleuroncodes planipes* and *Nyctiphanes simplex*) were transported northward and incorporated into the diets of the scombrid predators. A comparison of this study with other food habits studies during El Niño periods showed similar trends.

Pacific Bonito

In 1968 and 1969 (Pinkas et al. 1971), fish were the primary prey for bonito, with cephalopods next in importance (in 1968, NF for cephalopods = 13.9% and FO = 21.3%; in 1969, NF = 5.8% and FO = 28.2%). However, in our study, the importance of crustacea is about the same as fish (Figure 8). No

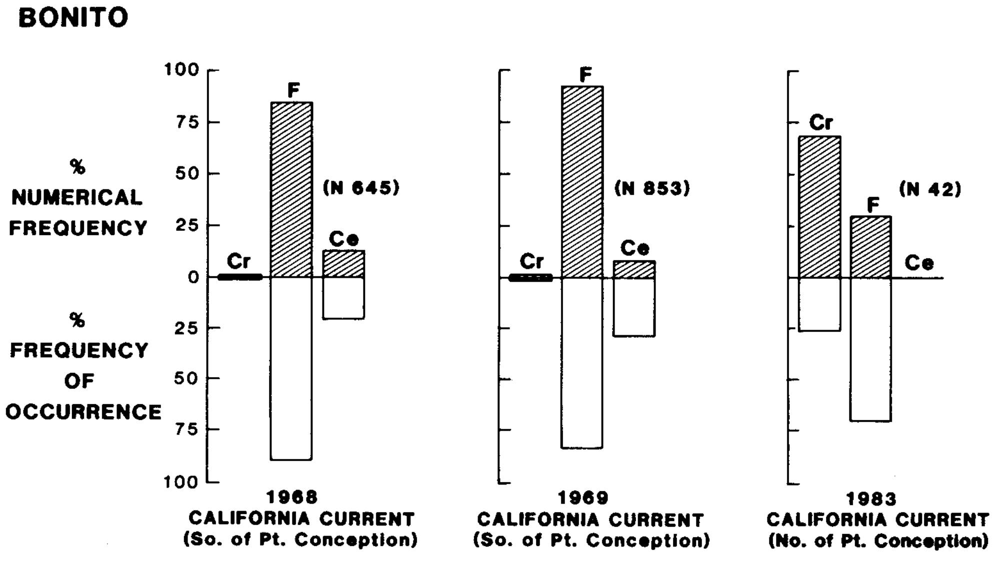

Figure 8. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by bonito caught in 1968 and 1969 (Pinkas et al. 1971) and those caught from August 15-September 1, 1983. Cr = crustaceans, Ce = cephalopods, and F = fish.

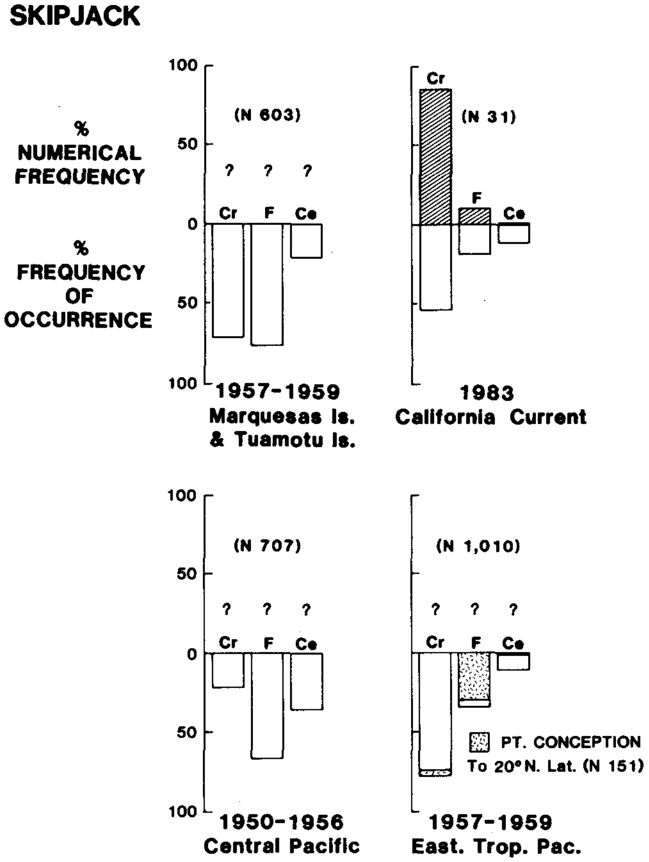

Figure 9. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by skipjack in several studies. On left are studies from central and south Pacific: 1957-59 (Nakamura 1965), and 1950-56 (Waldron and King 1963). On right are studies from the eastern tropical Pacific and California Current: 1983 (this study) and 1957-59 (Alverson 1963). Question marks represent unavailable data. Cr = crustaceans, Ce = cephalopods, and F = fish.

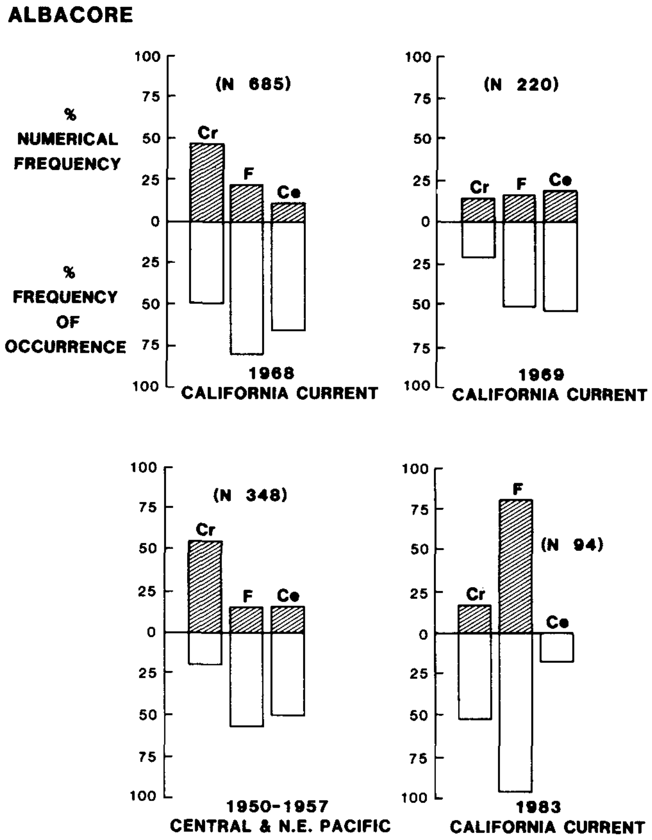

Figure 10. Comparison of percent numerical frequency and percent frequency of occurrence of prey consumed by albacore in 1968 and 1969 (Pinkas et al. 1971), 1950-57 (Iversen 1962), and 1983 (this study). Cr = crustaceans, Ce = cephalopods, and F = fish.

cephalopods were found in the bonito stomachs collected during the 1983 cruise. This suggests that cephalopods were not available to the bonito we sampled during the 1983 El Niño.

Skipjack

In Alverson's (1963) study conducted in the region between Point Conception and 20°N during the 1957-59 El Niño, crustacea were consumed most frequently, as in 1983 (Figure 9). In contrast to 1983, when euphausiids were the most important crustacean, the pelagic red crab was the most important crustacean in 1957-59.

Albacore

We used Pinkas et al. (1971) for a detailed comparison to our study because of the similar location (Iversen's 1962 data from the equatorial and northeastern Pacific were pooled together). Fish were the primary prey in 1968 and 1969, with anchovies the most important species in 1968, and sauries (*Cololabis saira*) the most important species in 1969 (Figure 10). In 1983, anchovies were almost equal in importance to all other fish combined.

MVRM versus IRI

The MVRM and the numeric and volumetric proportions (used in IRI calculations) gave similar results: anchovies were consumed almost as much in volume and numbers as all other fish combined. The mean numerical and volumetric percentages of anchovies consumed by albacore were slightly less (42.4% and 44.1%, respectively) than the numerical and volumetric percentages used for the IRI calculation (53.9% and 51.7%). This reflects the difference between establishing a measurement based on a pooled average (volumetric and numerical proportions) and a weighted average (MVRM and MNRM). The fact that numerical and volumetric proportions based on pooled (IRI-type) data are greater than the means of volumetric and numerical frequency shows that some albacore were primarily consuming anchovies, whereas, at other times, other albacore were consuming more of some other fish species. This suggests that the complementary use of the MVRM and volumetric frequency and the MNRM and the numerical frequency will provide insight into the feeding habits of fishes.

The MVRM calculation enabled us to perform statistical tests on these data and resulted in the conclusion that the distribution of anchovies as prey among individual albacore was not random. That is, it appears that some albacore encountered and fed on anchovy schools, while other albacore encountered and fed on schools of other fish, a possible reflection of the inherently patchy distribution of anchovy schools.

Gill-Raker Gap and Prey Size

In a previous study (Magnuson and Heitz 1971), the gill-raker gap (space between the first two gill rakers of the first gill arch) was measured or estimated by linear regression in tunas, mackerels, and dolphinfish. The results showed a positive correlation between gill-raker gap and fork length, and gill-raker gap and prey size—i.e., the predators with smaller gill-raker gaps consumed smaller prey.

We determined the mean gill-raker gaps for the scombrids in our study by linear regression (fork length vs gill-raker gap). Although bonito had a larger gill-raker gap (ca. 3.05 mm) than both skipjack (ca. 1.03 mm) and albacore (ca. 2.50 mm), we found that the proportion of prey items in bonito stomachs more closely resembled the contents of skipjack stomachs (mostly euphausiids) than albacore stomach contents.

Our findings were contrary to those of Magnuson and Heitz: most of the bonito prey were smaller than most of the albacore prey, even though albacore had a smaller gill-raker gap than bonito and they were caught in the same area on the same days. This information, added to the evidence that scombrids in previous studies have diverse and opportunistic feeding habits during similar and dissimilar environmental conditions, underscores the complexities of food-web dynamics.

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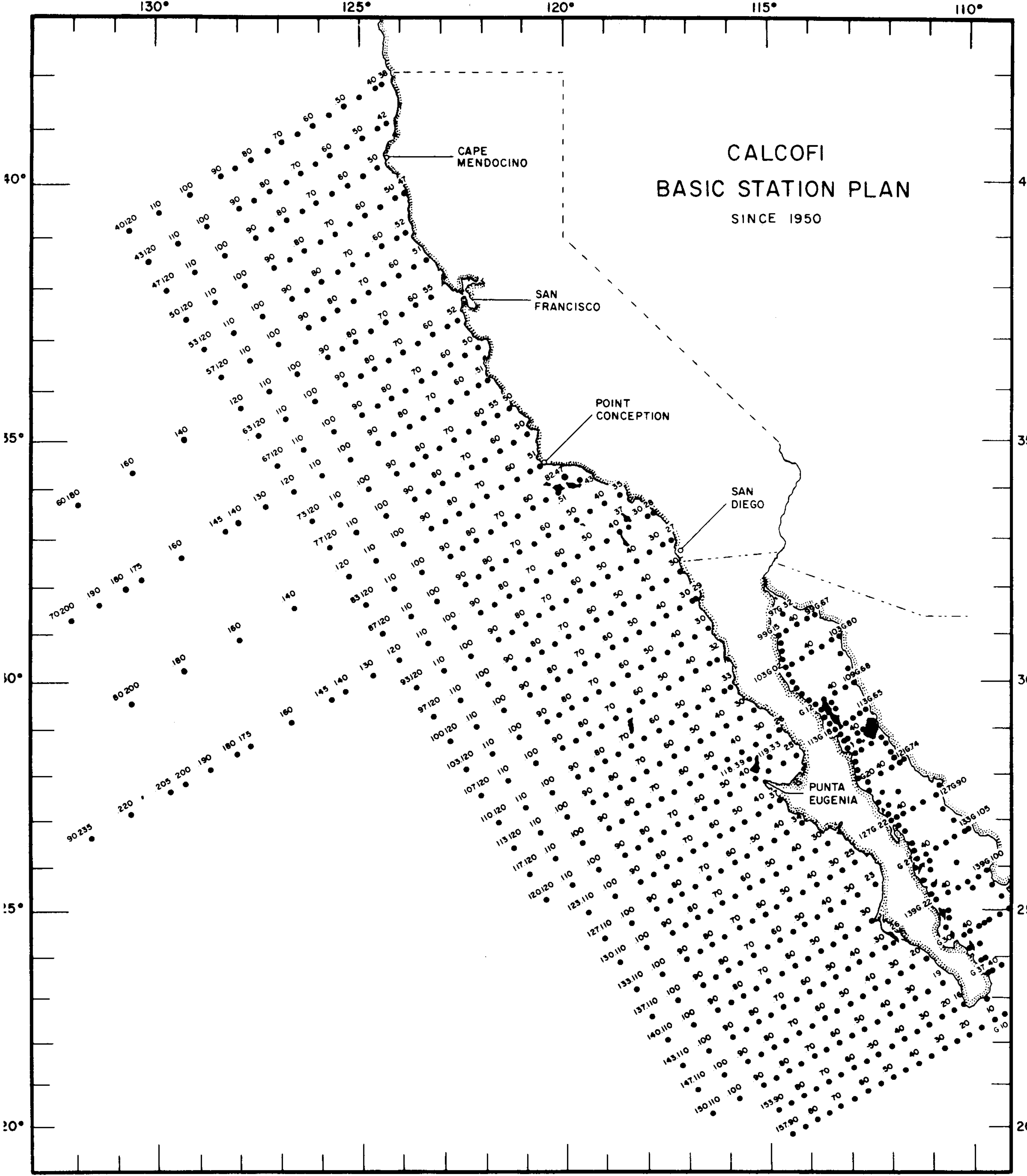

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